

ECOLOGICAL RESPONSES OF TWO MOJAVE DESERT SHRUBS TO SOIL HORIZON DEVELOPMENT AND SOIL WATER DYNAMICS

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Abstract. In the arid southwestern United States, subtle differences in soil horizon development affect seasonal soil hydrology and consequently influence plant performance and community structure. We measured canopy development, population structure, and seasonal ecophysiology (predawn water potential, ψ_{pd} , and midday net photosynthetic assimilation, A_{net}) of two co-dominant warm-desert shrubs, the evergreen *Larrea tridentata* and drought-deciduous *Ambrosia dumosa*, in five Mojave Desert soils varying in surface and sub-surface soil development, and we used process-based soil hydrology modeling output to determine longer-term soil water dynamics underlying soil/plant responses. We hypothesized that ecophysiological performance would covary with plant development, which would reflect soil hydrological characteristics.

Among three sites on alluvial fan deposits of different geological ages (Young Alluvial, <4000 yr BP; Intermediate Alluvial, ~12 000 yr BP; Old Alluvial, ~40 000 yr BP), total canopy volume of *Larrea* (cubic meters per 100 m² ground area) was highest on the Young Alluvial site, in close agreement with soil modeling results showing that these coarse-textured, weakly developed soils permit deeper water infiltration. In older, stronger developed soils, infiltration and persistence of soil water was sharply reduced, which was reflected by lower individual *Larrea* plant volumes. However, during peak spring conditions, ψ_{pd} and A_{net} were highest in *Larrea* at the Intermediate Alluvial site (-4.2 ± 0.32 MPa and 3.2 ± 0.91 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), where soils had substantial surface and subsurface horizons, and at the Pavement site, where soils had strong surface layers but little subsurface development. Concurrent plant performance at the Young Alluvial site was unexpectedly low (-4.8 ± 0.49 MPa and 1.7 ± 0.56 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, respectively). During summer drought ψ_{pd} and A_{net} remained high in Intermediate Alluvial plants, but were extremely low in Pavement site *Larrea* (-8.17 MPa and -0.04 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, respectively), due to curtailed infiltration of summer precipitation. These findings suggest that *Larrea* growing in older soils experience greater mortality and reduced growth but are not subject to strong intra-specific competition resulting from the persistence of large individuals apparent in younger, coarser textured soils.

In contrast to *Larrea*, density of *Ambrosia* increased with soil horizon development, but smaller plant sizes resulted in similar canopy volume per area, and identical ψ_{pd} and A_{net} across all soils where it occurred, suggesting greater plasticity to the transmittal of precipitation. These findings show that a strong geomorphology and soils context is essential for understanding the variation in plant responses and vegetation structure in desert environments.

Key words: alluvial fan; *Ambrosia dumosa*; bajadas; drought; *Larrea tridentata*; Mojave Desert; photosynthesis; seasonal productivity; soil development; water potential.

INTRODUCTION

Water is the principal limiting ecological factor in warm deserts (Ehleringer 1985, Smith et al. 1997). Different soil conditions greatly affect surface infiltration and subsurface percolation, depth of moisture storage, and the persistence of plant-available moisture (Alizai and Hulbert 1970, Noy-Meir 1973, Schlesinger and Jones 1984, Schlesinger et al. 1989). Consequently,

understanding ecological patterns and processes in deserts requires knowledge of the spatial variation and distribution of soils, the hydrological behavior of these soils, and ultimately, the ways in which varying soil hydrologies affect plants (McAuliffe 1994, 1999a, b, *in press*).

Recent linkages of ecological investigations to geological studies of Quaternary landform evolution and soils have proven essential for interpreting the spatial patterns of many ecological phenomena that occur on the extensive alluvial piedmonts (bajadas) of the Mojave and Sonoran Deserts (McAuliffe 1991, 1994,

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1999a). Bajadas are mosaics of alluvial fan deposits that can vary considerably in geological age. Time-dependent changes in soil properties in these deposits include the accumulation of clay minerals and calcium carbonate and incorporation of these materials into well-developed surface and subsurface soil horizons (McFadden et al. 1986, 1987, 1998, McDonald 1994, McDonald et al. 1996, McAuliffe 1999b). Age-dependent soil profile development is one of the strongest predictors of plant community composition in these environments (McAuliffe 1994, 1999a, b).

