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Bajadas

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# LANDSCAPE EVOLUTION, SOIL FORMATION, AND ECOLOGICAL PATTERNS AND PROCESSES IN SONORAN DESERT BAJADAS<sup>1</sup>

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Abstract. Three alluvial piedmonts (bajadas or alluvial fans) studied in the Sonoran Desert near Tucson, Arizona are complex mosaics of distinct geological landforms. These landscape mosaics have been produced through the temporally episodic and spatially discontinuous aggradation of alluvial surfaces and the destruction of other parts of the landscape by erosion. These geomorphic processes produce abrupt juxtapositions of soils of different ages and degrees of profile development. Vegetation patterns correspond closely to this geomorphic mosaic. Larrea tridentata predominates on most Holocene-aged surfaces and all parts of highly dissected, early Pleistocene surfaces. This shrub is generally excluded from Pleistocene-aged surfaces containing soils with strongly developed argillic (clay-rich) horizons. The highest species diversity is encountered on some of the most unstable, erosional slopes of early Pleistocene surfaces. Comparisons among the three study areas indicated the importance of igneous lithology (highly weatherable intrusives vs. weatheringresistant extrusives) in controlling geomorphic processes, and ultimately, vegetation patterns. The areal extent of late Holocene alluvial aggradation and patterns of erosion and dissection of older Pleistocene deposits are strongly influenced by the weatherability of different lithologies and provide a strong control over the spatial scale of ecological patterns.

Processes limiting the distributions and abundances of plants are directly linked to landscape characteristics in many ways. Landform age and stability affect the structure of populations of long-lived *Larrea tridentata*. Individuals of this shrub species can exhibit clone-like growth and increase considerably in size (diameter) over time spans of many centuries to millennia. The growth and persistence of these long-lived clones in some parts of the landscape apparently contribute to the exclusion of other species. However, development of large clones and dominance by *L. tridentata* are impossible or greatly inhibited in several landscape settings including: (1) extremely young alluvial deposits that have existed for too short a time for large clones to have developed, (2) hillslopes subject to considerable erosional disturbance, and (3) extremely thin soils underlain by impenetrable petrocalcic horizons (caliche), which magnify drought conditions and apparently contribute to episodic mortality in *L. tridentata*.

Soil horizon development as determined by landform age controls the vertical movement and distribution of soil water, in turn affecting the distribution of various plant life forms. Clay-rich (argillic) horizons that have required tens to hundreds of thousands of years to form greatly limit the downward infiltration, vertical distribution, and the temporal availability of soil water. Despite surficial stability for extremely long periods of times, sites with strongly developed argillic horizons lack *L. tridentata* and are instead occupied by drought-deciduous or succulent plants that are capable of highly seasonal activity in soils that exhibit high seasonal variability in water availability. Syntheses involving the study of various ecological processes (e.g., plant physiological, demographic, and interspecific interactions) with a larger landscape perspective provide a rich framework for further studies of arid land systems.

Key words: alluvial fan; argillic horizon; bajada; Basin and Range; calcic horizon; desert landforms; geomorphology; gradients; landscape ecology; Larrea tridentata; Quaternary Period; Silver Bell bajada; soils; Sonoran Desert; US/IBP Desert Biome.

#### Introduction

The deserts of the southwestern United States and adjacent Mexico are contained almost entirely within the Basin and Range Physiographic Province. An alternating pattern of long, narrow mountain ranges sep-

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arated by broad basins characterizes this extensive region. Crustal extension and faulting leading to the downdrop of basins in relation to uplift of ranges began 12–15 million years ago. Since that time, alluvium derived from the ranges has been deposited within the adjacent basins. Some of the basins within the Sonoran Desert contain depths of alluvium exceeding 3 km (Morrison 1985). The alluvial basins consist of two

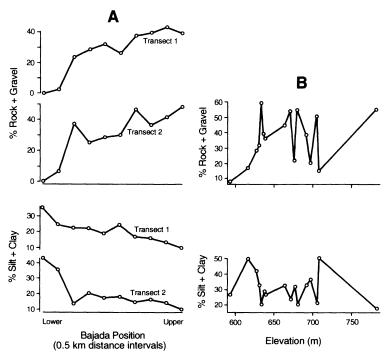


Fig. 1. Textural attributes of soils along elevational gradients of Sonoran Desert bajadas studied by (A) Phillips and MacMahon (1978) and (B) Solbrig et al. (1977).

physiographic parts (Peterson 1981): (1) the piedmont slopes (referred to as bajadas in most American ecological literature) and (2) nearly level basin floors. Considerable plant ecological research has been conducted in the gently sloping alluvial piedmonts or bajadas.

Research on vegetation patterns of Sonoran Desert bajadas over the past 25 yr has reflected the widespread shift in ecology away from a Clementsian focus on the distributions of distinct vegetational associations or climaxes (e.g., Yang and Lowe 1956) to examination of continuous changes in species distributions. The analytical tools of gradient analysis championed by Whittaker (1956, 1967, 1975) and ordination techniques (Curtis and McIntosh 1951, Bray and Curtis 1957) paved the way for studying many kinds of continuous changes in community composition. In the wake of these conceptual and methodological developments, research during the 1970s through the 1980s (e.g., Barbour and Diaz 1973, Solbrig et al. 1977, Phillips and MacMahon 1978, Bowers 1988) has contributed to and solidified a view that Sonoran Desert bajadas consist of simple spatial gradients with respect to soil texture. The bajada gradient has been represented as consisting of coarse-textured soils near mountain fronts and grading to finer textured soils toward basin floors. The bajada gradient model has emphasized that the spatial gradient in soil texture produces a vegetational continuum along the slope of the bajada (Solbrig et al. 1977, Bowers and Lowe 1986).

Although gradient analysis and its conceptual and methodological descendents have played an invaluable

role in vegetation studies in all kinds of environments, this same conceptual framework has greatly limited the way in which the physical and ecological nature of Sonoran Desert bajadas has been perceived, studied, and described by ecologists. The bajada gradient model greatly oversimplifies considerable spatial complexity in geomorphology, soils, and species distributions. A case in point from research conducted as part of the US/IBP (International Biological Program) Desert Biome investigations follows.

The work of Solbrig et al. (1977) and Phillips and MacMahon (1978) discussed soil textural changes along two different Sonoran Desert bajadas. Both groups of investigators presented tabular data on soil texture for their study sites; these data are plotted in Fig. 1. Although the data of Phillips and MacMahon (1978) indicated a rather clear gradient in soil texture (Fig. 1A), the data of Solbrig et al. (1977) collected at the Silver Bell Bajada site can at best be described as extremely irregular (Fig. 1B). Some of these soil data are clearly opposite the expected pattern of increasingly fine textures of bajada soils at increasing distances from the mountain front. For example, one of the uppermost bajada sites (elevation 708 m, Fig. 1B) has a higher clay content and considerably lower gravel and rock content than soils from any other site, including most of the sites in lower elevations of the bajada. Yet, despite such extreme departures of data from the expected soil textural gradient, the authors, in direct reference to the data plotted in Fig. 1B (and for additional soil data from another site in Argentina) stated "in

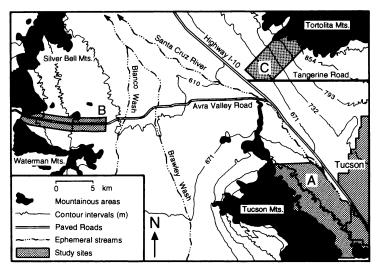


Fig. 2. Location of the three alluvial piedmont study areas near Tucson, Arizona. (A) Tucson Mountains, (B) Silver Bell Mountains, (C) Tortolita Mountains.

both areas soil texture becomes coarser with increased elevation" (Solbrig et al. 1977). Such a statement, despite clear evidence of a far more complicated pattern, demonstrates the extent to which preconceptions regarding gradients impaired the ability of the investigators to accurately observe, interpret, and describe the physical bajada environment as it actually existed.

Preconceptions of a continuous bajada gradient clashed with not only the reality of the physical environment, but also with observed plant distributions. For example, although most ecologists associated with the US/IBP Silverbell Bajada project stressed the spatially continuous nature of change in abundances of individual species, Barbour and Diaz (1973) briefly discussed a level of heterogeneity in vegetation within small areas that complicated sampling efforts and statistical estimation. Such spatial heterogeneity and departures from an idealized vegetational continuum, rather than simply being statistical noise, may represent important and general patterns deserving study and explanation. The recognition and understanding of these ecological patterns require a far more sophisticated view of both geomorphology and desert soils than has to date been presented in ecological discussions of the "bajada gradient."

This paper contains several parts. First, in the *Results* I develop a detailed picture of the geomorphic history and pedogenic diversity of three alluvial piedmonts in the Sonoran Desert. For each of these piedmonts, I present the relationships between landscape patterns and vegetational composition. Second, in the *Discussion* I examine ways in which processes that shape patterns of demographic structure, species composition, and the distribution of plant life forms are directly related to landscape attributes. Finally, I discuss how an enlarged and more realistic view of these desert

landscapes offers new perspectives for the study of physiological and population processes in arid environments.

# MATERIALS AND METHODS

#### Study sites

The research was conducted on three alluvial piedmonts in the northeastern part of the Sonoran Desert. The three study areas were adjacent to the Tucson, Tortolita, and Silver Bell mountain ranges near Tucson, Arizona (Fig. 2). The Tucson Mountains study area was  $\approx 16$  km in length and included fan deposits on the northeast side of the mountain range. The study area included the entire breadth (3–4 km) of the alluvial piedmont between the mountain front and the floodplain of the Santa Cruz River. The elevational range of the study area is  $\approx 670-760$  m (Fig. 3).

The Silver Bell Mountains study area was located in the same general area along the "Silver Bell Bajada Transect" studied by Barbour and Diaz (1973), Solbrig et al. (1977), and Barbour et al. (1977) (Fig. 4). The area of study was a band  $\approx 1 \times 12$  km along Avra Valley Road between the elevations of 634 and 805 m.

The Tortolita Mountains study area included fan deposits associated with two drainages that debouch from Wild Burro and Ruelas Canyons on the southwest side of the range (Fig. 5). The study area was ≈7 km in length from the mouths of the two canyons to the floodplain of the Santa Cruz River. This piedmont included an elevational range (640–820 m) similar to the two other study areas. The Tortolita site differs, though, in lithologic composition of alluvium. The Tucson Mountains and Silver Bell Mountains are composed primarily of extrusive igneous rocks (rhyolites and andesites), whereas the Tortolita Mountains are

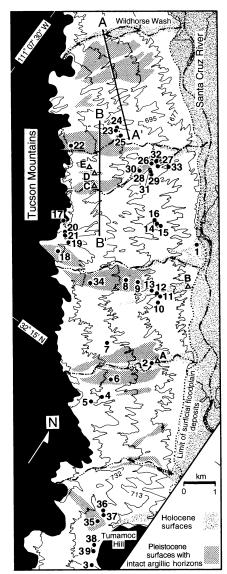


Fig. 3. Map of the Tucson Mountains piedmont study area. Numbered sites 1–39 are locations of vegetation sampling sites; lettered sites A–E are locations of soil profiles described in Appendix C. Transects A–A' and B–B' are diagrammed in cross section in Fig. 7. Elevations in metres; contour interval = 18.3 m.

composed primarily of granites and granodiorites (Arizona Bureau of Mines 1959, 1960, Katzer and Schuster 1984; J. R. McAuliffe, *personal observations*).

#### Methods

Tucson Mountains.—Most of the fieldwork at this site was conducted in 1986 and 1987. Geomorphic surfaces of the piedmont were mapped on 1:24 000 topographic maps published by the U.S. Geological Survey (Jaynes and Cat Mountain 7.5' quadrangles). A geomorphic surface is an area of land formed by deposition or erosion during a defined time period (see

Peterson 1981). Mapping was accomplished by ground reconnaissance and aided by color aerial photographs (1:24 000 scale). The 45 km² study area, broken down into  $0.8 \times 0.8$  km sectors, contained 83 such sectors. Intensive surveys on foot were conducted in 43 of these sectors; for 37 of the remaining 40 sectors, reconnaissance of geomorphology was conducted from roadsides along at least one 0.8-km border of each sector. Only three sectors (3.6% of the total study area) were not directly examined due to inaccessibility of privately held lands.

Field reconnaissance and mapping involved identification of stable relict surfaces as indicated by planar surficial configurations and color differences on aerial photographs. Relative ages of geomorphic surfaces were determined primarily from topographic relationships (Peterson 1981) and soil attributes (Gile et al. 1981). When available, roadcuts and other exposures were also used to determine stratigraphic relationships. This work was augmented by a map of surficial Quaternary deposits of the northernmost 3–4 km of the study area (Katzer and Schuster 1984). Detailed 1:24 000 maps of Quaternary deposits of the entire study area (McKittrick 1988) were also used to interpret geomorphic features.

Soils on different geomorphic surfaces were described from 19 profiles according to established methodology (USDA Soil Survey Staff 1975, Birkeland 1984). The following characteristics were recorded from each soil horizon: depth, Munsell color, dry and wet consistency, structure, texture, carbonate morphology, and effervescence (reaction with 10% HCl). Samples were collected from individual horizons for laboratory analyses in 17 of the 19 profiles. These analyses included (1) percentage by mass of gravel and rock retained in a 2-mm mesh sieve, (2) mechanical analysis of the fraction passing through the 2-mm mesh sieve (percent sand, silt, and clay) using the hydrometer method (Bouyoucos 1936, 1951, Black 1965), and (3) calcium carbonate content measured by mass loss of the soil sample after reaction with an excess of hydrochloric acid (Black 1965).

In addition to these soil profile descriptions and laboratory analyses, I examined 23 additional soil profiles within the study area that were exposed in road cuts and construction excavations. These examinations permitted a reliable determination of the correspondence between various soils and the different geomorphic surfaces. A knowledge of the general distribution of soils in relation to geomorphology was also augmented by four soil profile descriptions made by Katzer and Schuster (1984) near the north boundary of the study area.

Thirty-nine vegetation sampling sites were distributed throughout all of the identified geomorphic surfaces (Fig. 3, Appendix A). Slope and aspect were measured and additional soil samples were collected from depths of 0–5 cm and 15–20 cm at each site. Texture

of these samples (percent sand, silt, and clay) and calcium carbonate content were determined using the previously described methods; pH of saturated soil pastes was measured for each sample with a glass electrode pH meter calibrated against standard buffers.

Percentage canopy cover of perennial plant species was measured by the point-intercept method. At each site, 300 sample points were placed at 1-m intervals along a 100-m tape positioned in three nonintersecting locations. When sampling sites were adjacent to noticeable discontinuities in vegetation compositions, detailed examination of geomorphic and soils transitions was made along these discontinuities.

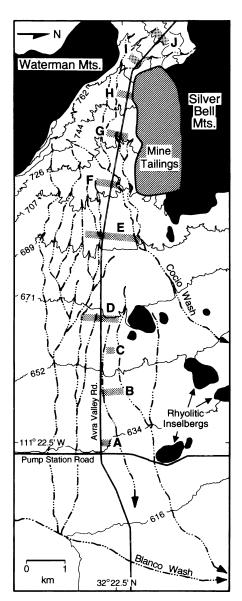


Fig. 4. Map of the Silver Bell Mountains piedmont study area. Shaded bands A–J show the locations of the 10 study transects along the elevational gradient. Elevations in metres; contour interval = 18.3 m.

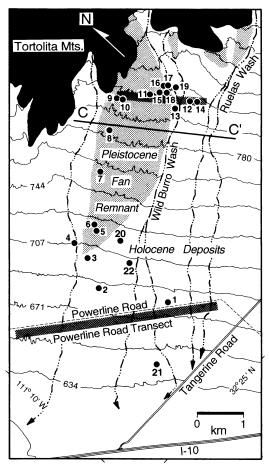


Fig. 5. Map of the Tortolita Mountains piedmont study area. Numbered sites 1–22 are locations of vegetation sampling sites. The shaded strip along the Powerline road indicates the region over which vegetation samples were collected at 0.16 km intervals. The shorter shaded strip near the mountain front is a transect along which detailed examinations of geomorphic and soils transitions within the Pleistocene surface were made. Transect C–C' is diagrammed in cross section in Fig. 7. Elevation in metres; contour interval = 18.3 m.

Silver Bell Mountains.—Geomorphology, soils, and vegetation were studied in 1991 and 1992 along 10 transects spaced along the 12-km elevational gradient (Fig. 4, Appendix B). The individual transects ranged between 0.25 and 1.5 km in length and were oriented parallel to the average elevational contours. Within each transect, transitions among geomorphic surfaces were determined by topographic discontinuities, elevational differences, soil characteristics, and when available, stratigraphic information obtained from natural and anthropogenic exposures. Schematic cross sections of the geomorphic surfaces and soils were prepared in the field for each transect.

Perennial vegetation was characterized in a total of 24 sampling sites located within the 10 transects (Appendix B). At each sampling site, vegetation was sampled in five circular, 100-m<sup>2</sup> plots. Data collected from

each plot included density and canopy cover of the median-sized individual of each species recorded on a log<sub>2</sub> scale according to the Log-series sampling method described by McAuliffe (1991a). The sum of these two values yields an estimate of canopy cover on a log<sub>2</sub> scale. The antilogarithm base 2 of the difference between this sum and the logarithm of total plot area provides an estimate of percent cover per species. This method was used because it provided better information on species richness (species per unit area) than can be attained with point-intercept sampling.

Tortolita Mountains.-The work of Katzer and Schuster (1984) provided a general Quaternary map of the Tortolita study area. This map, however, only distinguished "undifferentiated Holocene fans" from "undifferentiated Pleistocene fans." Additional surveys in 1987, 1989, and 1991 were used to characterize geomorphology and soils of the piedmont at a finer scale. These surveys were aided by the use of 1:24 000 color aerial photographs and topographic maps. Eight soil profiles were described from various topographic and geomorphic settings. The surveys also consisted of mapping changes in major soil characteristics (presence or absence of argillic horizons, surficial petrocalcic rubble) on diagrams of landscape cross sections made in transects across the piedmont. Vegetation data consisted of species lists and total cover of dominant perennial species estimated by eye in 22 locations (Fig. 5). On the basis of these estimates, the relative cover of each species was assigned to 1 of 6 classes based on a geometric scale: class 0 = absent, class  $1 = \le 5\%$ relative cover, class 2 = 6-12%, class 3 = 13-25%, class 4 = 26-50%, and class 5 = >50% relative cover.

Additional investigations on Holocene deposits in lower elevations of the Tortolita piedmont were conducted in 1992 along a 4.4-km transect located along a southeast–northwest trending power line corridor (Fig. 5). At 0.16-km intervals, densities of five dominant shrub and tree species were recorded from a 500-m<sup>2</sup> circular plot located 50 m to the south of the Powerline Road. An optical rangefinder was used to delimit the radius of each plot and plant densities were recorded in intervals arranged on a log<sub>2</sub> scale as described by McAuliffe (1991a).

# RESULTS

# Tucson Mountains

Geomorphology.—The piedmont slope of the Tucson Mountains is composed of several distinct alluvial landforms of different geological ages. These landforms exhibited various levels of either soil development or erosional incision and soil truncation as a function of their ages. Knowledge of the history of landscape development during the Quaternary Period is essential for understanding present-day landscape patterns. Fan deposits associated with one drainage system, Wild-

horse Wash, in the northernmost 3 km of the study area (Fig. 3) provide an illustration of general landscape patterns and the processes responsible for their creation. The alluvial history of the Wildhorse Wash system has been studied in more detail by Katzer and Schuster (1984) and is briefly recounted here.