Different plant life forms exhibit distinct responses to various soil conditions. For example, the drought-tolerant, evergreen shrub *Larrea tridentata* and smaller, drought-deciduous shrubs in the genus *Ambrosia* predominate over much of the Sonoran and Mojave Deserts. Variation in relative abundance of these shrubs is associated with the strength of development of various soil horizons (McAuliffe 1994, 1999a, McAuliffe and McDonald 1995). *Larrea* reaches its greatest development (individual size, density, and relative abundance) in weakly developed soils of geologically young (Holocene-aged) deposits or on erosionally truncated soils of much older (early Pleistocene) surfaces. In contrast, *Ambrosia* typically predominates in soils with strongly developed clay-enriched B-horizons on Pleistocene age surfaces (McAuliffe 1991, 1994).

The responses of *Larrea* and *Ambrosia* are undoubtedly a function of the hydrological behavior of soils and the developmental and phenological adaptations of these two species (McAuliffe 1994, 1999a, Smith et al. 1997). Water can potentially infiltrate and be stored at considerable depth in relatively coarse-textured soils with weak profile development. In contrast, high moisture-holding capacities of strongly developed, clay-enriched (argillic) B-horizons impede deep infiltration of water (McDonald et al. 1996). Although upper parts of soils with such profiles may be very moist for brief periods, these soils probably experience far greater seasonal amplitude in moisture availability than do zones of deeper moisture recharge in soils lacking such horizons. Relatively shallow root systems and the drought-dormant habit enable *Ambrosia* to effectively use soil water when it is available in upper soil layers, then survive extended periods when it is not. *Larrea* lacks the capacity for drought dormancy, and so extreme drought eventually causes death of entire branches (Runyon 1934). *Larrea* remains photosynthetically active during lengthy dry periods by extracting limited, but more seasonally constant, supplies of water from deeper soil layers (Smith et al. 1997). Soil horizons impeding the recharge of deeper soil layers apparently inhibit this shrub (Gile et al. 1998), as reflected by the diminished individual size, evidence of bouts of stem mortality, and lower densities on surfaces with such soils (McAuliffe 1994, Atchley et al. 1999).

Here, we examine soil hydrological behaviors and responses of *Larrea tridentata* and *Ambrosia dumosa*

where the two species exhibit marked variation in growth characteristics and density across an array of geomorphic surfaces where soil profile development and attendant soil water dynamics vary systematically with surface age. Our results include (1) a description of soil characteristics, (2) data on shrub canopy morphology and vegetation structure, (3) water relations and photosynthetic gas exchange in the two shrub species, and (4) soil hydrological modeling based on measured soil characteristics, which provides a basis for understanding the variable ecological responses across the various soils. We hypothesized that variation in ecophysiological performance underlies the observed patterns in vegetation structure across the contrasting surfaces. Specifically, we expected *Larrea* to perform best in soils with the least degree of horizon development, while *Ambrosia* was expected to perform best in soils with higher clay accumulation and water-holding capacity. Thus, we expected that plant water potentials and photosynthetic gas exchange would be highest at sites where plants were largest (Franco et al. 1994). Conversely, we predicted lower xylem pressure potentials and lower net assimilation on the sites where plants were smaller.

MATERIALS AND METHODS

Study site and soil characteristics

The study area was located in the East Mojave National Preserve, California on the west-sloping piedmont of the Providence Mountains (34°54'–58' N, 115°36'–39' W). Plants were studied on five Quaternary-aged geomorphic surfaces that varied in age, parent materials, and degree of soil development. With the exception of one site located on an eolian deposit, each site was located within 50 m of the soil profiles originally described by McDonald (1994).

Site names follow designations assigned to Quaternary geomorphic surfaces (Qe, Quaternary eolian; Qf, Quaternary fluvial) by McDonald (1994). The Qe3 site (hereafter referred to as the Dune site) is on a late Holocene (<4000-yr-old) eolian (sand dune) deposit. The VX Qf 5 site (the Pavement site) is a late Pleistocene (~12 000-yr-old) fluvial deposit consisting of sand derived from fluvially reworked dune deposits mixed with pebble-sized clasts, primarily of rhyolite that form a tightly packed surface stone pavement. Three additional sites were located on a chronosequence of soils formed in fluvial deposits from mixed plutonic (PM, syenogranite and syenite) parent material. The PM Qf7 site is a late Holocene (<4000-yr-old) gravelly deposit. The PM Qf5 and PM Qf4 sites are located on late Pleistocene deposits (~12 000 and ~50 000-yr-old, respectively) of cobbly to bouldery alluvium. These sites are referred to as the Young Alluvial (PM Qf7), Intermediate Alluvial (PM Qf5), and Old Alluvial (PM Qf4) sites. These deposits and soils

were dated, described, and mapped by McDonald (1994).

Surface clast size distributions were tallied at each site except the Dune site. A 12-m tape was stretched across each of the vegetation sampling plots (see *Plant morphology and vegetation*, below) with the 6-m mark positioned on the plot center. The maximum diameters of clasts located directly below 20-cm interval point intercepts were recorded in classes on a geometric scale: class 1, <1 cm; class 2, 1–2.5 cm; class 3, 2–5 cm; class 4, 5–10 cm; and so on. These tallies yielded 60 point intercepts per plot (300 per site) to estimate the proportion of clast size classes covering the soil surface.

Soil profiles were described using standard field methods and terminology in Soil Conservation Survey (1981) methods, with genetic soil horizon classification made to reflect current desert soil pedological concepts (McFadden et al. 1998). Soil pits were excavated to 1–2 m and into the C horizon. Samples were collected from each horizon for analysis of soil texture using the pipette method (Janitzky 1986), and bulk density estimated either by wax-coated clod (Singer 1986) or by in situ volume of removed soil (McDonald 1994).

Plant morphology and vegetation

Plant morphology and vegetation data were collected from five 100-m² circular plots at each site in April–May 1994, and from 10 plots at the Dune site in October 1996. Plot centers were uniformly spaced along transects within each of the study sites. With the exception of the Dune site, transects were positioned next to soil profiles studied by McDonald (1994). Data collected from each plot included the number of individual plants of each species and dimensions of all perennial plant canopies. Canopy height (H), diameter (D ; major and minor axes), and basal diameter (B) were measured for all *Larrea* shrubs in each plot. Additional *Larrea* plants outside the study plots were randomly selected on the Dune site because of low plant density. Canopy volume (V) of individual *Larrea* was computed as the frustrum of an inverted, right circular cone: $V = [1/3]\pi H[(D/2)^2 + (B/2)^2 + (D/2 + B/2)]$. Canopy diameter was measured for all *Ambrosia* plants in the plots. Heights of individual canopies were measured from a sample of 262 *Ambrosia* plants at one of the sites (Young Alluvial, PM Qf7) and a contrasting soil containing a well-developed argillic on an early Pleistocene-aged surface (PM Qf3) located near the three mixed-plutonic alluvium study areas. Pooled regression analysis of these data established a predictive relationship between H and D ($\log_{10} H = 0.224 + 0.744 \log_{10} D$; $r^2 = 0.87$) that was used to predict canopy heights and estimate individual plant volumes. Changes in *Ambrosia* canopy height with increasing canopy diameter required use of different mensuration formulae. Small, young plants are taller than wide, and volumes were modeled as prolate spheroids ($V = [4/3]\pi(H/2)(D/2)^2$).