The oldest alluvial deposits associated with Wildhorse Wash consist of a series of long, subparallel ridges, some more than a kilometre in length. Many of these ridges join upslope, forming a series of digitate spurs (Fig. 6, upper left). A few of the ridge-like landforms are isolated from other interconnected ridges, and due to their hump-backed shapes, are called ballenas (Spanish for "whales") by geomorphologists (Peterson 1981) (Fig. 6). Crests of ridges are elevated as much as 20 m above drainages and adjacent ridgelines are typically separated by 200-500 m (Fig. 7, Transect A-A'). These ridges and ballenas are erosional remnants of an ancient, originally undissected fan surface. A slightly convex plane resting across or slightly above the adjacent ridges indicates the approximate elevation and surface configuration of the original alluvial fan (Fig. 7A, dotted line). The great degree of erosional incision indicates great antiquity for this part of the landscape. On the basis of comparisons of this dissected landscape with other geomorphic studies in this region (McFadden 1978, Gile et al. 1981, Menges and McFadden 1981), Katzer and Schuster (1984) suggested these ancient fan deposits date to the Pliocene/ Pleistocene boundary,  $1.8-1.9 \times 10^6$  yr BP. Some of these deposits may even be as old as late Tertiary (Pearthree et al. 1988).

The present-day surface area of this highly dissected, early Pleistocene surface represents but a fraction of the area once occupied by the original alluvial fan. Incision and erosion of the ancient fan completely obliterated much of the northern part of the fan in early to mid-Pleistocene times. After this erosional period, another, distinct fan was deposited by the Wildhorse Wash system in mid-late Pleistocene times. This younger fan deposit abuts the northwestern edge of the highly dissected, early Pleistocene surface (Figs. 6 and 7A). The younger, mid-late Pleistocene surface is only slightly dissected and retains the slightly convex cross section of a typical alluvial fan (Figs. 6 and 7A). The absence of extremely deep incisions in this surface and the degree of soil development on it suggest the fan was formed a few hundred thousand years ago (Katzer and Schuster 1984).

During the formation of the mid-late Pleistocene fan, alluvial deposits eventually aggraded to a point where the course of Wildhorse Wash switched to a still more northerly direction (Katzer and Schuster 1984). Consequently, the aggrading mid-late Pleistocene fan became topographically severed from the extensive upland watershed that supplied both run-off and alluvium. The only drainages across this fan surface today are those originating from precipitation falling directly

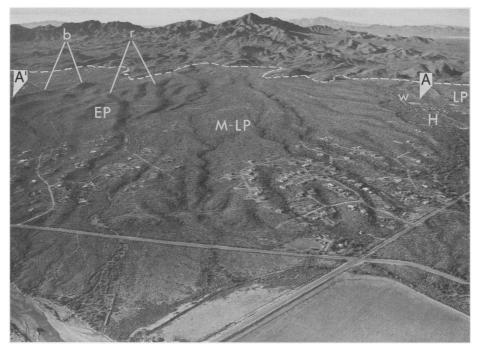


FIG. 6. Northern part of the Tucson Mountains study area: aerial view toward the southwest from the intersection of Silverbell Road (left to right in foreground) and Ina Road (diagonally across lower right). The broken white line shows the approximate border between alluvial surfaces in the foreground and exposed bedrock pediments and mountain slopes in the background. Wildhorse Wash (w) and associated Holocene (H) and late Pleistocene (LP) deposits are at the far right. The extensive, relatively planar surface of the mid–late Pleistocene fan (M-LP) occupies much of the center. The highly dissected, interconnected ridgeline remnants (r) and ballenas (b) comprising the early Pleistocene fan surfaces (EP) are at the left. Letters A-A' indicate approximate endpoints of the landscape cross section diagrammed in Fig. 7. Photograph by Peter Kresan, copyright 2 December 1984.

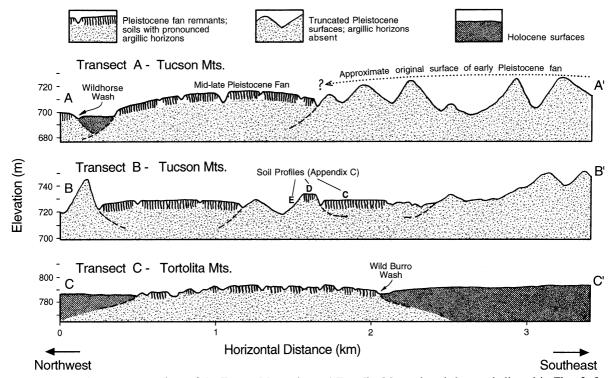


Fig. 7. Landscape cross sections of the Tucson Mountains and Tortolita Mountains piedmonts indicated in Figs. 3, 5, and 6. Vertical scale is exaggerated in comparison to the horizonal scale by a factor of 13.5:1.

on the limited area of the fan (referred to as on-fan drainages) (Fig. 6). The substantially smaller and less energetic flows originating solely as run-off from within the mid-late Pleistocene fan surface are generally incapable of moving the larger alluvial particles (large cobbles, stones, and boulders) that were deposited during the fan's original creation by the considerably larger flows of the Wildhorse Wash drainage. Consequently, erosion of the fan surface has occurred rather slowly by the selective removal of finer particles, and much of the original planar surfaces of the fan, as well as the soils on them, are relatively intact.

The northward shift of the locus of deposition from this mid-late Pleistocene fan surface led to the aggradation of an additional late Pleistocene fan surface with a degree of soil development that indicates an age of  $25\,000-75\,000$  yr (Katzer and Schuster 1984). These deposits are located directly northwest of Wildhorse Wash (Fig. 7). Holocene deposits (<11 000 yr old) are found in terraces elevated  $\approx 1$  m above the active channel in the lower reaches of Wildhorse Wash and in a fan deposit at the mouth of the wash (Figs. 3, 6, and 7A).

The general pattern of (1) extensive areas covered by deeply dissected early Pleistocene surfaces, (2) largely intact mid-late Pleistocene fans, and (3) limited areas of Holocene terraces and fans repeats itself across the study area to the south of the Wildhorse fan deposits (Fig. 3) (see also McKittrick 1988, Pearthree et al. 1988). The deeply dissected, early Pleistocene surfaces occupy the largest fraction of the landscape; midlate Pleistocene deposits appear as both broad fans and as narrower terraces 100-300 m wide inset within the topographic confines of older, dissected surfaces (Figs. 3 and 7B). Finally, the most recent Holocene deposits form terraces ranging between a few metres to  $\approx 100$ m wide and elevated 1-1.5 m above active channels of major washes. Several small fan-like deposits of Holocene age occur where these washes debouch onto the Santa Cruz River floodplain (Fig. 3).

Soil development over time. - The Tucson Mountains alluvial fan piedmont, like others studied by ecolegists (Solbrig et al. 1977, Phillips and MacMahon 1978) generally consists of gravelly to stony alluvium deposited in areas near the mountain front and finer alluvium in more distal locations. This textural change is clearly seen in alluvium contained in active wash channels debouching from drainages in the Tucson Mountains. This alluvial texture gradient is also expressed on the surfaces of stable remnants of older fan deposits but not within soil profiles. For example, the percentage of gravel and rock (material retained in a 2-mm mesh sieve) in surface samples (0–5 cm depth) taken from stable remnant surfaces of mid-late Pleistocene fans is negatively correlated (albeit weakly) with distance from the mountain front (r = 0.55, P = .05, n = 13). The surficial stoniness of a soil may reflect, to an extent, the textural nature of the original alluvium, but generally indicates little of the texture and structure of some underlying soil horizons. Samples taken at 15-20 cm depth from the same mid-late Pleistocene fan remnants discussed above show no significant relationship between the percentage of gravel and rock in the samples and distance from the mountain front (r = 0.30, P > .10, n = 13). A lack of any relationship between percentage clay at 15-20 cm depth and distance from the mountain front in these samples (r = 0.06, P > .50, n = 13) demonstrates even more strongly that subsurface soil texture is unrelated to distance from the mountain front on these mid-late Pleistocene surfaces.

The andesitic and rhyolitic alluvium comprising these fan deposits is relatively resistant to physical weathering in arid and semiarid climates (Bull and Schick 1979, Bull 1991). Because of this resistance to weathering, gravelly and stony materials remaining on the surfaces of these fan deposits may reflect the textural attributes of the original alluvium, even after the passage of several hundred millennia. However, pedogenic changes within these ancient deposits have formed soil horizons that differ greatly from the nature of the original rocky or gravelly parent materials.

In warm arid and semiarid climates of the American Southwest, two distinct soil horizons typically form and become increasingly developed over time in noncalcic alluvium in stable landscape positions. These horizons are a clay-enriched argillic horizon and a calcic horizon enriched with calcium carbonate (Gile et al. 1966, 1981, Gile and Grossman 1968, Machette 1985). The accumulation of clay and calcium carbonate within profiles of desert soils is a time-dependent process. A principal source of both materials in these arid regions (especially for calcium carbonate in noncalcic parent materials) is wind-transported dust and materials deposited by precipitation (Gile et al. 1981, Machette 1985, McFadden and Tinsley 1985, Mc-Fadden et al. 1986, 1987, McFadden 1988, Marion 1989).

Soils on the most recent Holocene surfaces exhibit very weak profile development with little or no accumulation of clay and carbonate in distinct horizons (Fig. 8, Appendix C: Profile A). The physical nature of these soils is largely determined by the characteristics (texture, chemistry, etc.) of the original alluvium. Some soils on Holocene surfaces possess cambic B horizons characterized by weak structural development and slight accumulation and vertical redistribution of calcium carbonate (Appendix C: Profile B). All of the Holoceneaged soils are coarse textured throughout their depths (sand, loamy sand, and sandy loam textural classes).

In contrast to the little-altered alluvium of Holocene deposits, soils developed on stable, planar surfaces of Pleistocene fan remnants show very strong profile development. In these soils, the textural, structural, and chemical characteristics of some horizons differ dramatically from those of the original, coarse alluvium.

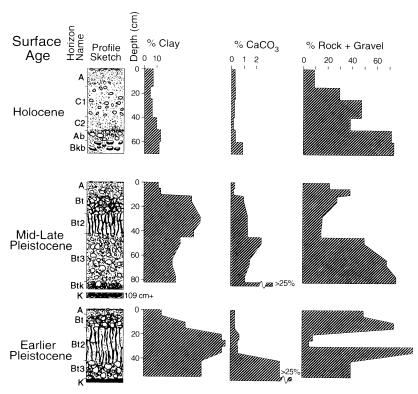


Fig. 8. Soil profile characteristics from a chronosequence of alluvial deposits in the Tucson Mountains study area. These three soils are profiles A, C, and D listed in Appendix C.

Strongly developed argillic horizons containing up to 45% clay are present in soils from mid-late Pleistocene surfaces and argillic horizons from the soil of a somewhat older Pleistocene fan remnant contained >65% clay (Fig. 8, Appendix C: profiles C, D). The two soils from Pleistocene surfaces represented in Fig. 8 were located only a kilometre from the mountain front, and the original parent materials for these clayey soils were very coarse rhyolitic gravels and angular cobbles. Yet the zone of maximum clay accumulation in each profile is nearly devoid of coarse fragments (Fig. 8, Appendix C). These strongly developed argillic horizons are similar to those described in other studies of soil development in coarse, noncalcic parent materials in the American Southwest (McFadden 1978, Gile et al. 1981, Pearthree and Calvo 1987). These argillic horizons are the result of pedogenic changes (accumulation of illuvial clay) over long periods of time, not the original presence of layers of clay-rich alluvium. The argillic horizons contained in all soils of remnant, noneroded Pleistocene surfaces are underlain at depths of 60–100 cm by moderately to strongly cemented, stage III-IV (Gile et al. 1966) calcic and petrocalcic horizons (caliche) (Appendix C).

Erosional truncation of soils.—Unless a fan surface is buried by younger alluvium, on-fan drainages increasingly incise and eventually eliminate the fan's original planar surface (Christenson and Purcell 1985). In this process, soil profiles that may have developed on the original surface are altered or destroyed. The erosional truncation of well-developed soils of Pleistocene surfaces involves thinning and removal of original A and argillic B horizons and the exposure of deeper calcic horizons (Fig. 9). On the largely preserved, original surfaces of mid-late Pleistocene fans, soil truncation has typically occurred only in the immediate vicinity of small drainages that are usually incised no more than a few metres into the fan surface (Figs. 6 and 7A, B). On highly dissected early Pleistocene deposits, though, virtually all of the planar features of the original fan have been removed together with surficial argillic horizons. Consequently, soils that are present on these highly dissected surfaces are very distinct; two factors contribute to this distinctness. First, the exposure of carbonate-rich materials at the surface profoundly affects soil-forming processes. Second, soils in these environments often have relatively weak horizon development because of the dynamic nature of the erosional settings in which they are found.

Within the study area, accumulations of pedogenic carbonate are found throughout extensive vertical sections of the highly dissected, early Pleistocene fan deposits. Examinations of two extremely deep trenches (new excavations for sewer lines) showed petrocalcic horizons present throughout at least the upper 10 m of alluvium comprising these ancient surfaces. The ver-

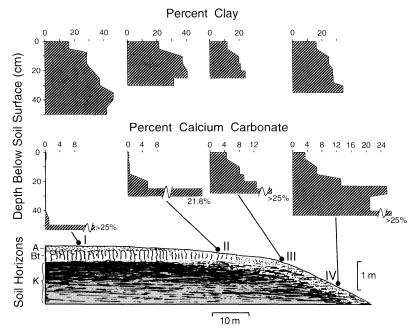


FIG. 9. Pattern of soil truncation at the edge of a Pleistocene fan remnant with intact argillic horizons. Site is located in the immediate vicinity of soil profiles C, D, and E (Fig. 3; Appendix C). Data for location IV in the figure are from soil profile E (Appendix C).

tical extent of carbonate accumulations represents a vertical succession of ancient alluvial deposits and buried soil horizons (including calcic horizons). Because of the great depth of carbonate-rich material in ancient fan deposits of the study area, extensive and profound landscape dissection continually exposes carbonate-rich materials on erosional slopes of early Pleistocene deposits.

Partial dissolution and deterioration of originally highly cemented petrocalcic horizons occurs when these horizons are brought near the surface in the process of soil truncation (Fig. 9). Abundant calcium carbonate flocculates clay particles (Gile et al. 1981). Since the downward movement of clays occurs in colloidal sus-

pension, flocculation of clay particles into aggregates inhibits downward clay translocation and formation of an argillic horizon. As a consequence, carbonate-rich soils derived from former calcic horizons typically have weak structure, relatively soft, dry consistency, and more homogeneous texture with depth in comparison to soils on noneroded remnants of Pleistocene fan surfaces (Figs. 9 and 10A, B, Appendix C).

The dynamic nature of these erosional environments also directly limits soil development. Erosion on hill-slopes exposes underlying materials in upslope locations; materials eroded from upslope are transported downslope and accumulate at the lower parts and bases of slopes. The relatively great (and probably episodic)

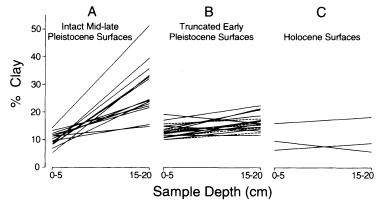


Fig. 10. Magnitude of textural transitions (percent clay) indicated by steepness of slope between surficial (0–5 cm depth) and deeper (15–20 cm depth) soil samples taken at the 39 vegetation sampling sites. – – in B indicate soils from relatively level, erosional summits (Groups D1, D2 in Table 1); ——represent soils from adjacent erosional sideslopes.

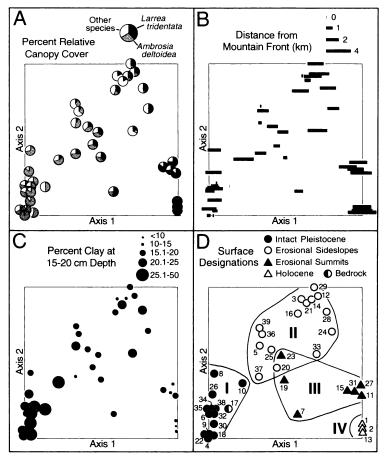


Fig. 11. Polar ordinations of the 39 vegetation samples from the Tucson Mountains study area. Arabic numerals marking individual sites in part D are the sample site identifications.

flux of materials to and from these surfaces interrupts pedogenesis and inhibits the formation of strongly developed soil profiles (Gile et al. 1981, Peterson 1981).

Vegetation responses. - Differences in relative abundances of two shrubs, Larrea tridentata and Ambrosia deltoidea, accounted for much of the variability in vegetational composition across the Tucson Mountains piedmont. A polar ordination (see Gauch 1977 for computational methods used) of the 39 sample sites based on relative cover of 29 perennial species clearly separated the sites on the basis of variation in relative cover of these two shrub species (Fig. 11A). Sites positioned to the left of the ordination are dominated by A. deltoidea, whereas L. tridentata exhibits greater dominance in sites plotted to the right. Vertical separation within the ordination is largely due to variation in the contributions of other species to cover. Species other than L. tridentata and A. deltoidea typically contribute > 50% of total canopy cover in sites plotted in the upper half of the ordination. Sites plotted in the lower half the ordination are those more fully occupied by either L. tridentata, A. deltoidea, or these two species combined.

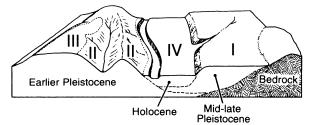


Fig. 12. Landscape designations of sites in the Tucson Mountains study area based on geomorphic and soils attributes. (I) Stable mid-late Pleistocene fan remnants mantled by soils containing well-developed argillic horizons. (II) Erosional sideslopes of earlier Pleistocene deposits. Soils in these locations lack argillic horizons, have relatively homogeneous texture with depth, and are highly calcic, but typically have depths in excess of 20 cm above cemented petrocalcic horizons. (III) Wide, moderately level (<3° slope) summit areas of truncated early Pleistocene surfaces listed in (II) above. These summit areas exhibit complete truncation of any former argillic horizon and have soils developed from the degraded remnants of former calcic horizons. These summit areas range from 10 to 50 m in width. Also included in this group is one younger Pleistocene surface (site 7) from which all original soils have been truncated but not taking the highly dissected topography of the early Pleistocene landforms. (IV) Holocene surfaces in which little pedogenesis has occurred.

Table 1. Ordered table of relative canopy cover of perennial species of the Tucson Mountains piedmont study site. 1: <5% relative cover, 2: 5–21%, 3: 12.1–25%, 4: 25.1–50%, 5: >50% relative cover.

				San	iple s	ites 1-	-39 (gr	oupe	d as i	n den	drogi	am o	f Fig.	13)			
	A	-		B-1				-		B-2					С	-1	
Species	17	22	4	6	18	34	8	9	30	32	26	38	35	39	3	36	21
Olneya tesota		1															
Opuntia fulgida		1	1	1	1	1	1	1					• • •				• • •
Opuntia spinosior		1				1	2	1	1							• • •	
Acacia gregii	2																
Janusia gracilis	2							• • •					• • •				
Opuntia versicolor	1	3	1	1	1	1	1	1		1	1	3	2	1		1	
Ambrosia deltoidea	4	5	5	5	5	5	5	5	5	5	5	5	5	4	1	4	
Opuntia leptocaulis						1						1		1	• • •		
Simmondsia chinensis	2	2	1	1	3	1											3
Ferocactus wislizeni	1													1			
Opuntia phaeacantha		1		1	2	2		1					1	1	1	2	
Fouquieria splendens		1		1	1							1		2	2	1	
Cercidium microphyllum	1			2	1	2	3	1	1	2	2	2	1	2		1	1
Acacia constricta	2								1		1	1	1	2	1	2	
Krameria parvifolia	2										1						
Calliandra eriophylla	$\bar{2}$															2	1
Krameria gravi	$\bar{2}$	1		1						1	1	1	2	3	2	3	3
Larrea tridentata						1			1	1	1			2	3	2	3
Jatropha cardiophylla																	
Muhlenbergia porteri																	
Condalia warnockii																	
Zinnia acerosa															1	1	1
Tiquilia canescens															1		
Lycium berlandieri																	1
Psilostrophe cooperi														3	4	1	ī
Poaceae														ĭ	2	2	2
Bouteloua eriopoda																	1
Parthenium incanum																1	
Aristida purpurea														1	1		3

Although the ordination indicates a compositional continuum, there is no clear or simple relationship between vegetation composition and distance to the mountain front (Fig. 11B). The plot does show that sites completely dominated by *L. tridentata* (lower right in Fig. 11B) are typically at great distances from the mountain front. But many sites where *L. tridentata* was either rare or absent were located both near and far from the mountain front. Similarly, species-rich sites in which *L. tridentata* and *A. deltoidea* were codominant were as likely to be found either immediately adjacent or at great distances from the mountain front.