As the plants grow, they become spherical ($V = [1/6] \times \pi D^3$) and eventually hemispherical. Hemispherical canopies were modeled as the segment of one base of a sphere, with volume calculated for different height/diameter relationships ($H \geq D$, $V = [1/3]\pi H^2[3(D/2) - H]$; $H \leq D$, $V = [1/6]\pi H[3(D/2)^2 + H^2]$). One-way analysis of variance (ANOVA) was used to determine differences between the sites in plant density (plants per 100 m²) and total canopy volume (cubic meters per 100 m²) between the sites, using least significant differences (LSD) for comparisons of means, with an associated α of 0.05.

Environmental and plant functional measurements

Rainfall was measured at each site with rain gauges set 1.5 m above the ground. Mineral oil was added to eliminate evaporative losses, and measurements were made 24–48 h after notification of a storm by staff at the University of California Riverside's Sweeny Granite Mountain Desert Reserve, located ~16 km from the study area. Air temperature (T_{air}) was measured with a shaded, ventilated copper/constantan thermocouple in the open cuvette of a LICOR LI-6200 portable photosynthesis system (LICOR, Lincoln, Nebraska). Leaf-to-air vapor pressure deficit (VPD) was estimated from leaf temperature and relative humidity measured with a Vaisala Humicap sensor within the cuvette.

Predawn xylem water potentials (ψ_{pd}) of *Larrea* and *Ambrosia* were measured between 0100 and 0400 using a Scholander pressure chamber (Soil Moisture Equipment Corporation, Santa Barbara, California). Five plants of each species at each site were sampled, with sampled branches marked for midday gas exchange measurements. *Ambrosia* was sampled only on the PM Alluvial sites. We sampled *Ambrosia* on the Pavement site, but it is restricted to channels at the edge of the deposit, and so did not include this data in our analysis. Estimations of midday (1100–1430) net photosynthesis (A_{net}) and stomatal conductance to water vapor (g_s) were made on terminal shoots with a closed system portable photosynthesis system (LICOR 6200). Each shoot was enclosed in a 0.25-L cuvette, allowed to adjust to cuvette conditions for 10 to 15, then measured over a 10-s sampling period under full sunlight (~1400–1800 $\mu\text{mol photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). Shoots were harvested for determination of leaf area for correcting gas exchange measurements.

Ecophysiological measurements were made monthly from 16 January (DOY 16) to 27 September (DOY 272) 1996. One-way, repeated-measures ANOVA (Systat v. 8.0, SPSS 1998) was used to detect soil effects on ψ_{pd} and A_{net} within each species. Soil site was the between-subjects factor, and time (DOY 64, 94, 124, 179, 213, and 242) as the within-subject factor. Linear, single degree polynomial contrasts were used to test for the significance of within-subject effects of time and the time-by-site interactions. Sampling centered around two significant rainfalls, DOY 76 (31.5 mm, for DOY

64, 94, and 124) and DOY 209 (9.9 mm, for DOY 179, 213, and 242), allowing comparison of plant performance in response to rainfall under seasonal "peak" springtime and hot summer "dry" conditions. Peak and dry season measurements for *Ambrosia* were taken on DOY 94 and 124, the only sampling dates this species was active. We were specifically interested in the within-subjects site-by-time interaction, which would indicate site-specific responses to precipitation through time (SPSS 1998). Adjusted α a posteriori linear contrasts were made for pairwise comparisons of sites within sampling dates.

Soil hydrological responses

A one-dimensional, process-based model, Simultaneous Heat and Water (SHAW; Flerchinger and Saxton 1989) was used to evaluate daily changes in soil water. Precipitation, air temperature, solar radiation, relative humidity, and wind speed from the Daggett, California weather station located 116 km W of the study sites were used for simulating hourly changes in soil heat and water flux, runoff, and evaporation. Daggett is at similar elevation and experiences similar temperature and precipitation as the study sites (McDonald et al. 1996).