A plot of the ordinated sites showing clay content of soils (15–20 cm depth) (Fig. 11C) indicates the sites dominated by A. deltoidea in which L. tridentata is absent or extremely rare are characterized by soils with higher clay content, regardless of distance from the mountain front. These higher clay contents indicated the presence of strongly developed argillic horizons as diagrammed for Pleistocene surfaces in Fig. 8. Sites in which L. tridentata dominates to the exclusion of all other species (plotted in lower right of ordination) have consistently lower clay contents than other sites.

The sample sites fall into four relatively distinct classes on the basis of geomorphic characteristics and associated soil attributes (Fig. 12). Much of the vari-

ability expressed in the original ordination can be accounted for by these geomorphic and soil characteristics. When the ordination is plotted showing the landscape attributes based on geomorphology, soils, and slope characteristics, sites within each of these landscape groupings form relatively distinct groupings within the ordination (Groups I-IV; Fig. 11D). Assemblages dominated by A. deltoidea, in which L. tridentata is absent or rare (Group I), are located exclusively on stable Pleistocene fan remnants mantled by soils containing strongly developed argillic horizons. One of these sites (Site 17) is located on rhyolitic bedrock, but it too has soils with strongly developed argillic horizons (Appendix A). Sites located on erosional sideslopes of ridges and ballenas and other erosional landforms typically associated with early Pleistocene surfaces have vegetational compositions that are distinct (Group II, Figs. 11D and 12) from most sites located on the relatively level summits above erosional sideslopes (Group III). The overlap between ordination groups II and III (especially sites 19 and 23) is discussed in detail at a later point. Group IV consists of assemblages almost completely dominated by L. tridentata that occur on Holocene surfaces. Additionally, the compositional similarity between some members of Group III (especially sites 15, 31, 27, and 11) from sites on summits

TABLE 1. Continued.

						C-	2							D	-1		D-2			D-3	
19	20	37	25	5	10	23	12	16	28	33	24	29	14	15	7	27	11	31	1	13	2
										• • • •											
	• • •	• • •	• • •		1							• • •		• • •							
	• • •		• • •																• • •		
			• • •			• • •			• • •	• • •	• • •	• • •	• • •	• • •			• • •		• • •	• • •	
								• • •		• • •		• • •			• • •		• • •	• • •			
				1				• • •	• • •	1	• • •		• • •	• • •		• • •	• • •	• • •		• • •	• • •
4	4	4	4	4	5	4	2	3	1	3	1	2	2	1	4		• • •	• • •	• • •	• • •	• • •
				1		• • •	• • •	• • •		• • •	• • •	• • •	• • • •	• • •		• • •	• • •	• • •	• • •	• • •	
1	1		• • •	1		• • •		• • •	• • •	• • •	• • •	• • •		• • •	• • •	• • •	• • •	• • •		• • •	
	• • •			• • •				• • •	• • •	• • •	• • •	• • •	• • •		• • •		• • •	• • •	• • •	• • •	
	• • •	• • •	• • •	1				• • •	• • •	• • •	• • •	• • •	• • •		• • •	• • •	• • •	• • •		• • •	
1	1	1	1	1				• • •		• • •	1	1		1		1	• • •		• • •	• • •	
1		1	2	3	2	3	4	3	3	1	3	3	2	2	1	1	1	• • •	• • •	• • •	
• •	1	1	1			• • •	2	• • •	1	1	1	1	1		• • •	• • •		• • •		• • •	
				• • •	• • •				1	1			1	3	• • •	• • •	1			• • •	• • •
	• • •	1		• • •				• • •	• • •	• • •	1	1		• • •	• • •	• • •	• • •		• • •	• • •	• • •
3	3	3	4	4	2	2	3	3	4	4	3	3	3	2	1	3	2	4	• • • •		• • •
4	4	3	3	3	3	4	4	4	4	4	4	4	4	5	5	5	5	5	5	5	5
	1	1		1				• • •		• • •			• • •	• • • •		• • •		• • •		• • •	• • •
• •	• • •	• • •		• • •			• • •	• • •	1	• • •	• • •	1	• • •	• • •	• • •		• • •	• • •	• • • •	• • •	• • •
	• • •	• • •	• • •				• • •	• • •		• • •	1	• • •	1	• • •	• • •	• • •			• • •		
	• • •		• • •	• • •	• • •			1	1	1	2	1	3	• • • •	• • •	• • •	• • •	• • •	• • •	• • •	• • •
	• • •				• • •			1			• • •		2	• • • •		1		• • •	• • •		
• •	• • •		1	• • •		1		• • •	• • •	• • •	1	• • •	• • •		• • •	• • •	• • •	• • •		• • •	• • •
	• • •	• • •	• • •	1	• • •	1	1	• • •	1	2	2	1	• • •		• • •		• • •	• • •	• • •	• • •	
• •		• • •	• • •	• • •	• • •	• • •		• • •	• • •	• • •		• • •	• • •	• • •	• • •	• • •	• • •			• • •	
• •	• • •	• • •	• • •			• • •	• • •	• • •	• • •	• • •	• • •	• • •	• • •	• • •	• • •	• • •	• • •	• • •		• • •	• • •
					• • •			• • •	• • •		• • •	• • •				• • •		• • •	• • •	• • •	• • • •
	1	• • •	1	• • •	• • •				• • •		• • •		• • •	• • •			• • •	• • •		• • •	

of early Pleistocene surfaces and sites from Holocene surfaces of Group IV is shown by their proximity in the ordination.

A hierarchical classification (TWINSPAN procedure described in Hill 1979 and Gauch 1982) (Fig. 13) and accompanying ordered table (Table 1) of sites complement the ordination by providing more detailed information on compositional affinities among the 39 sample sites. The primary division in the dendrogram (Fig. 13) distinguishes sites where L. tridentata is absent or extremely rare (left side of division 1) from those in which L. tridentata is predominant (right side of division 1). Secondary division of the primary, lefthand cluster separates one site (17) labelled "Cluster A" from 12 other sites labelled "Cluster B" based on the presence or absence of the shrub species Calliandra eriophylla. Site 17 is the only site located on bedrock (rhyolite) but as already pointed out, contains a welldeveloped argillic horizon (41.6% clay at 15-20 cm depth; Appendix A).

Cluster B contains sites that are compositionally and physiognomically distinct from sites on the right side (Clusters C and D) of the primary dendrogram division. The shrub species A. deltoidea accounts for >50% of all perennial plant cover in the sites included in Cluster B and other shrub species (Simmondsia chi-

nensis, Krameria spp., L. tridentata), if present, contribute relatively little to total cover (Table 1). Three architecturally similar cylindro-opuntia species (Opuntia fulgida, O. spinosior, and O. versicolor) are collectively more abundant in these sites than those included in clusters C and D. Although these cacti usually contribute but a small fraction of total canopy cover, they are conspicuous components of the vegetation due to their greater height above the short canopies of A. deltoidea. The small tree Cercidium microphyllum is commonly interspersed within the relatively uniform matrix of closely spaced canopies of A. deltoidea. With the exception of site 10, Cluster B corresponds with the group of sites dominated by A. deltoidea from intact Pleistocene surfaces located in the lower left of the polar ordination (Group I, Fig. 11D).

The right side of the dendrogram, representing sites where *L. tridentata* accounts for >5% relative cover is further subdivided on the basis of the degree of dominance by this shrub. Cluster C contains sites where *L. tridentata* accounts for <50% of all canopy cover; Cluster D contains sites with >50% relative cover by *L. tridentata*. Within sites contained in Cluster C, *L. tridentata* typically shares dominance with two other shrub species, *A. deltoidea* and *Krameria grayi*, and the small tree *Cercidium microphyllum*. Many other species of

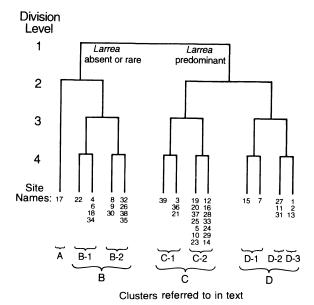


Fig. 13. TWINSPAN dendrogram of the 39 vegetation sample sites, Tucson Mountains study area. Cut levels (Hill 1979) used in the classification were 0, 5, 12, 25, 50% relative cover.

woody perennials (Fouquieria splendens, Acacia constricta, Calliandra eriophylla, Jatropha cardiophylla, Condalia warnockii, Zinnia acerosa, Tiquilia canescens, Lycium berlandieri, and Psilostrophe cooperi) are much more common in sites of Cluster C than in those of any other cluster (Table 1). The variable heights of the many shrub and small tree species found in sites included in Cluster C produce a more complex vertical architecture of the vegetation than possessed by sites contained in other clusters. Perennial C<sub>4</sub> grasses, including Muhlenbergia porteri, Aristida purpurea, Tri-

A) Dependent variable = number of species

dens muticus, and Bouteloua eriopoda, are most abundant in some of the sites included in Cluster C. Various Opuntia species, so prominent in sites in Cluster B, are considerably less abundant in sites of Cluster C (Table 1). Sites within Cluster C contain the most diverse perennial plant assemblages in terms of the numbers of species and evenness of species' abundances. With the exception of three sites (sites 10, 19, and 23), members of dendrogram Cluster C are all located on erosional sideslopes of early Pleistocene surfaces and correspond to Group II in the ordination (Fig. 11D). Site 10 was classified by the TWINSPAN classification as a borderline case between Clusters B and C and likewise was positioned in an intermediate position between ordination groups I and II. Similarly, the TWIN-SPAN classification listed sites 19 and 23 as borderline cases between Clusters C and D. These two sites were located on summits above erosional sideslopes of early Pleistocene surfaces (surface designation III, Figs. 11 and 12). The polar ordination indicated a similar ambiguous affinity of these two summit sites with ordination Group II representing sites from erosional sideslopes (Fig. 11D). The ambiguous classification of these two sites is apparently related to the influences of an extremely shallow, indurated petrocalcic horizon (site 19) or a unique, extremely narrow, ridge-like shape of summit site 23. These two exceptions are examined in more detail in the Discussion.

Sites included in Cluster D are characterized by far greater dominance of *L. tridentata* and an absence or extreme rarity of other species. This extreme dominance of *L. tridentata* is expressed in two very different geomorphic and soils settings: several of the relatively level summits of the oldest (early Pleistocene) surfaces and the Holocene surfaces (landscape designations III and IV; Fig. 12). As already indicated, the polar or-

TABLE 2. Analyses of covariance: effects of distance from the mountain front and landscape position on species richness and relative cover of *Larrea tridentata* at the Tucson Mountains study area.\*

Source of variation	df	SS	MS	F	P
Covariate (distance)	1	16.67	16.67	6.30	.017
Treatments (landscape position)	3	205.2	68.39	25.85	<.00001
Residual	33	87.32	2.646		
Total	37	306.19			
	Covariate	$R^2 = 16.67/309$	19 = 0.052		
R) Dependent variable - relative cov		$R^2 = 205.2/309.$			
B) Dependent variable = relative cov Source of variation				F	P
Source of variation	er of <i>Larrea tric</i>	dentata	19 = 0.664	F 9,454	.004
Source of variation  Covariate (distance)	er of <i>Larrea tric</i>	dentata SS	19 = 0.664 MS		
B) Dependent variable = relative cov Source of variation  Covariate (distance)  Treatments (landscape position)  Residual	er of <i>Larrea tric</i>	dentata ss 1041	19 = 0.664  MS  1041	9.454	.004

<sup>\*</sup> n = 38 sites; one site (Site 17) was excluded because it was located on bedrock rather than alluvial fan deposits.

dination revealed the same similarity of the perennial vegetation of sites from these two extremely different landscape settings.

Two major components of compositional variability indicated in the polar ordination and the hierarchical classification (changes in the relative dominance of L. tridentata and the relative contributions of a diverse set of other species) have also been a focus of gradient studies of other Sonoran Desert bajadas. Both the number of species encountered in point-intercept sampling and the relative cover of L. tridentata are significantly, but weakly correlated with distance from the mountain front ( $r^2 = 0.18$  and 0.24, respectively). However, a considerably greater amount of variation in the relationship between distance and either species richness or relative dominance by L. tridentata is explained with the inclusion of landscape position as an independent factor.

Analysis of covariance (Table 2) indicated the relative contributions of distance of sites from the mountain front (a continuous covariate) and landscape position (four levels of this categorical factor as shown in Fig. 12) as determinants of species richess and dominance by L. tridentata. Although species richness is significantly related to distance (P < .02), only 5% of the total variation in species richness is explained by this covariate (Table 2A, Fig. 14). A considerably greater percentage of total variation in species richness among the sample sites (66%) is explained by separating out geomorphic and soils attributes as an independent factor. Similarly, the pattern of dominance by L. tridentata is significantly but weakly related to distance from the mountain front. Analysis of covariance indicated that only 3.5% of the total variation in relative cover of L. tridentata is explained by distance from the mountain front, whereas 84% was explained by the four levels of geomorphic and soils characteristics (Table 2B, Fig. 14). Within any single elevational contour, the magnitude of variation in species richness or dominance by L. tridentata is nearly as great as the variation over the entire elevational gradient.

# Silver Bell Mountains

One might argue that the very weak expression of a vegetational gradient with distance from the mountain front in the Tucson Mountains study area is due to a rather abrupt and atypical truncation of the piedmont gradient by the Santa Cruz River. However, the second study area in the Silver Bell Mountains piedmont provides a further clarification of the importance of geomorphic surfaces and soils variability to vegetation patterns.

Geomorphology and soils.—The same diversity of alluvial deposits and landforms observed in the Tucson Mountains piedmont was present in the Silver Bell study area. Principal alluvial landforms included (1) stable fan remnants of Pleistocene age, (2) erosionally

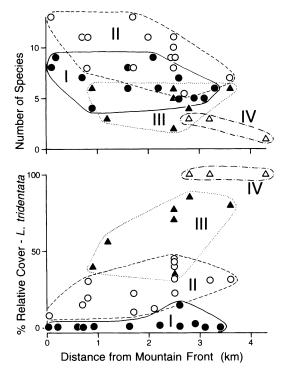


Fig. 14. Number of species and relative cover of *Larrea* tridentata as functions of distance from mountain front and landscape positions (I–IV) designated in Fig. 11.

truncated Pleistocene surfaces, and (3) Holocene deposits of at least two different ages.

Transversely level, stable remnants of Pleistocene fan surfaces are found along nearly the entire elevational range of the study area but are more extensive in mid- to upper elevations (Fig. 15). Soils mantling these surfaces contain reddened and strongly developed argillic horizons (sandy clay loam, sandy clay, and clay textural classes) beneath coarser textured, more permeable A horizons. The argillic horizons are underlain at depths of 50–100 cm by weakly to strongly cemented (stage II–IV, Gile et al. 1966) calcic horizons (Appendix C). These soils are very similar to those found on the mid–late Pleistocene fan surfaces of the Tucson Mountains piedmont.

Soils on Pleistocene fan remnants in the lowermost elevations (Transects B–D) possess moderately extensive areas (up to 10 m wide at site B3) of tightly packed and lightly to moderately varnished stone pavements that are relatively barren of perennial vegetation. Vesicular A horizons (McFadden et al. 1987) up to 5 cm thick are present immediately below the stone pavements (Appendix C). Areas covered with varnished stone pavements diminish in areal extent with increasing elevation (e.g., to areas <4 m wide at site D3) and are completely absent on mid–late Pleistocene fan remnants of the uppermost elevations.

Highly eroded, ridgeline remnants of even older Pleistocene fan deposits are found throughout the up-

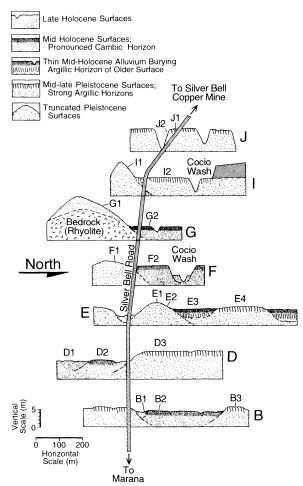


Fig. 15. Landscape cross sections of 7 of the 10 transects studied on the Silver Bell piedmont. Vertical scale is exaggerated in comparison to the horizonal scale by a factor of 16:1.

per half of the study area (Transects E through I, Fig. 15). The crests of these ridges and isolated ballenas are elevated from a few to  $\approx 10$  m above adjacent, younger fan surfaces. Like the same landforms in the Tucson Mountains site, these ridges and ballenas represent the erosional remnants of ancient fan deposits (probably early Pleistocene age) whose original surfaces would have been elevated somewhat above the level of the remaining ridges. Degraded remnants of petrocalcic horizons can be found on the surfaces of these landforms and indicate truncation of original soils. Because of the abundance of calcium carbonate at the surface and the more dynamic nature of hillslopes, the soils that mantle these landforms are calcic and lack argillic horizons.

The relative area covered by Holocene deposits in the Silver Bell piedmont is greater than the very limited areal extent of Holocene surfaces in the Tucson Mountain piedmont. The extent of Holocene deposits is largely related to the size, location, and behavior of the major streams draining basins. The close proximity of the Santa Cruz River to the east flank of the Tucson Mountains and the relatively deep incision of the river has led to corresponding deep incision of the narrow piedmont and removal of most Holocene alluvium directly to the Santa Cruz floodplain. Extensive Holocene surfaces are not present in most distal parts of the Tucson Mountains piedmont because occasional voluminous flows of the Santa Cruz River remove large quantities of alluvium from the basin. The considerably smaller stream systems (Blanco and Brawley Washes) on the basin floor directly below the Silver Bell piedmont (Fig. 2) do not have the capacity to transport volumes of alluvium comparable to those transported by the Santa Cruz River. In addition, these washes are located a greater distance from the Silver Bell Mountains ( $\approx$  14 km) and are not incised as deeply into the valley floor as is the Santa Cruz River.

As a consequence, extensive areas in lower elevations of the Silver Bell piedmont are covered by Holocene deposits that bury older deposits. Much of the alluvium comprising these Holocene deposits has been derived from the erosion of extensive Pleistocene fan deposits located upslope. The extent of Holocene deposits diminishes in upper parts of the piedmont. In middle reaches of the study area (e.g., transects D–G, Fig. 15), Holocene surfaces are limited to deposits inset within the topographic confines of more elevated, older surfaces. In the uppermost parts of the study area, Holocene surfaces are virtually absent and are limited to very small bar-like deposits and terraces associated with wash channels.

Soils on Holocene-aged deposits in lower to middle reaches (Sites B-G, Fig. 15) exhibit considerable complexity due to repeated episodes of aggradation during the last 11 000 yr and varying degrees of soil development as a function of surface age. Variation in soil development indicated at least two distinct Holocene surfaces of different ages. A well-defined Holocene surface observed from transects A to G (Sites A2, B2, D2, F2, and G2; Fig. 15, Appendix B) possessed a soil with a slightly altered B horizon exhibiting weak structural development (i.e., a cambic horizon) and advanced stage I carbonate accumulation and carbonate redistribution within the profile (Appendix C). Textures of all horizons in these soils were coarse (loamy sand or sandy loam textural classes; Appendix C). The weak developmental characteristics exhibited by these soils are similar to the degree of pedogenic development found in dated Holocene deposits in the Chihuahuan Desert of southern New Mexico that range between 2600 and 7500 yr old (Fillmore Alluvium described by Gile et al. 1981: 45, 80, 106-107). On the basis of this pedogenic similarity, I refer to these surfaces as mid-Holocene surfaces. One mid-Holocene surface encountered in transect E exhibited more complex features due to the shallow burial of what is probably a latest Pleistocene surface. The buried surface contained

a moderately well-developed argillic horizon (Appendix C; Silver Bell soil profile E3). Inset below the mid-Holocene surface at transects A, B, and D are small areas of late Holocene deposits that lack any substantial pedogenic modification, including structural and textural changes or accumulation and redistribution of carbonate.

Vegetation patterns.—Relative cover of the two dominant species, A. deltoidea and L. tridentata, as well as the contributions of a diverse set of other species can be pictured as a compositional continuum (Fig. 16A) that closely resembles the polar ordination of sites from the Tucson Mountains piedmont (Fig. 11A). However, this compositional continuum does not signify a pattern of spatially continuous change over the face of the piedmont. The repeated lateral juxtaposition of the various, distinct geomorphic surfaces along the entire elevational gradient typically produces abrupt vegetational transitions at the scale of metres to tens of metres (Figs. 15 and 17).

The correspondence between geomorphic surfaces and vegetation composition within the Silver Bell study area is very similar to that observed in the Tucson Mountains study area. Despite distance from the mountain front, stable Pleistocene fan remnants mantled by soils containing well-developed argillic horizons are dominated by the shrub *Ambrosia deltoidea* (Group I, Fig. 16B). Although *Larrea tridentata* is present on these surfaces of the lower elevation sites, this shrub species is completely absent from Pleistocene fan remnants with comparable argillic horizons in the upper elevations of the site (Table 3, Fig. 17, Appendix C: soil profiles C1, J1). Cacti reach their greatest densities on soils with strong argillic horizons in the uppermost elevations (Table 4).

Erosional sideslopes of truncated Pleistocene surfaces have a more even mix of many species and possess the greatest number of species (Fig. 16B: Group II; Fig. 17; Table 3). On these sites, like those from similar erosional sideslopes of the Tucson Mountains area, *L. tridentata*, *A. deltoidea*, *Krameria grayii*, and *Cercidium microphyllum* share codominance. Erosionally truncated but nearly level sites (sites E1, H1) are dominated by *L. tridentata* and *A. deltoidea* and possess fewer species than do adjacent erosional slopes (Table 3).

Throughout the elevational gradient, mid-Holocene surfaces are strongly dominated by *L. tridentata* and contain the lowest numbers of other species (Tables 3 and 4; Fig. 17). An exception is site E3, which has low cover of *L. tridentata*, substantially greater coverage of *A. deltoidea* (Table 3), considerably higher densities of the cactus *Opuntia acanthocarpa* (Table 4), and more species than contained in any of the other mid-Holocene surfaces (Fig. 17). The anomalous composition of site E3 is clearly related to its unique soil attributes. As indicated previously, the soils of this site consist of a relatively thin veneer (<50 cm) of mid-Holocene

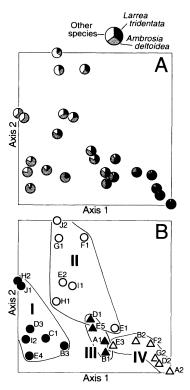


FIG. 16. Polar ordination of the Silver Bell vegetation samples. (A) Samples plotted as relative cover of *Larrea tridentata*, *Ambrosia deltoidea*, and other species. (B) Same ordination as (A), except plotted as geomorphic surfaces of each sample site (I = relict Pleistocene surfaces with well-developed argillic horizons, II = erosionally degraded, earlier Pleistocene fan remnants, III = late Holocene surfaces, IV = mid-Holocene surfaces).

alluvium burying a moderately well-developed argillic horizon of a latest Pleistocene surface. None of the other sites on mid-Holocene surfaces contain a buried argillic horizon so close to the surface (e.g., compare Silver Bell soil profile descriptions from sites E3 and F1, Appendix C).

Late Holocene surfaces possess more equable abundances of *L. tridentata* and *A. deltoidea* and more species than do adjacent mid-Holocene surfaces (Fig. 16, Group III; Fig. 17).

Although the greatest amount of compositional variability along the elevational gradient arises from the vegetational differences among various geomorphic surfaces, some clear compositional gradients are expressed within the individual geomorphic surfaces. For example, even though *L. tridentata* is a minor component of the vegetation on mid–late Pleistocene fan remnants of lower elevations (Fig. 17), relative cover of this shrub on mid–late Pleistocene surfaces gradually declines and eventually becomes completely absent with increased elevation. On these same Pleistocene fan remnants, trees (*Cercidium microphyllum* and *Olneya tesota*), other shrub species (Table 3), and various cactus species (Table 4) show increased representation in

Table 3. Relative cover of nonsucculent perennial plants at the Silver Bell study area. Individual sites (see Fig. 4) are arranged by distance from the basin floor within separate landscape groupings. 1: <1% relative cover, 2: 1.1-5%, 3: 5.1-12%, 4: 12.1-25%, 5: 25.1-50%, 6: 50.1-75%, 7: >75% relative cover.

				San	nple si	tes wit	hin sep	arate la	ndscap	e grou	pings			
										Trunca	ited Pl	eistocer	ne	
		1	Remna	nt Plei	stocen	e			Eros	ional s	lopes		Le	vel
Species	В3	C1	D3	E4	H2	12	J1	E2	F1	G1	I1	J2	E1	H1
Krameria parvifolia			• • • • • • • • • • • • • • • • • • • •	• • • • •	2	1	1							
Janusia gracilis					1	1	1					1		
Prosopis velutina						1								
Fouquieria splendens					1	2	2	2	3	2	4			
Olneya tesota			1			2	1	2	1	2	1	2		1
Cercidium microphyllum		3	3	2	4	2	4	4	4	4	1	5	2	3
Ambrosia deltoidea	7	7	7	7	6	7	6	5	5	5	5	4	4	6
Larrea tridentata	4	3	2	1				4	5	4	4	4	6	4
Acacia constricta					2		1	2	2	3	2	3		2
Krameria gravi			1		1			3	3	2	3	1	3	1
Lycium berlandieri						1	1	1		2	2	2		2
Jatropha cardiophylla							1			1	2	1		
Psilostrophe cooperi								1	1	3	1			
Polygala macradenia								1		1				
Ephedra trifurca								1		1	1	1		
Trixis californica								1				1		
Encelia farinosa										2				
Calliandra eriophylla										2	1			
Tiquilia canescens										2		1		
Ayenia microphylla										1	1	1		
Hibiscus denudatus												1		
Abutilon incanum												1		
Sphaeralcea ambigua												1		
Menodora scabra										1				
Muhlenbergia porteri												1		
Zinnia acerosa														
Lycium sp. 1		1				1		1						
Ambrosia dumosa														

upper elevations. The presence of these additional species contributes to a gradual increase in species richness with elevation on the mid-late Pleistocene surfaces (Figs. 17 and 18). Other individual geomorphic surfaces are not as widely distributed over the entire elevational gradient, but show similar elevational trends in species richness (Fig. 18).

An analysis of covariance provided an estimate of the proportion of variation in species richness explained by position along the elevational gradient (distance from the Silver Bell Mountains, a continuous covariate) and landscape position (a categorical factor with four levels: stable Pleistocene fan remnants, erosional sideslopes of truncated Pleistocene surfaces, mid-Holocene surfaces, and late-Holocene surfaces). Both distance and landscape position are highly significant predictors of species richness. Distance along the elevational gradient accounted for an estimated 36% of

TABLE 4. Density classes of succulent species at the Silver Bell study area. Individual sample sites (see Fig. 4) are arranged within separate geomorphic surfaces according to distance from the basin floor. Values listed are median values of density classes recorded on a log<sub>2</sub> scale (McAuliffe 1991b).\*

				San	nple si	tes wit	hin sep	arate la	ndsca	pe grou	pings			
										Trunca	ited Pl	eistocer	ne	
		J	Remna	nt Ple	stocen	e			Eros	ional s	lopes		Le	vel
Species	В3	C1	D3	E4	H2	12	J1	E2	F1	Gl	I1	J2	El	HI
Opuntia acanthocarpa			2	2	5	3	6	1			3	4		
Opuntia phaeacantha				1	1	1	2			1	2	3		
Opuntia fulgida		1	1		1						1			
Opuntia leptocaulis			1				1		1			2		
Carnegiea gigantea				1	3	2	1	1				3		
Echinocereus fasciculatus		1			2	3	2				1	3		
Ferocactus wislizeni			1		2	1	2				1			
Mammillaria microcarpa					2	4	7				1	5		

<sup>\*</sup> Codes: 1: <1 plants/100-m<sup>2</sup> plot, 2: 1, 3: 2, 4: 3-5, 5: 6-11, 6: 12-23, 7: 24-47 plants/100-m<sup>2</sup> plot.

TABLE 3. Continued.

Sample sites within separate landso	ane grounings

L	ate H	olocer	ne		Mi	iddle I	Holoce	ene	
A1	В1	Dl	E5	A2	B2	D2	E3	F2	G2
								2	
							2		
	1	3					2 2	1	
5	5	5	5	2	5	3	5	4	3
6	6	5 3	6	7	7	7	5 5 2	7	7
3		3	2				2		
							1	2	1
	• • •	• • •	• • •				1		• • •
• • •	• • •	• • •	• • •						
							• • •	• • •	• • •
• • •	• • •	• • •							
		• • •	• • •			• • •	• • •	• • •	• • •
• • •	• • •	• • •	• • •	• • •					
	• • •	• • •	• • •			• • •			
• • •	• • •	• • •	• • •	• • • •		• • •			
	• • •	• • •	• • •	• • • •	• • •	• • •			• • •
• • •	• • •		• • •			• • • •			
• • •	• • •	1	• • •	• • •					
• • •	1		1			• • •			• • •
1	• • •	• • •	• • •			• • •		• • •	• • •
3	2	2	2			1	1		• • •
1	• • •	1	•••	1	• • •	2	1	• • •	• • •

the total variation in species richness, whereas landscape position accounted for 48% of the total variation (Table 5, Fig. 18). Despite the apparent complexity of this piedmont and rather small number of sampling sites, only 16% of total variation is not explained by a combination of the two factors of distance and geomorphic/soils attributes. In effect, an accurate map of the geomorphic configuration of the landscape coupled with information on distance from the mountain front

Table 4. Continued.

	• .				
Sample s	2911	within	senarate	landscape	groupings
Sumpic 5	,,,,,,	** * CTTTTT	Separate	ania scupe	SICUPILIS

L	ate H	olocer	ne		Mi	iddle I	Holoc	ene	
A1	В1	DI	E5	A2	B2	D2	E3	F2	G2
	1	1	2				3	1	1
		1					1		
								1	1
1		1	1						
1		1	1				1		
	1	1	1						
			• • •	• • •					
• • •		• • •	• • •	• • • •	•••	•••	•••	• • •	•••

provides a high-resolution mapping of vegetation responses. However, distance alone explains slightly less variation in species richness than does information on geomorphic attributes of various parts of the piedmont. The differential distribution of the various geomorphic surfaces at varying distances from the mountain front contributes strongly to the pattern of changes in average vegetational composition at different points along the elevational gradient. For example, Holocene surfaces represent a disproportionately large fraction of the landscape in lower elevations of the piedmont, whereas surfaces such as erosional remnants of older Pleistocene surfaces are nonexistent in these lower elevations because of either complete erosional truncation and/or burial (Figs. 15 and 17).

#### Tortolita Mountains

Geomorphology. — In gross aspect, the geomorphology of the Tortolita Mountains study area is very different from that of the two other study areas. The smooth, regular elevational contour lines on a topographic map of the Tortolita piedmont indicate a relatively unbroken slope as compared to the more deeply dissected terrains of the Tucson Mountains and Silver Bell sites (compare Fig. 5 with Figs. 3 and 4; Fig. 7). The less dissected topography of the Tortolita site has two components. First, Holocene deposits cover a greater proportion of the Tortolita piedmont and are little dissected because of their recent deposition. Second, the older Pleistocene deposits of the Tortolita piedmont exhibit a different spatial pattern and degree of dissection compared to Pleistocene surfaces of the Tucson Mountains and Silver Bell piedmonts. On the Tortolita piedmont, Pleistocene fan remnants are primarily limited to areas in upper parts of the piedmont near the mouths of Wild Burro and Ruelas Canyons (Fig. 5). Although these older, slightly elevated surfaces are more dissected than the surrounding Holocene surfaces, the maximum depth of incision of these deposits is but a fraction of that of Pleistocene surfaces of the Tucson Mountains piedmont (Fig. 7).

Although Pleistocene fan remnants of the Tortolita piedmont are not as deeply dissected, these surfaces are covered with a more finely ramified system of closely spaced, on-fan drainage channels (Fig. 19). Average distances between on-fan drainage channels on Pleistocene surfaces at the Tucson Mountains and Silver Bell sites is on the order of 200 m or more. On-fan drainages on the Pleistocene fan remnants in the Tortolita study area are typically spaced no more than 50–100 m apart.

Both the areal extent of Holocene deposits and the pattern of dissection of older Pleistocene deposits is in part controlled by lithology of the alluvium. The granites and granodiorites of the Tortolita Mountains are highly susceptible to weathering and yield greater amounts of fine alluvium than do the more weathering-

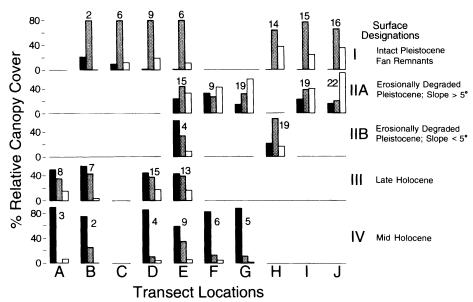


Fig. 17. Relative cover of the two dominant species *Larrea tridentata* (black histogram bars) and *Ambrosia deltoidea* (shaded bars) and other species (white bars) as a function of position along the elevational gradient and landscape position within the Silver Bell study area. Number above each histogram is the total number of species sampled at each site.

resistant rhyolites and andesites of the Tucson and Silver Bell Mountains. Hence, greater volumes of fine alluvium have been recently transported from the Tortolita Mountain slopes to the piedmont than have been transported from the Tucson or Silver Bell Mountains. This has led to the more extensive burial of older deposits by late Holocene deposits in the Tortolita piedmont (Katzer and Schuster 1984). [For a general discussion of the importance of lithology to geomorphic

Geomorphic Surfaces O Truncated Pleistocene ▲ Late Holocene 20 Number of Species Mid- Late Pleisto Mid Holocene 15 10 5 n. Ċ Ď Ė Ġ Ĥ Transect Locations

Ftg. 18. Number of species at the Silver Bell sample sites as a function of distance along the bajada gradient and land-scape position. One mid-Holocene site (E3) was excluded from the set of other mid-Holocene sites in the accompanying analysis of covariance because of the presence of buried soil horizons not typical of the other mid-Holocene surfaces. Similarly, two nearly level, but erosionally truncated early Pleistocene surfaces are not included with the erosional sites with steeper slopes shown here because of the uniqueness of these two sites. One of the five sites from steeper slopes of truncated Pleistocene surfaces contained an anomalously low species count (site indicated with an arrow; transect location F), but was included in the analysis of covariance.

processes in arid environments, see Bull (1991).] Indeed, the configuration of the basin floor with the Santa Cruz River confined against the northern flank of the Tucson Mountains (Fig. 2) is largely a consequence of the massive amount of alluvium transported from the Tortolita Mountains in comparison to considerably smaller volumes derived from the northernmost part of the Tucson Mountains.

The lithology of alluvium also exerts a strong control on the erosion of older parts of the piedmont. The fine network of on-fan drainages within the large Pleistocene fan remnant of the Tortolita site (Fig. 19C) may reflect the ability of run-off derived from relatively

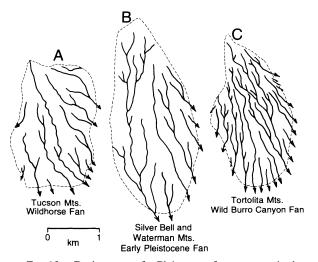


Fig. 19. Drainage nets for Pleistocene fan remnants in the three study areas. Taken from 1:24 000 U.S. Geological Survey topographic maps.

Table 5. Analysis of covariance: effects of distance from mountain front and geomorphic setting on species richness at the Silver Bell study area.\*

Source of variation	df	SS	MS	$\boldsymbol{F}$	P
Covariate (distance)	1	184.6	184.6	36.11	<.00001
Treatments (landscape position)	3	243.5	81.17	15.87	<.00001
Residual	16	81.82	5.114		
Total	20	509.92			
- C		te $R^2 = 184.6/50$	9.92 = 0.36		
		$R^2 = 243.5/509$			

<sup>\*</sup> n = 21 sites; sites E3, E1, and H1 were excluded from the analysis for reasons listed in Fig. 18 legend.

small areas to erode alluvium of highly weatherable granitic lithology. In contrast, the amount of water (and stream power) required to move larger, weatheringresistant particles of andesite or rhyolite up to several tens of centimetres in diameter comprising Pleistocene fan remnants of the Tucson Mountains and Silver Bell piedmonts is much greater than that necessary to move abundant finer particles weathered from granitic alluvium in the Tortolita piedmont. The widely spaced channels on Pleistocene fan remnants of the Tucson Mountains and Silver Bell piedmonts (Fig. 19A, B) may indicate that collection of run-off from considerably larger areas of these surfaces has been required to generate flows voluminous and powerful enough to carry larger particles and initiate incision. Due to the proximity and nearly identical elevational range of the three study areas, they experience similar ranges of precipitation; any small differences in precipitation that may exist between the sites cannot readily account for the considerably different patterns of landscape dissection. Instead, by generating differences in the type of alluvium and weathering and erosion of existing alluvial surfaces, lithology controls not only the evolution and distribution of geomorphic features (Bull 1991), but also the distribution of soils and plant species and the spatial scale of ecological pattern within alluvial piedmonts.

Soils.—Within the finely dissected Pleistocene fan remnants in upper parts of the Tortolita piedmont,

relict soils with strongly developed argillic horizons are present on relatively narrow, transversely level areas between the shallow drainageways (Fig. 20). These relict soils exhibit a level of development similar to the soils found on the mid-late Pleistocene fan remnants of the Tucson Mountains site and contain reddened argillic horizons (sandy clay loam and sandy clay textural classes) and stage III-IV calcic horizons (Appendix C). In the vicinity of the landscape cross section C-C' (Figs. 5 and 7C) approximately half of the surface area of the Pleistocene fan remnant is covered by relict soils containing well-developed argillic horizons. The short, erosional sideslopes typically possess soils derived from the degradation of exposed calcic horizons (Fig. 20). These soils, like those in similar erosional settings in the Tucson Mountains and Silver Bell sites, lack argillic horizons and have rather soft consistency and relatively weak structural development. Remnant. moderately to highly cemented calcic horizons are present, but usually at depths exceeding 20-25 cm (Appendix C).

Soils on Holocene surfaces include those located within the zone of catastrophic flooding and alluvial aggradation. No apparent soil development has occurred within accumulations of latest Holocene alluvium. As recently as 1988, a large flood originating in Wild Burro Canyon affected much of the area occupied by latest Holocene deposits (Fig. 21) (Pearthree 1991). To the sides and elevated slightly above the zone of

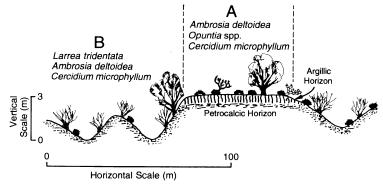


Fig. 20. Typical landscape cross section across a small part of the Pleistocene fan remnant at the Tortolita study area. Zone A consists of narrow, level areas with preserved argillic horizons; Zone B consists of erosional slopes and ridgelines from which argillic horizons have been completely truncated. Species listed are the dominant perennials found in each landscape position.

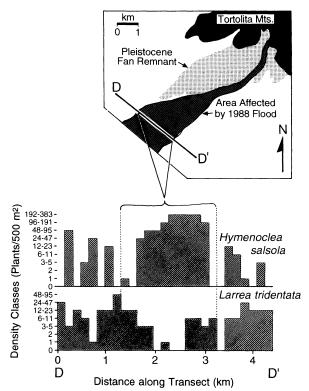


Fig. 21. Densities of *Larrea tridentata* and *Hymenoclea salsola* in relation to the flood and aggradational zone associated with the Wild Burro canyon drainage. Area affected by the 1988 flood taken from map of Pearthree (1991).

this considerable and recent alluvial activity are somewhat older Holocene surfaces with soils showing some pedogenic change (development of a weak cambic horizon in some areas). Some of these older Holocene soils are similar in appearance to soils on mid-Holocene surfaces in the Silver Bell study area.