The SHAW model treats the soil profile as discrete layers of unique texture, porosity, saturated hydraulic conductivity, and saturated water content. Infiltration (I) through the soil layers is calculated as a function of precipitation, ponding, and runoff produced by an explicit cumulative infiltration equation for each soil profile (Flerchinger et al. 1988), based on the Green-Ampt equation: $I = K_s t - (h_f - h_s)(\theta_s - \theta_0) \log_e [1 - (I / ((h_f - h_s)(\theta_s - \theta_0)))]$, where K_s is the hydraulic conductivity at surface water content, θ_0 and θ_s are the initial and saturated volumetric water contents, t is time, and h_f and h_s are head pressure at the wetting front and surface. Absorbed solar and long-wave radiation, turbulent heat and vapor transfer, and precipitation at the upper boundary and soil conditions at the lower boundary define water and heat fluxes into the soil. Heat and water fluxes between layers are determined and represented as nodes after computing initial fluxes at the upper boundary. Flux equations are solved simultaneously using implicit finite difference equations balancing net inward flux with changing conditions in the layer using a Newton-Raphson procedure. Several species-specific plant parameters for modeling evapotranspiration were unknown for this range of soils, so bare soil evaporation was modeled by maintaining equilibrium between water flux and water potential and simulating turbulent transport of water vapor away from the soil surface (McDonald et al. 1996). Contour plots of soil matric potential (ψ_{matric}) with intervals of -4 MPa between 0 and -16 MPa (SPSS 1997) were generated over two consecutive contrasting years, 1995 (fairly wet), and 1996 (very dry). The -16

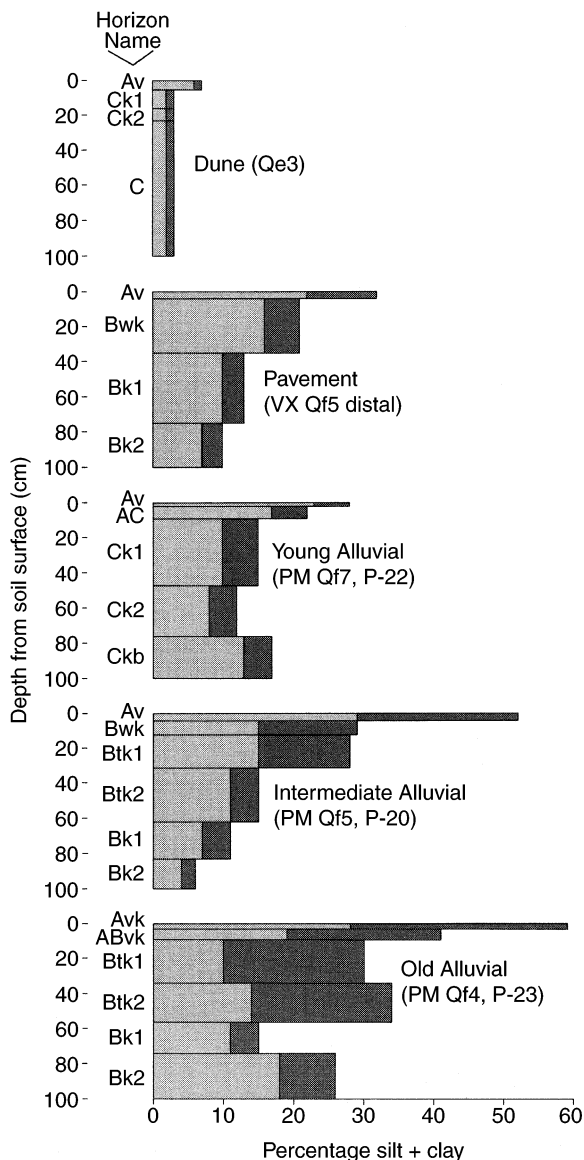


FIG. 1. Percentage of fine-earth fraction (≤ 2 mm diameter) of silt (light shading) and clay (dark shading) in soil horizons of the five study sites. Site names are followed by Quaternary surface designation and soil pit numbers of McDonald (1994).