Vegetation.—The general correspondence between geomorphology, soils, and vegetational composition on Pleistocene surfaces is nearly identical to that of the other two study areas. However, overall spatial pattern is more fine grained due to the scale of dissection of these surfaces (Figs. 7, 19, and 20). The narrow remnant Pleistocene surfaces mantled by soils with intact argillic horizons are dominated by A. deltoidea and Opuntia species, especially O. acanthocarpa. Larrea tridentata is virtually absent from these soils. Areas located on the short erosional sideslopes from which argillic horizons have been truncated are dominated by L. tridentata. Ambrosia deltoidea and cacti are less prominent in the erosional sideslopes (Table 6, Fig. 20). Within dissected parts of the landscape, wide, relatively level summit areas from which argillic horizons have been stripped are generally absent. Rather, ridgelike, erosional summits predominate, and the vegetation on these narrow ridges is similar to that of the erosional sideslopes (Table 6, Fig. 20).

Vegetation occupying the extensive Holocene deposits is extremely variable (Table 6). The shrub Hy-menoclea salsola is dominant in some areas but L. tridentata is dominant in others. Density classes of these two species recorded in  $500\text{-m}^2$  plots along the power line road transect (Fig. 21) are strongly negatively correlated (Spearman rank correlation,  $r_s = -0.82$ , P < .01, n = 27 plots). Within this transect, H. salsola is predominant on deposits of extremely recent geological origin that even today are subject to flooding and alluvial aggradation (Fig. 21). Larrea tridentata was largely absent from this zone even prior to the 1988 flood (J. R. McAuliffe, personal observa-

Table 6. Relative cover of various perennial species at the Tortolita study area. Sites are arranged by geomorphic surfaces and soil attributes. Site numbers correspond with those indicated in map of Fig. 5. 1: ≤5% relative cover, 2: 5.1–12%, 3:12.1–25%, 4: 25.1–50%, 5: >50% relative cover.

						San	iple s	sites	witl	nin se	para	te la	ndsc	ape	grou	ping	gs					
		Ren	nan	t	T	runca	ted F	Pleis	toce	ne												
		Pleist			Slo	pes		Ric	lges						]	Holo	cene	e				
Species	9	15	7	6	10	16	5	8	11	17	18	4	1	13	21	2	20	3	12	19	14	22
Ambrosia deltoidea	5	5	5	5	3	4	3	4	4	4	4	4	4			2	1	3	4		1	
Opuntia acanthocarpa	2	2	2	2	1	2		- 1	1	2	1				• • •		1	1	1	1	1	
Opuntia phaeacantha	1	1	1		1	1		1	1	1	1						1		1	1	1	
Cercidium microphyllum	3	1	3	3	2	4	3	2	1	2		3	4	1	1	3	3	4	1	1	1	3
Carnegiea gigantea	1	1			1		• • •		• • •	1				· · ·								
Fouquieria splendens	1	1				1																
Olneya tesota	1	1			1	1			• • •		3		3	1	1				• • •	1	1	2
Larrea tridentata	1	1	1	1	5	4	5	4	5	4	4	5	4	5	5	5	5	3				
Hymenoclea salsola																2	2	4	4	5	5	5
Isocoma tenuisecta																					3	
Prosopis velutina											1										1	
Acacia constricta		1										2						1			1	
Opuntia fulgida		1						1		1	1						1	1				
Ĉeltis pallida											1											
Opuntia leptocaulis							1															
Lycium sp.																	1					

tion), indicating that episodic flooding and alluvial aggradation over an extended period of recent geological history have apparently prevented or limited establishment. However, *L. tridentata* is the dominant species on slightly older, elevated surfaces to the sides of the extremely dynamic, latest Holocene surfaces.

#### DISCUSSION

### Ecological processes

Processes limiting the distribution and abundances of plants are directly linked to landscape characteristics in many ways. For example, landform age and stability can directly influence plant populations whose individual members may live for several centuries or even millennia [e.g., *L. tridentata* (Vasek 1979/1980, 1980)]. Soil profile development exerts a major control over the vertical movement, spatial distribution, and temporal availability of water. Run-off generated in one part of the landscape may augment incident precipitation in adjacent areas. These various relationships between landscape characteristics and ecological processes are the focus of this section.

Causes of variation in relative dominance of L. tridentata.-Among the sites from Holocene and erosionally dissected, early Pleistocene surfaces in the Tucson Mountains study area where L. tridentata is predominant (Fig. 13: right side of primary dendrogram division), this species exhibits considerable variability in relative dominance (Table 1). Enigmatically, vegetation composition of some of the relatively wide, level summits of dissected early Pleistocene surfaces (Fig. 12: landform component III) is most similar to that of Holocene surfaces. In particular, the polar ordination positioned a group of four sites from summits of dissected early Pleistocene surfaces (Fig. 11D: sites 15, 31, 27, and 11) closer to the three sites from Holocene surfaces (Group IV) than to ordination Group II containing sites from the adjacent sideslopes of early Pleistocene surfaces. The four indicated sites from summits of early Pleistocene surfaces and those from Holocene surfaces are clearly dominated by L. tridentata and contain few other species (Table 1).

Soils sampled at 0–5 and 15–20 cm depth from the four summits indicated above are indistinguishable from those of erosional sideslopes in terms of texture (Fig. 10B), or calcium carbonate content and pH (Appendix A). Soils of the Holocene surfaces contain considerably less calcium carbonate (Appendix A) and in two of the three sites, have slightly coarser textures than any of the sites from dissected early Pleistocene surfaces (Fig. 10B, C). Therefore, these soil characteristics cannot explain the vegetation dissimilarity between summits and erosional sideslopes and the greater similarity between some summits and Holocene surfaces.

Whereas no relationship between these soils attributes and vegetation compositions is apparent, the de-

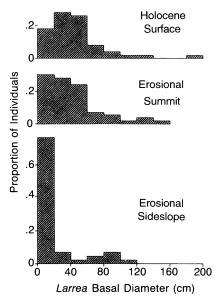


FIG. 22. Distributions of basal diameters of individuals of *Larrea tridentata* in different landscape positions in the Tucson Mountains study area. Holocene Surface = Site 13; Erosional Summit = Site 31; Erosional Sideslope = Site 28.

mographic structure of populations of *L. tridentata* in different landscape settings provides a key for understanding processes that may have led to variations in relative dominance of this species.

Individuals of *L. tridentata* can exhibit clone-like growth through basal stem splitting and outward propagation in the shape of a circular or elliptical ring (Vasek 1980). Sternberg (1976) demonstrated the genetic (isozymic) uniformity among the multiple basal stems forming individual clonal rings. On the basis of radiocarbon dates obtained from wood collected from the interior of clones, Vasek (1980) estimated that some individual clones of *L. tridentata* in sites in the Mohave Desert have increased in basal diameter at an average rate of slightly less than 1 mm per year. Large clones of this shrub species with diameters of several metres may have ages of several thousand years.

At the Tucson Mountains study area, circular clones of L. tridentata up to a maximum of 3 m basal diameter were found only on sites from Holocene surfaces and transversely level summits of dissected early Pleistocene surfaces. Basal diameters of L. tridentata were skewed considerably toward smaller plants in erosional sideslopes of early Pleistocene surfaces (Fig. 22) and large circular clones were never encountered in this part of the landscape. Similarly, sites from mid-Holocene surfaces of the Silver Bell study area showed a predominance of large clones, sometimes exceeding 5 m in basal diameter (Table 7) and an associated dominance of L. tridentata and presence of few other species. The maximum sizes of clones on these mid-Holocene surfaces are comparable to those reported for some Mohave Desert sites by Vasek (1983). [See Wright

TABLE 7. Size distributions of Larrea tridentata on various geomorphic surfaces at the Silver Bell study area.

		]	Numbers of in	idividuals pei	diameter clas	s	Maximum
			Bas	al diameters	(cm)		observed basal
Geomorphic surface	Site	0–25	25.1–50	50.1–100	100.1–200	>200	diameter (cm)
Mid-Holocene	A2	3	3	4	11	6	550
	B2	4	13	11	8	5	400
	D2	9	8	13	13	7	370
	F2	7	14	9	14	15	400
	G2	0	0	6	7	8	400
Late Holocene	B1	22	4	0	0	0	50
Truncated Pleistocene; level surface with shallow, restrictive petrocalcic horizon	H1	30	8	1	0	0	100
Remnant Pleistocene with strong argillic horizon	C1	18	17	13	2	0	200

(1970) for photographs of the appearance of clonal individuals in Avra Valley near the Silver Bell study area.]

The persistence and increase in size of individual L. tridentata, coupled with the filling of gaps between older individuals by additional recruitment, could conceivably lead to eventual, considerable reductions in populations of other species and even competitive exclusion of some species. Vasek (1979/1980) originally suggested this scenario for sites dominated by clones of L. tridentata on the basis of an observed lack of establishment of Ambrosia dumosa, whereas many A. dumosa rapidly established in adjacent, disturbed sites from which L. tridentata was removed. Mahall and Callaway (1991) showed that roots of L. tridentata strongly inhibited root elongation in both conspecifics and in A. dumosa, apparently by some chemical mechanism. Their experiments demonstrated that root elongation in A. dumosa ceased in the presence of active roots of L. tridentata, but that this interaction was not reciprocal: the roots of A. dumosa had no effect on root elongation of L. tridentata. In environments where individuals of L. tridentata increase in size over long periods of time and their extensive root systems increasingly exploit (and perhaps monopolize) the soil environment, such interactions may inhibit establishment and survival of young individuals of other species and ultimately contribute to lower species richness in these sites. The rarity of small individuals of L. trldentata in sites where large clones are found, especially the mid-Holocene surfaces at Silver Bell (Table 7), also suggests strong intraspecific inhibition.

Larrea tridentata may also inhibit establishment of some species by processes other than direct competitive interference. Establishment of many perennial species in these Sonoran Desert plant communities is largely restricted to areas beneath protective canopies of "nurse plants" (McAuliffe 1984a, 1986, 1988). In many parts of the Sonoran Desert, shrubby Ambrosia species are by far the most important nurse plants be-

neath which many species of woody perennials and succulents become established. Woody plants with more open, diffuse canopies, including *L. tridentata*, less frequently serve as nurse plants. If *L. tridentata* is capable of competitively eliminating or substantially reducing populations of *Ambrosia* spp., a reduction in establishment of other species, even those not affected directly by competition with *L. tridentata*, may be an eventual consequence. The consistently greater species richness and evenness of species abundances on erosional slopes of early Pleistocene surfaces may be due, at least in part, to the apparent diminished persistence of individual *L. tridentata* and resulting lower saturation of these environments by long-lived clones.

Importance of surface age and stability to dominance by L. tridentata. – A geomorphic surface must be stable for centuries and perhaps even several millennia for the developement of large clones of L. tridentata. Vasek (1983) originally pointed out that such clones are common "only on stable substrates of long duration." Mc-Auliffe (1991b) documented the correspondence between ages of three Holocene surfaces and clones size and relative dominance of L. tridentata at a site in central Baja California. Similarly, the contrast in size distributions and corresponding relative dominance of L. tridentata on late vs. mid-Holocene surfaces at the Silver Bell study area (Table 7) indicates the importance of the passage of considerable lengths of time for the development of clones and dominance of L. tridentata. The degree of soil development on mid-Holocene surfaces of the Silver Bell study area suggested an age of at least a few thousand years for these surfaces. It is possible that some of the largest clones of L. tridentata in these sites are nearly as old as the mid-Holocene deposits.

Zones of extremely recent, considerable alluvial aggradation such as those observed in latest Holocene deposits of the Tortolita piedmont (Fig. 21) are apparently too recently deposited and greatly disturbed for *L. tridentata* to have yet become widely established.

Webb et al. (1988) similarly documented the absence of *L. tridentata* from areas of similar, extremely recent aggradation in the Mohave Desert.

Clonal development in L. tridentata may also be inhibited in some of the relatively steep (5°-15°) side-slopes of early Pleistocene surfaces on account of considerable mortality and population turnover due to direct or indirect effects of erosion of these surfaces. Observations were made on mortality of L. tridentata at one Tucson Mountains site along a level ridgetop location (site 31) and the adjacent sideslopes (sites 28 and 29). Carcasses of dead individuals accounted for 10% of L. tridentata in the sideslope environments, but dead individuals were absent on adjacent, level summit areas. Similarly, there is a much higher frequency of individuals with considerable stem mortality in the sideslope locations (Table 8).

Two hypotheses regarding factors responsible for the higher mortality in the sideslopes were evaluated. The first hypothesis was that cold air drainage into the small, incised valleys between adjacent ridgeline remnants may kill *L. tridentata* on sideslopes located as much as 10 m in elevation below the summits. Of any topographic location, the lowermost bases of erosional sideslopes would be impacted most heavily by cold air drainage. Yet *L. tridentata* becomes even more prevalent at the bases of slopes and does not exhibit the mortality or stem death observed in upper sideslope locations, indicating that cold air drainage cannot account for the observed mortality in the upper sideslopes.

An alternative hypothesis is the higher mortality of L. tridentata is caused by either direct effects of slope instability or shallow soil conditions associated with soil loss. Several L. tridentata on sideslopes of sites 28 and 29 with moderately large basal diameters (up to 40 cm) were obviously pedestalled. Up to 15 cm of soil had been removed during the lifetimes of these plants, as indicated by the elevation of the original rooted bases of the plants above the present soil surface. Plants pedestalled to this degree were often completely dead or exhibited considerable stem death similar to that attributed to drought effects by Runyon (1934). These kinds of erosional losses of substrate and pedestalling of plants were never observed in the relatively wide (30-50 m), transversely level summits above the erosional sideslopes. Erosional losses of substrate from hillslopes in these kinds of semiarid environments are probably highly episodic (Peterson 1981, Bull 1991), and are probably considerable over the time scale required for the development of large clones of L. tridentata. Following surface erosion, the distribution of original, primary roots of L. tridentata would be considerably shallower and located in zones that would be subject to greater seasonality in the availability of water. This problem would be especially acute if restrictive layers (e.g., impervious petrocalcic horizons underlying soils of truncated Pleistocene surfaces)

TABLE 8. Mortality patterns of *Larrea tridentata* on transversely level summits vs. sideslopes of dissected early Pleistocene surfaces, Tucson Mountains study area. Data are numbers of individual plants. Date of observations: 18 October 1988.

	_		L. tridentatis that are d	
Location	0–25	26-50	51-99	100
Sideslopes Summit	20 48	14	11 0	5 0

prevented additional downward root growth (Shreve and Mallery 1933, Cunningham and Burk 1973). Relatively impervious calcic and petrocalcic horizons typically underlie soils on the erosional sideslopes, often at depths <50 cm (Appendix C: soil profile C).

One of the summit sites (site 23) was not dominated by L. tridentata as in most of the other summits. Instead, this site was grouped with others from the erosional sideslopes (Figs. 11 and 13). This exception among summit sites is explained by its peculiar morphology. Site 23 is located on the narrow, knife-like ridge crest of an isolated ballena. Geomorphically stable, transversely level summits areas are extremely narrow (<10 m wide) or altogether absent in this site. All other sites had much broader (30–50 m wide), relatively stable summit areas that were bounded by relatively sharp breaks to erosional sideslopes (see Fig. 12).

The greater instability of the erosional sideslopes in comparison to the more level summit areas and Holocene surfaces of sufficient age is also suggested by the greater occurrence of the short-lived species *Psilostrophe cooperi* and *Zinnia acerosa* in the sites from erosional sideslopes of both Tucson Mountains and Silver Bell study areas (Tables 1 and 3) [see Goldberg and Turner (1986) for information on longevity of these species in relation to other perennials]. In particular, *P. cooperi* rapidly invades many kinds of disturbed areas such as excavated sites and roadsides (J. R. Mc-Auliffe, *personal observations*).

Restrictive petrocalcic horizons, soil water variability, and equilibrium vs. nonequilibrium communities.—The most vigorous growth of L. tridentata occurs in sites where relatively deep rooting is possible (Shreve and Mallery 1933). Extremely shallow, strongly cemented petrocalcic horizons (caliche) inhibit development of large clones and dominance of L. tridentata, even on geomorphically stable surfaces. For example, site 19 of the Tucson Mountains study area was located on one of the widest (50 m), transversely level and geomorphically stable summits of early Pleistocene surfaces, but was the only summit that contained a strongly cemented, laminated, and impenetrable petrocalcic horizon at shallow depth (18 cm). The calcic horizons present in all other summit sites were neither as strongly cemented nor as shallow and undoubtedly permitted both root and water penetration to considerably greater depths. The shallow petrocalcic horizon of site 19 is apparently responsible for the lesser dominance of *L. tridentata* and greater abundance of relatively shallow-rooted, drought-deciduous *Ambrosia deltoidea*. The same diminished abundance of *L. tridentata* and increased abundance of *A. deltoidea* on a relatively level, geomorphically stable early Pleistocene surface with a shallow, highly cemented petrocalcic horizon at 27 cm depth was observed at the Silver Bell study area (site H1, Table 3). Additionally, *L. tridentata* at this site were characterized by extremely small basal diameters; large clonal individuals were completely absent (Table 7).

Another example of impacts of shallow petrocalcic horizons on L. tridentata and community structure is site 3 (Tucson Mountains) at the base of the southwest slope of Tumamoc Hill (Fig. 3). This site, although classed as an erosional slope because of its location with respect to the slope of Tumamoc Hill, is relatively level (3° slope), geomorphically stable, but possesses a very shallow, indurated petrocalcic horizon that is occasionally exposed at the surface. At this site, individuals of L. tridentata exhibit considerable amounts of past stem mortality, large clones are absent, and the short-lived shrub Psilostrophe cooperi contributed more canopy cover than did L. tridentata. Similarly, one of the nearby Tumamoc Hill permanent plots located 1.4 km north of site 3 (Tumamoc Plot 16 of Goldberg and Turner 1986) contains a shallow, highly cemented petrocalcic horizon. Goldberg and Turner (1986) documented considerable mortality and a lack of recruitment of L. tridentata in this plot during the first half of this century that were followed by considerable increases of Psilostrophe cooperi. These authors also suggested a connection between shallow petrocalcic horizons and episodic mortality of L. tridentata. They documented that populations of L. tridentata on considerably deeper soils located nearby (Area B of Goldberg and Turner 1986) have not experienced the same declines.

Shallow, indurated petrocalcic horizons greatly limit rooting depth and the storage of soil water. Furthermore, soil moisture limited to shallow reserves is subject to greater evaporative losses than moisture stored at greater depth in deeper soils (Schlesinger et al. 1987). Consequently, shallow, relatively impenetrable petrocalcic horizons greatly amplify the intensity of severe droughts. Despite its considerable drought tolerance, L. tridentata is not capable of complete drought dormancy and death of branches and even entire plants may occur in response to extreme drought (Runyon 1937). In the wake of such drought-induced mortality of L. tridentata, considerable space would be freed for occupation by more rapid colonizers such as Psilostrophe cooperi and other shorter lived species. Extreme droughts in arid environments can be thought of as a special kind of environmental disturbance because they

can cause episodic mortality of perennial plants. Where certain kinds of soil attributes such as shallow petrocalcic horizons intensify the impact and increase the frequency of severe droughts, the resulting more frequent episodic mortality of L. tridentata (and of other species as well) followed by pulses of establishment of a variety of species may prevent the community from attaining any long-term equilibrium (T. L. Burgess, University of Arizona Desert Laboratory, personal communication, February 1993). Conversely, the extremely long-term persistence and dominance of clones of L. tridentata may represent one equilibrium state determined by interspecific interactions (competition and other mechanisms preventing establishment of other species discussed previously). However, this state apparently can be achieved only in parts of the landscape that are most stable in terms of surficial geological processes and soil water availability.