MPa cutoff was used to reflect realistic minimum ψ_{pd} (Syvertsen et al. 1975).

RESULTS

Soil conditions

The five sites varied in development of stone surface pavements, fine-textured surface A_{vk} , and subsurface B_{ik} soil horizons (Fig. 1). The A_{vk} (vesicular A horizon: k indicates an accumulation of calcium carbonate) is a silt- and clay-rich horizon located directly beneath the desert pavement, resulting from the long-term accumulation of eolian dust (McFadden et al. 1987). The

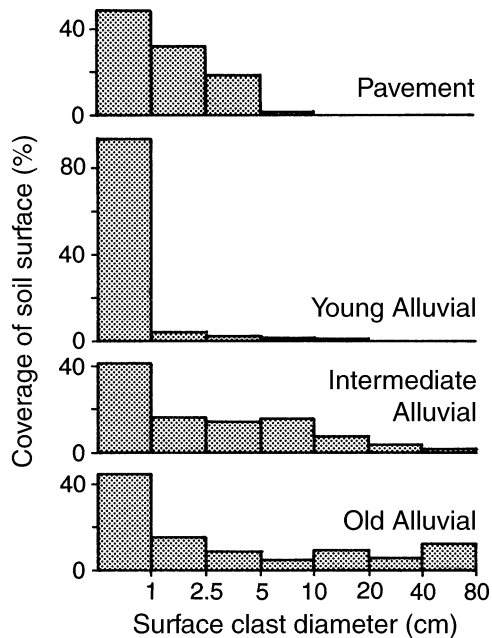


FIG. 2. Surface clast size distributions at the study sites. The Qe3 Dune site lacked surface clasts.

B_{tk} horizon is an argillic (clay-rich) B-horizon, also with an accumulation of calcium carbonate. The Dune site lacked significant soil development, consisting of parent material of unaltered eolian sand (C-horizon). Pavement site soil has a well-developed A_{vk} horizon beneath a surface pavement, and a weak underlying B_{tk} horizon with little clay accumulation in the sandy parent material. The three mixed-plutonic alluvium sites

(PM- Qf7, Qf5, Qf4) showed age-dependent development of pavements, and A_{vk} and B_{tk} horizons (Fig. 1).

The size distribution of surface clasts differed among the four alluvial surfaces. The Pavement, Intermediate Alluvial, and Old Alluvial sites possessed well-developed stone pavements. Clasts at the Pavement site were small (≤ 5 cm diameter), whereas pavements at the Intermediate Alluvial and Old Alluvial sites had a greater fraction of large clasts (>40 cm diameter; Fig. 2). The Young Alluvial site had a much larger percentage ($>90\%$) of surface clasts <1 cm diameter, reflecting the lack of pavement development on this surface.

Plant morphology and size structure of populations

Larrea on the different sites attain different maximum heights, basal diameters, and canopy diameters. Within each site, the relationship between canopy height and basal diameter was asymptotic, but with different asymptotes (Fig. 3). Plants on the Dune site were 2–3 m high. In contrast, plants from the Old Alluvial site never reached 1 m height, with intermediate canopy heights at the other three sites. The greatest maximum basal and canopy diameters were achieved on the Dune and Young Alluvial sites, where plant basal diameters commonly exceeded 100 cm, with the other sites having plants with basal diameters <75 cm.

Differences in canopy dimensions produced substantial inter-site variation in individual *Larrea* canopy volume. Median plant canopy volumes at the Dune site exceeded 10 m^3 , over 10-fold higher than median volumes at the other sites (Fig. 4). On a logarithmic scale, individual plant canopy volumes were approximately normally distributed at all sites except the Pavement

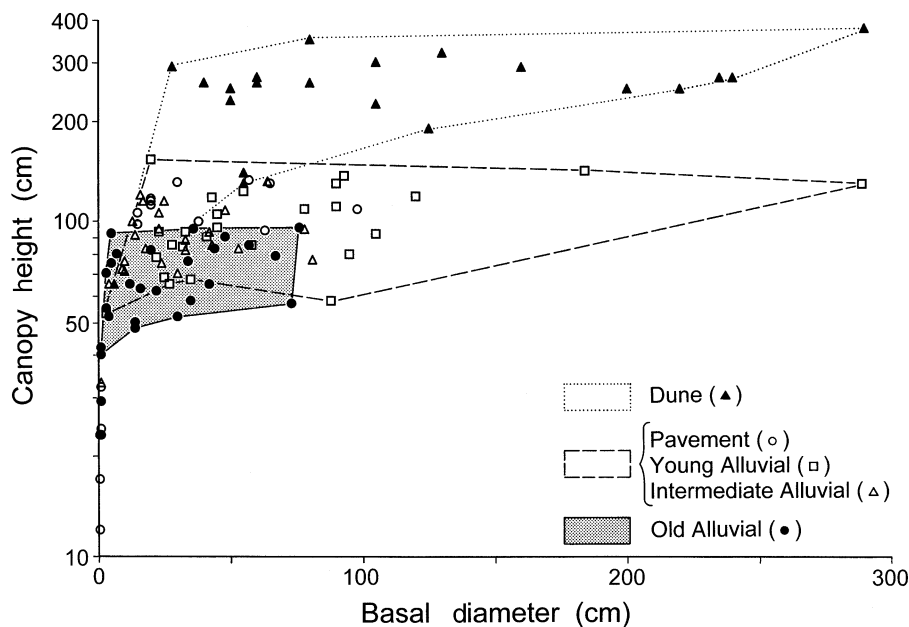


FIG. 3. Relationship between *Larrea tridentata* canopy height (note log scale) and basal diameter. Lines represent the dimensional spaces achieved by *Larrea* at various sites.

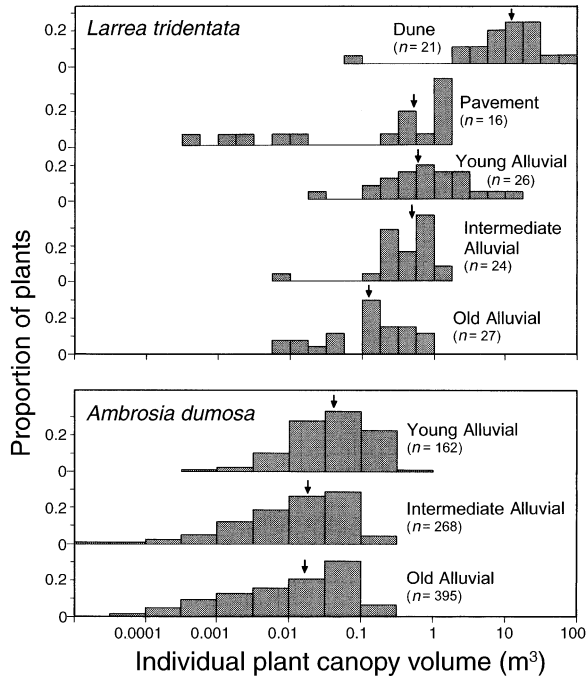


FIG. 4. Distributions of individual *Larrea tridentata* and *Ambrosia dumosa* canopy volumes across the study sites. Data are log-scale interval histograms; arrows indicate median values.

site. There the distribution had a long, left-handed tail representing small, young plants, with an abrupt truncation of the upper distribution at a modal volume of $\sim 1 \text{ m}^3$. Although median canopy volumes at the Young and Intermediate Alluvial sites were similar to the Pavement site, these sites lacked a large number of small individuals, and the Young Alluvial site contained plants of substantially larger volumes. *Larrea* at the Old Alluvial site had the lowest median canopy volume, with maximum canopy volumes $< 1 \text{ m}^3$. Distributions of canopy volumes of *Ambrosia* exhibited slight differences among the three mixed plutonic sites, but with median canopy volumes on the Young Alluvial site 2–3 times greater than the other PM sites (Fig. 4).