The absence or rarity of Larrea tridentata on soils with well-developed argillic horizons. - Even though shallow petrocalcic horizons may have detrimental impacts on L. tridentata that apparently prevent extreme dominance, this species is nevertheless at least relatively common on such soils. In contrast, L. tridentata is either completely excluded or extremely rare on soils with strongly developed argillic horizons. These soils lack any appreciable accumulations of calcium carbonate in upper parts of their profiles (Fig. 8, Appendices A and C). On the other hand, all of the sites from deeply dissected, early Pleistocene surfaces contain abundant carbonate throughout their soil profiles and L. tridentata is either dominant or subdominant on these calcic soils. This same kind of positive association of L. tridentata with carbonate-rich soils has been widely documented and discussed (Hallmark and Allen 1975, Musick 1978, Lajtha et al. 1987). However, the question of whether this association reflects a causal link between soil carbonate levels and responses of L. tridentata has not been resolved. The presence of substantial amounts of calcium carbonate in upper parts of soil profiles is clearly associated with other soil attributes such as texture. For example, in the Tucson Mountains study area, 13 of 14 sites with strong argillic horizons had <1% calcium carbonate in upper parts of soil profiles, whereas soils from only one of 25 sites lacking argillic horizons (Holocene and dissected Pleistocene surfaces) had <1% calcium carbonate (Appendix A). The strong intercorrelation of these various soil characteristics makes it difficult, if not impossible, to decipher cause-and-effect relationships between the distribution of L. tridentata and individual soil characteristics with linear statistical models (Hallmark and Allen 1975, Green 1979, Lajtha et al. 1987).

Laboratory experiments with germination, seedling growth, and seedling survival have provided only limited insights regarding factors that influence distributions of L. tridentata in nature. High salinities and pH ( $\geq 9.0$ ) clearly inhibit germination in the laboratory

(Barbour 1968, Barbour et al. 1977) but do not explain the absence of L. tridentata in neutral to slightly acid, carbonate-free and nonsaline soils of mid-late Pleistocene surfaces of the three study areas (Appendices A and C). The hypothesis that high carbonate content of soils protects seedlings of L. tridentata from phosphorus toxicity (Musick 1978) has been reexamined and rejected on the basis of further, more carefully controlled laboratory experiments (Lajtha et al. 1987). Field experiments, although in theory capable of providing insights into cause-and-effect relationships, are difficult, if not impossible, to apply in this system because particular combinations of soil conditions (complex horizonation, structural attributes, etc.) that have required perhaps hundreds of millennia to form in intact soils cannot be realistically mimicked. However, much more about factors directly responsible for the distribution of L. tridentata can be learned from a more thorough comparative approach.

Data from the Tucson area studies clearly indicated that presence or absence of L. tridentata is not causally related to levels of soil carbonates. The three sample sites on Holocene surfaces in the Tucson Mountains study area contain soils with very small to moderate quantities of carbonate (Table 9). Regardless of variation in carbonate contents of these sites, L. tridentata is dominant in all of them (Table 1). Carbonate-free Holocene soils are more common on the fan-piedmont of the Tortolita Mountains because of the derivation of much of the Holocene alluvium directly from the granitic Tortolita Mountains. Some Holocene soils completely dominated by L. tridentata in the Tortolita piedmont typically contain scarcely more than a measurable trace of calcium carbonate within the upper 50 cm of the soil surface (Table 9). These extremely low levels of soil carbonate are equal to or less than the carbonate levels contained in soils with strong argillic horizons from which L. tridentata is excluded (Appendix A). The dominance of Hymenoclea salsola in some sites is related to the recentness of alluvial aggradation and cannot be attributed to differences in soil carbonates (Table 9).

An additional relevant comparison that indicates the unimportance of soil carbonates per se to the distribution of L. tridentata is the response of this species in sites with strong argillic horizons and abundant carbonate in uppermost soil horizons. Such a combination was not encountered in any of the three study areas near Tucson. However, one site with this combination of characteristics was located in a unique geological setting near the Chiricahua Mountains in southeastern Arizona. The site was the east-facing slope of a small hill composed of quartzite located along the Portal Road on the east side of the Chiricahua Mountains (31°59.8' N, 109°10.0′ W; 1400 m elevation). This quartzite hill is a small, isolated island of noncalcic parent material embedded in a landscape dominated by paleozoic limestones and calcic alluvial deposits derived from

Table 9. Calcium carbonate contents of Holocene surfaces of the Tucson and Tortolita Mountains study areas.

Site	Depth (cm)	% CaCO <sub>3</sub>	% clay	Dominant species
Tucso	n Mountains			
2	0–5 15–20	0.28 0.29	9.6 6.4	L. tridentata
13	0-5 15-20	0.12 1.41	5.6 10.0	L. tridentata
1	0–5 15–20	1.68 4.27	9.8 12.2	L. tridentata
Torto	lita Mountain	s		
20	0-5 15-20 30-35 45-50	0.01 <0.01 0.03 0.10	5.5 5.5 4.2 5.2	L. tridentata
21	0-5 15-20 30-35 45-50	0.08 0.07 0.17 0.15	4.2 4.7 6.0 4.7	L. tridentata
22	0-5 15-20 30-35 45-50	0.04 0.06 0.04 0.04	4.2 6.2 4.7 5.9	H. salsola

limestone. Quartzitic colluvium toward the base of the hill was mantled with a soil that contained strongly developed argillic horizons with clay content, color, and structural attributes strikingly similar to the soils with argillic horizons present on mid-late Pleistocene fan remnants of the Tucson Mountains piedmont. However, this soil was different in that it contained abundant carbonate throughout the profile (Table 10). The amount of carbonate contained throughout this profile is comparable to that of soils found on erosional, early Pleistocene fan surfaces of the Tucson Mountains site where material derived from degraded calcic horizons serves as a parent material (Appendix A). The superposition of carbonate within this well-developed argillic horizon may be due to recent (Holocene) and relatively great inputs of calcium carbonate in the form of dust derived from the surrounding limestone-dominated landscape. Alternatively, the abundant carbonate may represent vestiges of carbonate that originally engulfed an old argillic horizon and is in the process of dissolution and redistribution throughout the profile. Regardless of the process that has produced this soil pattern, the site provided a valuable comparison for evaluating the behavior of L. tridentata on a soil with both strong argillic horizons and large amounts of calcium carbonate throughout the soil profile. Larrea tridentata is virtually absent from this site. The hill instead is dominated by perennial C<sub>4</sub> grasses (primarily Hilaria belangeri and Bouteloua spp.), Agave palmeri, and the small drought-deciduous shrubs Parthenium incanum and Calliandra eriophylla. However, L. tridentata is a dominant species on adjacent limestone hills with same slope, aspect, and elevation as well as fan deposits composed of limestone alluvium (Table 11). Soils developed on limestone bedrock, colluvium, and alluvium all lacked argillic horizons.

Table 10. Characteristics of carbonate-rich soil found on quartzitic outcrop on the east side of the Chiricahua Mountains, southeastern Arizona.

Soil horizon	Depth	Munsell color	% clay	% car- bonate	Carbonate morphol- ogy*
A	0–6	5YR 4/4	28.4	2.54	diffuse
Btk	6-25	5YR 4/4	37.0	8.74	I
Btk2	25-35	5YR 4/6	50.4	21.2	I
	35-45	5YR 4/6	51.9	29.5	I–II
Btk3	45-55	5YR 4/6	53.0	34.7	III
	55-65	5YR 4.5/6	46.4	41.9	III
K	65+	•••		• • • •	IV

<sup>\*</sup> Morphological stages I-IV described by Gile et al. (1966, 1981).

Although this site is an isolated example, it provided additional evidence that the distribution of *L. tridentata* is not directly affected by the absence of soil carbonates, but rather, the exclusion of this shrub is related in a more direct way to other factors associated with strongly developed argillic horizons. These factors are probably related to how the argillic horizon affects the vertical movement and storage of water. Although ecologists have paid considerable attention to the effects of strongly cemented calcic horizons ("caliche") on desert plants (Shreve and Mallery 1933, Cunningham and Burk 1973), investigations of the extremely important roles of argillic horizons in desert plant communities have been largely overlooked.

Impacts of the argillic horizon on soil water dynamics and consequences to L. tridentata.—The argillic horizon exerts a dominant control over the infiltration, distribution, and temporal availability of water. Although argillic horizons of soils from mid-late Pleistocene surfaces have extremely low infiltration capacities, an overlying coarse-textured A horizon that is typical in these soils facilitates rapid infiltration and permits saturation of underlying argillic horizons. However, infiltration in soils with strong argillic horizons is considerably shallower than infiltration in coarser textured, deep soils lacking strong horizonation because of the considerably greater moisture-holding capacity of clay-rich horizons (Walter 1973). Strongly developed argillic horizons of mid-late Pleistocene surfaces can typically hold on the order of 2-5 times the volume of water than can equivalent volumes of overlying, coarse-textured A horizons or all horizons of coarse-textured soils such as those occurring on Holocene surfaces (Birkeland 1984:14, Saxton et al. 1986). Furthermore, because of the infrequency and unpredictability of relatively large rainfall events in this semiarid climate (see Turner 1963, Monson and Smith 1982 for typical annual patterns of individual precipitation events in the Sonoran Desert), water may seldom infiltrate to deeper soil layers in soils with strong argillic horizons. Coarse-textured soils lacking strong horizonation would be moistened to greater depths by more frequently occurring, smaller precipitation events.

Because of the considerably shallower storage of water in soils with strong argillic horizons, these soils no doubt experience considerable seasonal amplitude in water availability due to greater losses of shallowly stored water to evaporation (Schlesinger et al. 1987). Although upper parts of soil profiles with strong argillic horizons may be extremely wet during short periods, the rapid use of this water by shallow rooted plants coupled with substantial evaporative losses produce extremely dry soil conditions through much of the year (J. R. McAuliffe, personal observations from freshly excavated soil profiles). Larrea tridentata is absent or rare in sites with this kind of highly episodic and more limited vertical distribution of soil water, even though strongly developed argillic horizons may not represent the same kind of physical obstruction to root development as do petrocalcic horizons.

The few L. tridentata present on some surfaces with strong argillic horizons invariably exhibited signs of stress in the form of repeated episodes of death of branches (as indicated by numerous stubs of branches that had died at various times in the past). They also exhibited considerably less vigorous growth as judged by sparse canopy foliage density than do L. tridentata growing on deep, coarse-textured soils (J. R. McAuliffe, personal observations, Silver Bell transects B, C, and D containing juxtaposed Pleistocene and mid-Holocene surfaces). Additionally, despite the stability and antiquity of the Pleistocene surfaces, these surfaces never possess large clones of L. tridentata (Table 7), which indicates that individual shrubs, once established, either do not persist for long or experience little net increase in basal diameter due to repeated bouts of stem mortality. These responses on the mid-late Pleistocene surfaces may indicate the impacts of seasonal and acute water shortages and suggest that strong argillic horizons may inhibit L. tridentata in an even more extreme manner than do physically restrictive soil horizons, such as shallow, strongly cemented pet-

TABLE 11. Relative cover of dominant perennials at the Chiricahua study sites. 1: <5% relative cover, 2: 5–12%, 3: 13–25%, 4: 26–50%, 5: >50% relative cover.

		Sites	
Species	Quartzite hill	Lime- stone hill	Calcic alluvium
Perennial C <sub>4</sub> grasses	5	0	1
Agave palmeri	3	1	0
Calliandra eriophylla	3	2	0
Gutierrizia sarothrae	1	2	3
Fouquieria splendens	1	4	2
Parthenium incanum	1	1	3
Prosopis juliflora	1	0	1
Larrea tridentata	0	4	3
Acacia greggii	0	1	2
Opuntia phaeacantha	0	1	1
Aloysia wrightii	0	1	0
Erioneuron pulchellum	0	0	3

rocalcic horizons (Shreve and Mallery 1933, Cunningham and Burk 1973).

However, data from the Silver Bell study area suggest that the exclusion, rarity, or poor condition of L. tridentata from soils with strong argillic horizons may be due to factors far more complicated than the simple effects of acute, seasonal water shortages. At this study area, L. tridentaia is present on sites with strong argillic horizons in lower elevations but is completely absent from soils with comparable argillic horizons in the three transects in the uppermost elevations (Table 3, Fig. 17, Appendix C). The upper elevation sites receive slightly more precipitation than do lower sites due to the orographic influences of the Silver Bell and Waterman Mountains (Fig. 2) (Bailey et al. 1977). Therefore, complete absence of L. tridentata from slightly more mesic sites of upper elevations is opposite the pattern expected if a seasonal soil moisture deficit was the exclusive mechanism eliminating this species from the Pleistocene fan remnants.

An alternate hypothesis for the exhusion of L. tridentata from soils with strongly developed argillic horizons in the more mesic parts of the Silver Bell precipitation gradient (and also the more moist parts of the Sonoran Desert) is the occasional saturation of argillic horizons beyond that which can be tolerated by this shrub species. Lunt et al. (1973) demonstrated the high oxygen requirements of roots of L. tridentata. In sites where permeable A horizons facilitate infiltration and the immediately underlying argillic horizons episodically become saturated, exchange of soil gases could be seriously impaired, impeding root function and elongation of L. tridentata. This effect may be especially acute during the winter rainy season when transpirational activity of all plants and direct evaporation of soil water would be extremely low, thereby allowing extremely wet soil conditions to persist.

These two hypotheses regarding mechanisms for exclusion of *L. tridentata* involving extreme drought vs. occasional and detrimental soil saturation are not necessarily mutually exclusive. It is possible that the two mechanisms act synergistically. Lack of extensive root development during times of soil saturation could further inhibit the ability of *L. tridentata* (with poorly developed root systems) to extract adequate amounts of soil water during seasonal droughts, which are amplified on the clay-rich soils. An additional factor that may influence the response of *L. tridentata* on these surfaces is potential competitive interaction with abundant drought-deciduous shrubs that rapidly exploit shallow soil moisture.

Soils, landscape processes, and plant life form distributions.—The various life forms of desert plants represent morphological expressions of different modes of water aquisition and use (Shreve and Wiggins 1964, Bowers and Lowe 1986). Because of the control exerted by soil characteristics on the vertical distribution and temporal storage of water, knowledge of landscapes

and associated soils is necessary for an understanding of the distribution of various plant life forms in alluvial piedmont environments of the Sonoran Desert.

The distinctive vegetational physiognomy of midlate Pleistocene surfaces with strong argillic horizons is due to the dominance of the small, drought-deciduous shrub Ambrosia deltoidea and an abundance of stem succulents, especially several *Opuntia* species. Despite the differences between these two groups in terms of both morphology and physiology, they are similar in their capacities to use water on an extremely seasonal basis. Water stored at rather shallow depth within the argillic horizon during the winter and spring rainy seasons is exploited by shallow-rooted Ambrosia deltoidea. The desiccation and loss of leaves of this shrub species following the commencement of the 2-3 mo presummer drought (Halvorson and Patter 1974, Szarek and Woodhouse 1977) indicate the depletion of shallow reserves of moisture contained in argillic horizons. On the other hand, cacti exhibit greater activity during the hot summer rainy period, during which most water uptake and apical stem growth occurs [e.g., see growth data for Carnegiea gigantea in Hastings (1961)]. For Ambrosia deltoidea and the many stem succulents that are most abundant on mid-late Pleistocene surfaces, drought-deciduousness or water storage are two very different water use strategies that enable highly seasonal activity on soils that have extremely high seasonal variability in available water.

The erosional sideslopes of early Pleistocene surfaces possess a greater diversity of species and different plant life forms than any other landform setting (Tables 1, 3, and 4). The erosional slopes undoubtedly yield much more run-off than do the level surfaces of mid-late Pleistocene fan remnants. Nevertheless, the absence of argillic horizons in the soils of these erosional landscapes (Fig. 10, Appendices A and C) may permit infiltration of water in at least some places where restrictive petrocalcic horizons are absent to relatively great depths. Examination of wetting fronts in soils 48 h after 2.7 cm of precipitation on ridges and sideslopes of an eroded, early Pleistocene ridgeline remnant with 5° slope (Site 37, Tucson Mountains study area) indicated depths of wetting of 21-25 cm, whereas an immediately adjacent, level surface of a mid-late Pleistocene fan remnant with well-developed argillic horizons (Site 35) was wetted to an average depth of 18 cm. A somewhat greater depth of wetting, possible greater variability in the vertical and horizontal distribution of soil water, and the previously described greater instability of erosional sideslopes are some of the many factors that may contribute to the greater diversity of species and life forms in these environments than in any other setting.

At the Silver Bell study area, late Holocene surfaces have higher species richness and diversity of life forms than do mid-Holocene surfaces. These differences are related to two factors: (1) proximity of drainages that are areas of local concentration of water received as run-off from adjacent areas and (2) apparently a lack of sufficent time for *L. tridentata* to increase in size and/or numbers, thereby excluding other species. Sites with the lowest diversity of life forms in which large clones of *L. tridentata* predominate are those with relatively deep, coarse-textured soils that have been geologically stable for perhaps millennia.

Topographic variation and surficial hydrology.—Runoff from some parts of the landscape contributes supplies of water to other landscape positions in excess of incident precipitation and exerts an important control on vegetation (Schlesinger and Jones 1984, Schlesinger et al. 1989). The late Holocene surfaces of the Silver Bell piedmont (Fig. 15, transects B and D) consist of narrow surfaces inset within the slightly elevated topographic confines of older geomorphic surfaces. These late Holocene surfaces receive run-off generated by the more extensive surfaces that surround them. The presence of larger tree species such as Cercidium microphyllum, Olneya tesota, and Acacia constricta on the late Holocene surfaces, but the absence or rarity of these species on adjacent, slightly elevated surfaces indicate the importance of the augmentation of incident precipitation by run-off from the surrounding landscape.

## Synthesis and conclusions

Continuous spectra of relative abundances of different species such as those presented in the polar ordinations of Figs. 11 and 16 are the consequences of individualistic responses of species to varying environmental conditions. However, a spatial continuum of vegetation composition can be expected to occur only in the latter case where environmental variables also vary continuously. McIntosh (1967) clearly pointed out the distinction between study of spatial environmental gradients and analyses of vegetational continua and stated that neither the individualistic nor continuum concepts of community composition imply that all vegetation change be spatially continuous or that discontinuities be absent.

The bajada gradient model as presented by Solbrig et al. (1977), Phillips and MacMahon (1978), Bowers (1988), and others is far too simplistic to enable an understanding of either the physical environment or predominant ecological patterns within alluvial piedmonts in the Sonoran Desert. Viewed from a considerable distance, the silhouetted profile of a Sonoran Desert bajada may indeed appear as the epitome of an ideal physical gradient. Yet, upon closer inspection, the seemingly continuous change along a "bajada" gives way to a landscape of distinct patches with rather abrupt discontinuities. The boundaries between patches may involve slight elevational jumps or pronounced changes in color, texture, or structure of soils. Variability in the landscape is typically as noticeable within a single elevational contour as it is along an entire elevational gradient. At this finer resolution, landscape change is

not spatially continuous. Rather, the alluvial piedmont consists of a complex mosaic of discrete landforms. This landscape mosaic is the result of the temporally episodic and spatially discontinuous creation of new patches through aggradation of fresh alluvium coupled with the destruction of other parts of the landscape through erosion (Gile 1975a, b, Bull 1991). Knowledge of how the physical face of the alluvial piedmont is formed by these geological fits and starts is needed to understand the distribution of landforms, soils, and ultimately, ecological patterns within the landscape.

Some of the variability in species distributions discussed in the original US/IBP Desert Biome research conducted on the Silver Bell Bajada is due to the abrupt juxtaposition of different geomorphic surfaces with markedly different soils. For example, Barbour and Diaz (1973) commented on the problem of statistical estimation of mean densities of L. tridentata within individual elevations along the Silver Bell Bajada and the difficulty of finding homogeneous areas of at least 1 ha for sampling. They illustrated this variability with data obtained from two sites (ARIZ-003 and ARIZ-022) located at the same elevation (675 m) but separated by a distance of only 250 m. Despite the proximity of their two sites, Barbour and Diaz (1973) reported a fourfold difference between the two sites in density and relative cover of L. tridentata.

One of my sampling transects at Silver Bell (transect D) was located at 671 m elevation, only 4 m lower in elevation and an estimated 0.5 km downslope from the sites of ARIZ-003 and ARIZ-022 of Barbour and Diaz (1973). I observed the same kind of vegetational differences within this transect as did Barbour and Diaz (1973). The differences in abundances of L. tridentata in this area are clearly related to an abrupt geomorphic boundary. The area is located at the interface between a large, stable Pleistocene fan remnant mantled with soils containing strongly developed argillic horizons where L. tridentata is extremely rare (north side of Avra Valley Road) and Holocene (both mid and later Holocene) deposits to the south side of Avra Valley Road where L. tridentata is dominant (Fig. 15, transect D).

Common references to desert soils as "immature" (Solbrig et al. 1977) or having little pedogenic modification (Walter 1973) have failed to recognize the pronounced pedogenic changes that occur in soils of arid and semiarid regions over time (Fig. 8, Gile et al. 1981). Some soils of alluvial piedmonts (such as very recent Holocene deposits or areas of accumulation of recent colluvium at the bases of erosional hillslopes) may indeed exhibit little or no pedogenic alteration. However, large parts of desert alluvial piedmonts typically consist of stable relict surfaces mantled by soils that have been forming for tens to several hundreds of thousands of years. The superficial stony or gravelly surfaces and coarse-textured horizons of these soils deceptively mask deeper, well-developed horizons that bear little or no

resemblance to chemical or physical characteristics of the original parent materials. These patterns of soil horizonation are extremely important to the infiltration, movement, and storage of water and must be recognized in order to understand ecological patterns. Vegetation studies in arid and semiarid systems that limit the examination of soils to shallow surface samples miss important features of deeper soil horizons that may in fact exert the strongest controls over vegetation.

A better understanding of landscape-level patterns and processes provides an essential framework for some investigations of population and community structure in arid and semiarid environments. For example, population structure of Larrea tridentata and potential impacts of this species on plant community structure make sense only in the context of a knowledge of the geological histories of different parts of the landscape. Populations of L. tridentata containing large, clonal individuals such as those on the mid-Holocene surfaces of the Silver Bell site typically exhibit an extremely unbalanced demographic structure. The predominance of large, old clones coupled with the rarity or complete lack of small, younger individuals suggests strong intraspecific interactions that prevent additional recruitment, possibly by the mechanism revealed by Mahall and Callaway (1991). Similarly, the diminished abundance of other shrub species may be due at least in part to similar and intense interspecific competition. The hypothesized competitive exclusion of other shrub species by L. tridentata is analogous to the declines of species richness in many ecological systems due to the increase of a dominant competitor over time. Examples of such competitive effects on community structure are found in studies of marine intertidal communities (Connell 1961, Paine and Levin 1981), sessile insects in streams (McAuliffe 1984b), sessile, marine intertidal algae (Sousa 1979), and compositional change in deciduous forests during the course of succession (Horn 1975, Pickett 1980). The principal difference between these systems and the desert plant communities discussed here is the time scale involved in community dynamics. Rather than the few years or less required for the competitive exclusion in intertidal communities or many decades to a few centuries in deciduous forests, exclusion of some species by slowgrowing L. tridentata may require several centuries and perhaps even several millennia. Vasek (1983) suggested the same, extremely long-term process of competitive exclusion for sites dominated by long-lived clones of L. tridentata in the Mohave Desert. Sites subject to relatively frequent and severe physical perturbations (e.g., droughts intensified by shallow soils; erosional loss of substrate) apparently never reach such a competitive equilibrium.

Given the great length of time involved in the development of community structure in these arid environments, the type of information required to un-

derstand population and community patterns involving L. tridentata in some parts of the landscape may typically be far beyond that which can be obtained exclusively from the study of populations over small spatial scales (e.g., small permanent plots) or short time scales (even the consecutive lifetimes of several investigators). Considerably larger temporal and spatial scales of investigation that are more familiar to the Quaternary geomorphologist need to be combined with knowledge gained from long-term plot studies (e.g., Goldberg and Turner 1986) for studies of plants with great potential individual longevities. In addition, the time-dependent processes of landform development and soil genesis provide the population and community ecologist working in arid environments with potential chronological tools for deciphering some kinds of longterm dynamics of plant communities during the last few thousand years (McAuliffe 1991b).

A broadened landscape perspective also provides a valuable context for ecophysiological studies in arid environments. Heterogeneous plant distributions on desert piedmonts ultimately need to be understood in terms of ecophysiological attributes of species that permit varying manners of water extraction and use. Variation in the distribution of different plant life forms across these landscapes implies considerable variability in the seasonal or vertical distributions and availabilities of water. Much more research needs to be done on the dynamics of water movement and seasonal and vertical distributions of water in soils of different parts of alluvial piedmonts. This information, combined with novel physiological approaches such as the determination of plant use of soil water stored either during periods of summer or winter precipitation through stable isotope studies (Ehleringer and Rundel 1989, Ehleringer et al. 1991), can provide a far better understanding and predictive accuracy concerning physiological responses.

A better understanding of landscape patterns in arid environments has important implications for dealing with problems of land management. For example, increases of undesired woody species such as mesquite (Prosopis spp.) and L. tridentata in semiarid grasslands have been widely discussed (Hastings and Turner 1965, Bahre 1990, Schlesinger et al. 1990). Yet, such invasions are highly variable and depend to a great degree on geomorphology and associated soil characteristics (McAuliffe, in press). In semiarid grasslands of Arizona, soils on Pleistocene alluvial fan surfaces with strongly developed argillic horizons and more permeable, overlying A horizons are typically not heavily invaded by deep-rooted woody species. However, adjacent erosionally degraded lands and Holocene surfaces with little pedogenic alteration of gravelly parent materials have typically experienced the greatest increases of woody species during this century. It is important to link knowledge of the dependence of these kinds of vegetation alterations on landscape attributes

with more information on soil water dynamics and theoretical insights into the dynamics of semiarid grazing systems (Walker and Noy-Meir 1981, Walker et al. 1981).

Likewise, responses of vegetation in arid regions to possible future climate change will undoubtedly be highly dependent on local geomorphic, edaphic, and hydrologic contexts. Models of possible vegetation shifts in the western United States (Nielsen et al. 1989) under different scenarios of climate change might be able to predict average, region-wide shifts. However, land managers will require knowledge of how such potential ecological changes (see review by Schlesinger et al. 1990) are dependent on the site-specific qualities of distinct parts of the landscape.

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# LITERATURE CITED

- Arizona Bureau of Mines. 1959. Geologic map of Pinal County, Arizona. Arizona Bureau of Mines, Tucson, Arizona, USA.
- —. 1960. Geological map of Pima and Santa Cruz Counties, Arizona. Arizona Bureau of Mines, Tucson, Arizona, USA.

- Bahre, C. J. 1990. A legacy of change: historic human impact on vegetation of the Arizona borderlands. University of Arizona Press, Tucson, Arizona, USA.
- Bailey, H. P., B. B. Simpson, and F. Vervoorst. 1977. The physical environment: the independent variable. Pages 13–49 in G. H. Orians and O. T. Solbrig, editors. Convergent evolution in warm deserts. Dowden, Hutchinson and Ross, Stroudsburg, Pennsylvania, USA.
- Barbour, M. G. 1968. Germination requirements of the desert shrub *Larrea divaricata*. Ecology **49**:915–923.
- Barbour, M. G., G. Cunningham, W. C. Oechel, and S. A. Bamberg. 1977. Growth and development, form and function. Pages 48–89 *in* T. J. Mabry, J. H. Hunziker, and D. R. DiFeo, Jr., editors. Creosote bush. Biology and chemistry of *Larrea* in New World deserts. Dowden, Hutchinson and Ross, Stroudsburg, Pennsylvania, USA.
- Barbour, M. G., and D. V. Diaz. 1973. *Larrea* plant communities on bajada and moisture gradients in the United States and Argentina. Vegetatio 28:335-357.
- Birkeland, P. W. 1984. Soils and geomorphology. Oxford University Press, New York, New York, USA.
- Black, C. A., editor. 1965. Methods of soil analysis. American Society of Agronomy, Madison, Wisconsin, USA.
- Bouyoucos, G. J. 1936. Directions for making mechanical analyses of soils by the hydrometer method. Soil Science 42:225–229.
- . 1951. A recalibration of the hydrometer method for making mechanical analysis of soils. Agronomy Journal 43: 434–438.
- Bowers, M. A. 1988. Plant associations on a Sonoran Desert bajada: geographical correlates and evolutionary source pools. Vegetatio **74**:107–112.
- Bowers, M. A., and C. H. Lowe. 1986. Plant-form gradients on Sonoran Desert bajadas. Oikos 46:284–291.
- Bray, J. R., and J. T. Curtis. 1957. An ordination of the upland forest communities of southern Wisconsin. Ecological Monographs 27:325–349.
- Bull, W. B. 1991. Geomorphic responses to climatic change. Oxford University Press, New York, New York, USA.
- Bull, W. B., and A. P. Schick. 1979. Impact of climatic change on an arid watershed: Naha Yael, southern Israel. Quaternary Research 11:153–171.
- Christenson, G. E., and C. Purcell. 1985. Correlation and age of Quaternary alluvial-fan sequences, Basin and Range province, southwestern United States. Pages 115–122 *in* D. W. Weide, editor. Soils and Quaternary geology of the southwestern United States. Geological Society of America Special Paper 203.
- Connell, J. H. 1961. The influence of interspecific competition and other factors on the distribution of the barnacle *Chthamalus stellatus*. Ecology **42**:710–723.
- Cunningham, G. L., and J. H. Burk. 1973. The effect of carbonate deposition layers ("caliche") on the water status of *Larrea divaricata*. American Midland Naturalist **90**:474–480
- Curtis, J. T., and R. P. McIntosh. 1951. An upland continuum within the prairie-forest border region of Wisconsin. Ecology 32:476–496.
- Ehleringer, J. R., S. L. Phillips, W. S. F. Schuster, and D. R. Sandquist. 1991. Differential utilization of summer rains by desert plants. Oecologia 88:430–434.
- Ehleringer, J. R., and P. W. Rundel. 1989. Stable isotopes: history, units, and instrumentation. *In* P. W. Rundel, J. R. Ehleringer, and K. A. Nagy, editors. Stable isotopes in ecological research. Ecological Studies Analysis and Synthesis **68**:1–15.
- Gauch, H. G., Jr. 1977. ORDIFLEX: a flexible computer program for four ordination techniques: weighted averages, polar ordination, principal components analysis, and reciprocal averaging. Release 3. Department of Ecology and Systematics, Cornell University, Ithaca, New York, USA.

- ——. 1982. Multivariate analysis in community ecology. Cambridge University Press, New York, New York, USA.
- Gile, L. H. 1975a. Causes of soil boundaries in an arid region. I. Age and parent materials. Soil Science Society of America Proceedings 39:316–323.
- 1975b. Causes of soil boundaries in an arid region.
   II. Dissection, moisture, and faunal activity. Soil Science Society of America Proceedings 39:324–330.
- Gile, L. H., and R. B. Grossman. 1968. Morphology of the argillic horizon in desert soils of southern New Mexico. Soil Science 106:6–15.
- Gile, L. H., J. W. Hawley, and R. B. Grossman. 1981. Soils and geomorphology in the Basin and Range area of southern New Mexico—guidebook to the Desert Project. Memoir 39. New Mexico Bureau of Mines and Mineral Resources, Socorro, New Mexico, USA.
- Gile, L. H., F. F. Peterson, and R. B. Grossman. 1966. Morphological and genetic sequences of carbonate accumulation in desert soils. Soil Science 101:347–360.
- Goldberg, D. E., and R. M. Turner. 1986. Vegetation change and plant demography in permanent plots in the Sonoran Desert. Ecology 67:695–712.
- Green, R. H. 1979. Sampling design and statistical methods for environmental biologists. John Wiley & Sons, New York, New York, USA.
- Hallmark, C. T., and B. L. Allen. 1975. The distribution of creosotebush in west Texas and eastern New Mexico as affected by selected soil properties. Soil Science Society of America Proceedings 39:120–124.
- Halvorson, W. L., and D. T. Patten. 1974. Seasonal water potential changes in Sonoran Desert shrubs in relation to topography. Ecology 55:173–177.
- Hastings, J. R. 1961. Precipitation and saguaro growth. University of Arizona Arid Lands Colloquium 1959–1960/1960–1961:30–38.
- Hastings, J. R., and R. M. Turner. 1965. The changing mile: an ecological study of vegetation change with time in the lower mile of an arid and semiarid region. University of Arizona Press, Tucson, Arizona, USA.
- Hill, M. O. 1979. TWINSPAN: a FORTRAN program for arranging multivariate data in an ordered two-way table by classification of the individuals and attributes. Department of Ecology and Systematics, Cornell University, Ithaca, New York, USA.
- Horn, H. S. 1975. Markovian properties of forest succession. Pages 196–211 in M. L. Cody and J. M. Diamond, editors. Ecology and evolution of communities. Belknap Press of Harvard University Press, Cambridge, Massachusetts, USA.
- Katzer, K. L., and J. H. Schuster. 1984. The Quaternary geology of the northern Tucson Basin, Arizona, and its archaeological implications. Thesis. Department of Geosciences, University of Arizona, Tucson, Arizona, USA.
- Lajtha, K., J. Weishampel, and W. H. Schlesinger. 1987. Phosphorus and pH tolerances in the germination of the desert shrub *Larrea tridentata* (Zygophyllaceae). Madroño 34:63-68.
- Lunt, O. R., J. Letey, and S. B. Clark. 1973. Oxygen requirements for root growth in three species of desert shrubs. Ecology **54**:1356–1362.
- Machette, M. N. 1985. Calcic soils of the southwestern United States. Pages 1–21 in D. L. Weide, editor. Soils and Quaternary geology of the southwestern United States. Geological Society of America Special Paper 203.
- Mahall, B. E., and R. M. Callaway. 1991. Root communication among desert shrubs. Proceedings of the National Academy of Sciences (USA) 88:874–876.
- Marion, G. M. 1989. Correlation between long-term pedogenic CaCO<sub>3</sub> formation rate and modern precipitation in deserts of the American Southwest. Quaternary Research 32:291–295.

- McAuliffe, J. R. 1984a. Prey refugia and the distributions of two Sonoran Desert cacti. Oecologia 65:82–85.
- . 1984b. Competition for space, disturbance, and the structure of a benthic stream community. Ecology 65:894– 908
- . 1986. Herbivore-limited establishment of a Sonoran Desert tree, *Cercidium microphyllum*. Ecology 67:276– 280
- ——. 1988. Markovian dynamics of simple and complex desert plant communities. American Naturalist 131:459– 490.
- . 1991a. A rapid survey method for the estimation of density and cover in desert plant communities. Journal of Vegetation Science 1:653–656.
- ——. 1991b. Demographic shifts and plant succession along a late Holocene soil chronosequence in the Sonoran Desert of Baja California. Journal of Arid Environments 20:165–178.
- In press. Landscape evolution, soil formation, and Arizona's desert grasslands. In M. McClaran, editor. The desert grassland. University of Arizona Press, Tucson, Arizona, USA.
- McFadden, L. D. 1978. Soils of the Cañada del Oro Valley, southern Arizona. Thesis. University of Arizona, Tucson, Arizona, USA.
- ——. 1988. Climatic influences on rates and processes of soil development in Quaternary deposits of southern California. Pages 153–177 in Geological Society of America Special Paper 216.
- McFadden, L. D., and J. C. Tinsley. 1985. Rate and depth of pedogenic-carbonate accumulation in soils: formulation and testing of a compartment model. Pages 23–41 *in* D. L. Weide, editor. Soils and Quaternary geology of the southwestern United States. Geological Society of America Special Paper 203.
- McFadden, L. D., S. G. Wells, and J. C. Dohrenwend. 1986. Influences of Quaternary climatic changes on processes of soil development on desert loess deposits of the Cima volcanic field, California. Catena 13:361–389.
- McFadden, L. D., S. G. Wells, and M. J. Jercinovich. 1987. Influences of eolian and pedogenic processes on the origin and evolution of desert pavements. Geology 15:504–508.
- McIntosh, R. P. 1967. The continuum concept of vegetation. Botanical Review 33:130–187.
- McKittrick, M. A. 1988. Surficial geologic maps of the Tucson metropolitan area. Arizona Geological Survey Open-File Report 88-18.
- Menges, C. M., and L. D. McFadden. 1981. Evidence for a latest Miocene to Pliocene transition from basin-range tectonic to post-tectonic landscape evolution. Arizona Geological Society Digest 13:151–160.
- Monson, R. K., and S. D. Smith. 1982. Season water potential components of Sonoran Desert plants. Ecology 63: 113–123.
- Morrison, R. B. 1985. Pliocene/Quaternary geology, geomorphology, and tectonics of Arizona. Pages 123–146 in
   D. L. Weide, editor. Soils and Quaternary geology of the southwestern United States. Geological Society of America Special Paper 203.
- Musick, H. B. 1978. Phosphorus toxicity in seedlings of Larrea divaricata grown in solution culture. Botanical Gazette 139:108–111.
- Neilson, R. P., G. A. King, R. L. DeVelice, J. Lenihan, D. Marks, J. Dolph, B. Campbell, and G. Glick. 1989. Sensitivity of ecological lanscapes and regions to global climate change. Report EPA/600/3-89/073, U.S. Environmental Protection Agency, Environmental Research Laboratory, Corvallis, Oregon, USA.
- Paine, R. T., and S. A. Levin. 1981. Intertidal landscapes: disturbance and the dynamics of pattern. Ecological Monographs 51:145–178.

- Pearthree, P. A. 1991. Geologic insights into flood hazards in piedmont areas of Arizona. Arizona Geology 21:1-5.
- Pearthree, P. A., and S. S. Calvo. 1987. The Santa Rita fault zone: evidence for large magnitude earthquakes with very long recurrence intervals, Basin and Range Province of Southeastern Arizona. Bulletin of the Seismological Society of America 77:97–116.
- Pearthree, P. A., M. A. McKittrick, G. W. Jackson, and K. A. Demsey. 1988 Geologic map of Quaternary and upper Tertiary deposits: Tucson 1° × 1° Quadrangle, Arizona. Arizona Geological Survey Open-File Report 88-21.
- Peterson, F. F. 1981. Landforms of the Basin and Range Province defined for soil survey. Nevada Agricultural Experiment Station Technical Bulletin 28.
- Phillips, D. L., and J. A. MacMahon. 1978. Gradient analysis of a Sonoran Desert bajada. Southwestern Naturalist 23:669–680.
- Pickett, S. T. A. 1980. Non-equilibrium coexistence of plants. Bulletin of the Torrey Botanical Club 107:238–248.
- Runyon, E. H. 1934. The organization of the creosote bush with respect to drought. Ecology 15:128–138.
- Saxton, K. E., W. J. Rawls, J. S. Romberger, and R. I. Papendick. 1986. Estimating generalized soil-water characteristics from texture. Soil Science Society of America Journal 50:1031–1036.
- Schlesinger, W. H., P. J. Fonteyn, and G. M. Marion. 1987. Soil moisture content and plant transpiration in the Chihuahuan Desert of New Mexico. Journal of Arid Environments 12:119–126.
- Schlesinger, W. H., P. J. Fonteyn, and W. A. Reiners. 1989. Effects of overland flow on plant water relations, erosion, and soil water percolation on a Mojave Desert landscape. Soil Science Society of America Journal 53:1567–1572.
- Schlesinger, W. H., and C. S. Jones. 1984. The comparative importance of overland runoff and mean annual rainfall to shrub communities of the Mojave Desert. Botanical Gazette 145:116–124.
- Schlesinger, W. H., J. F. Reynolds, G. L. Cunningham, L. F. Huenneke, W. M. Jarrell, R. A. Virginia, and W. G. Whitford. 1990. Biological feedbacks in global desertification. Science 247:1043–1048.
- Shreve, F., and T. D. Mallery. 1933. The relation of caliche to desert plants. Soil Science 35:99–112.
- Shreve, F., and I. L. Wiggins. 1964. Vegetation and flora of the Sonoran Desert. Volume 1. Stanford University Press, Stanford, California, USA.
- Solbrig, O. T., M. A. Barbour, J. Cross, G. Goldstein, C. H.
  Lowe, J. Morello, and T. W. Yang. 1977. The strategies and community patterns of desert plants. Pages 67–106 in G. H. Orians and O. T. Solbrig, editors. Convergent evolution in warm deserts. US/IBP Synthesis Series Number

- 3. Dowden, Hutchinson and Ross, Stroudsburg, Pennsylvania, USA.
- Sousa, W. P. 1979. Disturbance in marine intertidal boulder fields: the nonequilibrium maintenance of species diversity. Ecology **60**:1225–1239.
- Sternberg, L. 1976. Growth forms of *Larrea tridentata*. Madroño 23:408–417.
- Szarek, S. R., and R. M. Woodhouse. 1977. Ecophysiological studies of Sonoran Desert plants. II. Seasonal photosynthesis patterns and primary production of *Ambrosia deltoidea* and *Olneya tesota*. Oecologia (Berlin) **28**:365–375.
- Turner, R. M. 1963. Growth in four species of Sonoran Desert trees. Ecology 44:760–765.
- USDA Soil Survey Staff. 1975. Soil taxonomy—a basic system of soil classification for making and interpreting soil surveys. United States Department of Agriculture Handbook 436. United States Government Printing Office, Washington, D.C., USA.
- Vasek, F. C. 1979/1980. Early successional stages in Mojave desert scrub vegetation. Israel Journal of Botany 28:133– 148
- ——. 1980. Creosote bush: long-lived clones in the Mojave Desert. American Journal of Botany 67:246–255.
- Walker, B. H., D. Ludwig, C. S. Holling, and R. M. Peterman. 1981. Stability of semi-arid savanna grazing systems. Journal of Ecology **69**:473–498.
- Walker, B. H., and I. Noy-Meir. 1981. Aspects of the stability and resilience of savanna ecosystems. Pages 556–590 in B. J. Huntley and B. H. Walker, editors. Ecology of tropical savannas. Springer-Verlag, Berlin, Germany.
- Walter, H. 1973. Vegetation of the Earth and ecological systems of the geo-biosphere. Second edition. Springer-Verlag, New York, New York, USA.
- Webb, R. H., J. W. Steiger, and E. B. Newman. 1988. The response of vegetation to disturbance in Death Valley National Monument, California. U. S. Geological Survey Bulletin 1793.
- Whittaker, R. H. 1956. Vegetation of the Great Smoky Mountains. Ecological Monographs 26:1-80.
- . 1967. Gradient analysis of vegetation. Biological Reviews 42:207–264.
- —. 1975. Communities and ecosystems. Second edition. Macmillan, New York, New York, USA.
- Wright, R. A. 1970. The distribution of *Larrea tridentata* (D.C.) Coville in the Avra Valley, Arizona. Journal of the Arizona Academy of Science **6**:58–63.
- Yang, T. W., and C. H. Lowe. 1956. Correlation of major vegetational climaxes with soil characteristics in the Sonoran Desert. Science 123:542.

APPENDIX A

Tucson Mountain site characteristics. Sites are listed sequentially as they appear in Table 1.

Slope		Land- form		Dis- tance to moun- tain	n- % clay			% gravel + rock		lcium onate		H paste)
Site (de-	Aspect	desig-	Soil	front	0-5	15–20	0-5	15–20	0–5	15-20	0–5	15-20
name grees)	(degrees)	nations*	types†	(km)	cm	cm	cm	cm	cm	cm	cm	cm
17 12 22 2	72 (E) 358 (N)	R P	3 3	0	9.6 8.2	41.6	42 35	49 55	0 0.11	0.12	5.93 6.33	5.84 6.36
4 1	53 (NÉ)	P	3	0.9	12.2	24.0	37	44	0	0.07	6.12	5.90
6 1	38 (NE)	P		1.6	12.2	14.8	35	56	0.32	0.34	6.11	5.98
18 2 34 1	38 (NE) 28 (NE)	P P	3	0.7 2.1	5.2 14.2	21.4 51.2	38 35	76 7	0.08	0.45 0.78	7.61 6.85	7.61 7.49
8 2	43 (NE)	P	3	3.1	9.6	15.6	22	38	0	0	6.00	6.30
9 1	38 (NE)	P	3	3.3	11.2	23.2	16	46	0.09	0.05	5.55	5.07
30 1	353 (N)	P	3	2.2	9.8	34.6	29	26	0.18	0.31	6.15	6.96
32 1	353 (N)	P	3 3	2.9	8.4	32.4	36	60	0.12	0.15	6.00	6.03
26 1	348 (N)	P		2.6	6.6	23.8	22	50	0.18	0.12	6.21	7.69
38 8	258 (W)	P	3	0.1	17.6	47.6	29	11	0.67	0.24	7.40	6.50
35 2	83 (E)	P		1.6	10.4	24.6	22	56	0.24	0.25	6.01	6.42
39 5 3 3 36 9	248 (W) 193 (S)	PT-1 PT-2 PT-1	4/5 5 4	0.1 0.2 1.7	13.8 8.0 10.8	18.8 12.0 15.2	35 34 39	47 61 64	6.54 7.20 9.92	8.42 11.91 16.03	7.80 7.87 7.86	7.81 7.85 7.69
21 12 19 2	328 (NW) 318 (NW) 38 (NE)	PT-1 PT-2	4 5	0.8 0.9	12.6 15.8	21.4 17.6	49 48	55 40	22.12 19.71	31.57 27.20	7.73 7.83	7.57 7.64
20 11	108 (E)	PT-1	4	0.8	14.8	18.8	45	49	13.36	21.04	7.93	7.85
37 5	133 (SE)	PT-1	4	1.7	11.6	11.6	41	54	12.18	13.73	7.92	7.80
25 8	148 (SE)	PT-1	4 4 2	2.5	14.8	13.2	52	52	2.87	10.31	7.84	7.92
5 7	108 (E)	PT-1		0.7	17.0	22.4	43	56	1.07	9.40	7.66	7.80
10 1	48 (NE)	P	3	2.6	8.8	35.8	20	74	0	0.22	6.10	6.44
23 1	48 (NE)	PT-2	4	2.5	13.8	15.4	51	55	19.90	17.44	7.79	7.76
12 15	73 (E)	PT-1	4	2.7	12.4	16.6	54	60	8.66	11.29	8.54	7.70
16 9	63 (NE)	PT-1	4	3.6	10.8	17.2	43	61	11.31	2.92	7.85	7.69
28 9	293 (W)	PT-1		2.5	13.8	20.8	45	51	10.08	13.36	7.83	7.71
33 8	303 (NW)	PT-1	4	2.5	17.4	21.4	43	44	0.58	3.94	7.67	7.71
24 12	328 (NW)	PT-1		2.5	19.2	15.8	57	43	12.95	4.56	7.62	7.76
29 8	103 (E)	PT-1	4	2.5	12.6	14.6	36	60	7.39	10.42	7.79	7.67
14 10	268 (W)	PT-1	4	3.7	10.0	14.0	41	36	5.79	9.81	7.93	7.78
15 3	333 (NW)	PT-2	4	3.6	13.2	16.0	40	63	10.18	16.13	7.84	7.78
7 2	18 (N)	PT-2	4	1.2	11.8	15.6	34	41	1.79	4.86	7.77	7.80
27 1	38 (NE)	PT-2		2.5	10.0	12.8	41	43	5.93	11.44	7.76	7.64
11 2	18 (N)	PT-2	4	2.8	12.2	17.0	27	62	4.30	11.77	8.59	8.46
31 3	278 (W)	PT-2		2.5	11.0	14.6	34	41	5.30	11.74	7.86	7.80
1 1	3 (N)	H	1/2	4.3	9.8	12.2	19	30	1.68	4.27	7.85	8.06
13 1	28 (NE)	H	1/2	3.2	5.6	10.0	19	44	0.12	1.41	7.17	8.61
2 1	33 (NE)	H	1/2	2.8	9.6	9.6	22	34	0.28	0.29	6.90	7.52

<sup>\*</sup> Landform designations: H = Late Holocene, P = Pleistocene (intact), R = exposed bedrock, PT-1 = Truncated Pleistocene (erosional sideslopes of ballenas and ridgeline remnants), PT-2 = Truncated Pleistocene (nearly flat erosional summits of ballenas and ridgeline remnants).

<sup>†</sup> Soil types [names of Great Groups according to nomenclature of U.S. Department of Agriculture Soil Survey Staff (1975) and Henricks (1985)]: 1 = Torrifluvents (horizon development absent), 2 = Camborthids (presence of cambic B horizon and stage I carbonate accumulation), 3 = Haplargids and Paleargids (strong argillic horizons with underlying stage III–IV carbonate horizons, 4 = Calciorthids derived from degraded calcic horizons; shallow petrocalcic horizon present.

APPENDIX B Locations and characteristics of Silver Bell study sites.

Tran- sect	Sample site	Distance west of intersec- tion of Avra Valley and Pump Station Roads (km)	Distance north (N) or south (S) of Avra Valley Road (m)	Elev. (m)	Slope class*	Aspect	Landform†	Soil type‡
A	A1 A2	0.1 0.1	20 (N) 100 (N)	634 634	0		H-1 H-2	1 2
В	B1 B2 B3	1.6 1.6 1.6	60 (N) 160 (N) 450 (N)	646 646 646	0 0 0		H-1 H-2 P	1 2 3
C	C1	2.8	200 (N)	658	0		P	3
D	D1 D2 D3	4.0 4.0 4.0	350 (S) 200 (S) 250 (N)	671 671 671	0 0 0		H-1 H-2 P	1/5 2 3
E	E1 E2 E3 E4 E5	6.2 6.2 6.2 6.2 5.9	100 (N) 125 (N) 200 (N) 420 (N) 1000 (N)	700 695 695 695 695	0 2 0 0	 N 	PT-2 PT-1 H-2§ P H-2	4/5 4 2 3 2
F	F1 F2	7.5 7.5	120 (S) 100 (N)	710 710	1 0	N 	PT-1 H-2	4 2
G	G1 G2	8.7 8.7	325 (S) 150 (S)	737 732	2 0	N–NE 	PT-1 H-2	4 2
Н	H1 H2	10.3 10.3	300 (S) 40 (N)	753 753	0 0	•••	PT-1 P	4 3
I	I1 I2	10.9 10.9	80 (S) 75 (N)	776 771	2 0	NE 	PT-1 P	4 3
J	J1 J2	11.9 11.9	120 (S) 50 (S)	805 805	0		PT-1 P	4 3

<sup>\*</sup> Slope classes: Class 0 = 0-3°, Class 1 = 3.1-5°, Class 2 = >5°.
† Landform designations: H-1 = Late Holocene, H-2 = Mid-Holocene, P = Pleistocene (intact), PT-1 = Truncated Pleistocene (erosional sideslopes of ballenas and ridgeline remnants), PT-2 = Truncated Pleistocene (nearly flat erosional summits of ballenas and ridgeline remnants).

<sup>‡</sup> Soil types: same as in Appendix A. § Site E3 is characterized by <50 cm of Mid-Holocene alluvium burying a Late Pleistocene or Early Holocene soil with a weakly developed argillic horizon (see soil profile description in Appendix C, Site E3).

**APPENDIX C**Field and laboratory data for selected soil profiles from the three study areas.

A) Tucson Mo	ountai	ns study	site					·				%	
Surface		Hori- zon	Depth	Munsell	Textural	%	St	ructur	e	Consis	tency	gra- vel +	CaCO <sub>3</sub>
age	Site	name	(cm)	color	class*	clay	Grade†	Size‡	Type§	Wet	Dry¶	rock#	stage**
		A	0–15	10YR 6/3	LS	7.2			sg	ns, np	so	9	0
		C1	15–25	10YR 6/3	fgS	4.7			sg	ns, np	so	29	0
Holocene	Α	C2	25–40	10YR 6/3	fgS	6.5			sg	ns, np	so	48	0
		Ab		l at 40 cm de		10.3		c	-1-1-		-1-	20	0
		Ao Bwkb	40–55 55–75	7.5YR 5/4 7.5YR 5/4	gSL fcoSL	10.2 12.7	W	f f	sbk sbk	ns, np	sh sh	38 72	0 I
						12.7	w	I		ns, np	SII		
		Α .	0–5	10YR 5/4	LS		W	me	pl	ns, np	so	(25)	0
		Bwk	5-35	10YR 5/4	LS	• • • •	w	me	sbk	ns, np	sh		0
TT-1	D	ICk	35–80	10YR 5/4	LS		W	f	sbk	ns, np	sh	(25)	I
Holocene	В	IICk	80–95 (Buried sei	10YR 5/4 l at 95 cm de	vgS	• • •			sg	ns, np	1	(75)	I
		Bwkb	95–134	10YR 5/4	SCL				ma	ss, sp	sh	(25)	I
		Α	0-11	7.5YR 5/4	SL	11.6		f	gr	ns, np	so	21.9	0
		Bt	11-20	7.5YR 4/4	gSCL	38.6		f	sbk	s, p	h	27.9	Ŏ
Late-mid		Bt2	20-45	5YR 4/4	ŠCL	43.0	mo	f	р	vs, p	vh	16.0	0
Pleistocene	C	Bt3	45-82	5YR 4/6	vgSCL	26.2			sbk	s, p	vh	60.0	I
		Btk	82-109				nted calci					90.0	III
		K	109+		(Strongly	y ceme	nted peti	rocalci	c horizo	n)			IV
		Α	0-7	7.5YR 6/4	gSL	13.4		f	gr	ns, np	so	50.0	0
		Bt	7-15	5YR 4/6	vgSCL	33.6		vf	sbk	s, p	h	74.7	0
Earlier Pleis-		Bt2	15-42	5YR 4/8	C	64.0	S	f	p	vs, vp	vh	6.8	0
tocene	D	Bt3	43–55	5YR 4/8	gС	47.0		f	sbk	s, p	vh	39.7	0
		Btk	55–60				weakly o				n)		III
		K	60+		(Strongly	y ceme	nted peti	rocalci	c horizo	n)			IV
Early Pleisto-		Α	0-7	7.5YR 5/3	gSL	16.2		f	gr	ns, np	so	41.0	0
cene (ero-		Bk	7–23	7.5YR 5/3	vgSCL	25.9		f	gr	ss, np	so	67.0	I
sionally		Bk2	23–28	7.5YR 6/3	vgSCL	27.4		f	gr	ss, np	so	71.6	II
truncated)	E	Bk3	28–40	7.5YR 6/3	vgSCL	34.2		f	gr	ss, np	so	81.2	II
		K	40+		(Modera	itely ce	mented o	calcic l	norizon)				III–IV

# B) Silver Bell study site

Surface			Depth	Munsell	Textural		tructur			stency	gravel +	CaCO <sub>3</sub> stage**
age	Site	name	(cm)	color	class*	Grade†	Size#	I ype§	Wet∥	Dry¶	rock#	stage**
Late Holocene	B2		ut, indicatir	7.5YR 4/5 ation; color and ng parent mater								
Middle Holo- cene	Fl	A Bwk Bk Ck	0-10 10-27 27-130 130-155	7.5YR 6/4 7.5YR 5.5/4 7.5YR 6/4 7.5YR 5/4	gSL SL SL SL	mo mo mo	f c c	sbk sbk sbk ma	ss, sp ss, sp ss, np ss, np	so sh so–sh sh	(30) (20) (15) (5)	0 I I+ I
Mid-Holocene with shallow buried soil	E3	A Bwk Btb	0-5 5-41 41-70	7.5YR 5/4 7.5YR 5/4 (Buried late 7.5YR 4/6	SL SL Pleistoce SCL	w ene or ea mo	me rly Ho me-c		ss, np ss, np surface b ss, sp	 elow 41	 cm)	0 I I+
Mid-late Pleis- tocene (upper elevation)	J1	A Bt Bt2 Bt3 K	0-2.5 2.5-30 30-52 52-90 90+	7.5YR 5/4 6.25YR 5/6 3.75YR 4/6 5YR 4/6 (Mo	gLS vgSCL C gSC oderately t	w w mo s mo o strong	f f me c me ly cem	p gr sbk abk sbk ented ca	ns, np ss, sp vs, vp vs, vp alcic hor	so sh vh sh izon)	(33) (60) (10) (65)	0 0 0 0 IV
Mid-late Pleis- tocene (low- er elevation)	C1		eightly packet tement area 0–4 4–12 12–37	ed pebble paven 10YR 6/4 5YR 4/6 3.75YR 4/6	nent, pebb SiL CL C	vs mo s	light do me me	sbk sbk	ss, np s, p vs, vp	so 	(25) (25) (20)	on absent 0 0 0

## APPENDIX C. Continued.

B) Silver Bell stu	dy sit	:e										
Surface		Hori- zon	Depth	Munsell color	Textural	St	ructur	e	Consis	stency		CaCO <sub>3</sub> stage**
age	Site	name	(cm)			Grade†	Size‡	Type§	Wet	Dry¶		
		Btk Btk2	37–51 51–80	2.5YR 4/6 5YR 7/4	C SC	S	me	sbk sbk	vs, vp s, p		(40) (50)	I II
Pleistocene (ero-	H1	Α	0–2	10YR 6/4	LS	w	me	p	ss, np	sh		0

SL

gSL

f

f

(Strongly cemented petrocalcic horizon)

w

w

gr

gr

ss, np

ss, np

SO

so

(20)

(50)

H

II-III

IV

# C) Tortolita study site

sionally trun-

cated)

Surface age	Site	Hori- zon name	Depth (cm)	Munsell color	Textural class*	St Grade†	ructur Size‡		Consis	stency Dry¶	% gravel + rock#	CaCO <sub>3</sub> stage**
Mid-late Pleistocene	9	A Bt Bt2 K	0–7 7–16 16–39 39+	7.5YR 4/6 5YR 4/6 6.25YR 4/4	SL gSC SC (Strongly	w mo vs cemente	me me c ed peti	gr sbk sbk ocalcic	ns, np s, p s, p horizon)	so sh vh	(20) (35) (5)	0 0 0 IV
Mid-late Pleisto- cene (erosion- ally truncated)	10	A Bk Bk2	0–8 8–17 17–?	10YR 5/4 10YR 4/6 (Soft, loose	SL SL e rubble de	w w erived fr	f f om de	gr gr graded o	ns, np ns, np	so so izon)		II-III 0

<sup>\*</sup> Abbreviations used in profile descriptions follow. Fine earth fraction: S, Sand; LS, Loamy Sand; SL, Sandy Loam; SCL, Sandy Clay Loam; SC, Sandy Clay; C, Clay; CL, Clay Loam; SiL, Silt Loam. Coarse fraction modifiers: f, fine; g, gravelly; vg, very gravelly; co, cobbly.

† Grade: w, weak; mo, moderate; s, strong; vs, very strong.

‡ Size: vf, very fine; f, fine; me, medium; c, coarse.

Bk

Bk2

2-20

20 - 27

27 +

7.5YR 5/4

7.5YR 5/4

<sup>§</sup> Type: ma, massive; sg, single grain; gr, granular; pl, platy; abk, angular blocky; sbk, subangular blocky; p, prismatic.

Wet Consistency: ns, nonsticky; ss, slightly sticky; s, sticky; vs, very sticky; np, nonplastic; sp, slightly plastic; p, plastic; vp, very plastic.

<sup>¶</sup> Dry Consistency: I, loose; so, soft; sh, slightly hard; h, hard; vh, very hard; (data on dry consistency absent from some profiles described when wet).

<sup>#</sup> Value enclosed in parentheses are visual estimates (volumetric) from field descriptions. Other values are laboratory measurements (by mass).

<sup>\*\*</sup> Morphological stages I–IV described by Gile et al. (1966) and Gile et al. (1981).