The Dune site had significantly lower density of *Larrea* than the other four sites where densities were similar (Fig. 5). Despite low variation in density among these latter four sites, individual plant size differences contributed to substantial variation in total canopy volume per 100 m^2 . Mean total canopy volume per plot of *Larrea* at the Young Alluvial site was seven times that of the Old Alluvial site; the Pavement and Intermediate Alluvial sites were intermediate (Fig. 5). For the Dune site, low densities and large sizes of individual plants yielded highly variable total volumes per 100 m^2 (Fig. 5). However, the arithmetic mean for total canopy volume at the Dune site was comparable to that of the Young Alluvial site. Densities of *Ambrosia* differed significantly among the sites, with the lowest density at the Young Alluvial site and highest at the Old

Alluvial site (Fig. 5). However, the larger canopy volumes of individual plants from the Young Alluvial site (Fig. 4) compensated for the low densities, yielding values for total canopy volume per 100-m^2 indistinguishable from those of the Old Alluvial site (Fig. 5) where *Ambrosia* had the highest total canopy volumes.

Establishment of young *Larrea* plants also differed among the sites. For plants with stem diameters $\leq 5 \text{ cm}$, the basal stem was single, circular in cross-section, with no stem-axis splitting. We arbitrarily categorized these small plants as young plants. Studies in the Mojave (Vasek 1980) and Sonoran Desert (McAuliffe 1991) show that basal stem diameters in such plants increase by slightly $< 1 \text{ mm/yr}$. Assuming similar growth rates in the Providence study area, plants with small basal stems likely established within the last 50 yr. The ratio of plants with stems $\leq 5 \text{ cm}$ to plants with stems $> 5 \text{ cm}$ differed significantly between the sites ($\chi^2 = 17.43, P \leq 0.0001$). Ratios at each site were 0/21 for the Dune, 5/11 for the Pavement, 1/25 for the Young Alluvial, 2/22 for the Intermediate Alluvial, and 9/18 for the Old Alluvial sites. Although higher proportions of young plants at the Pavement and Old Alluvial sites indicate higher per capita recruitment, dead remains of large plants at these sites also indicate higher mortality rates (data not shown).

Ecophysiological responses

During 1996, four precipitation events totaling $< 55 \text{ mm}$ of rain occurred, with 75% of the total coming

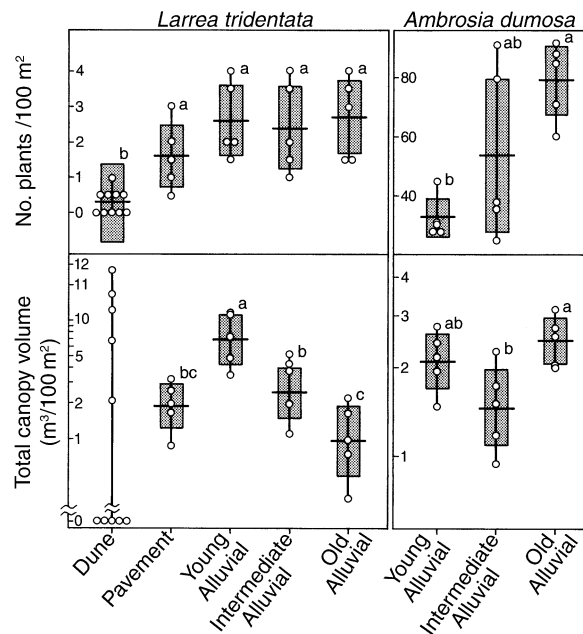


FIG. 5. Density and total canopy volume (note log scale) of *Larrea tridentata* and *Ambrosia dumosa* per area on the five study sites. Different lowercase letters indicate significant differences at $P \leq 0.05$ (ANOVA); vertical bars indicate range; horizontal bars indicate mean values, shaded boxes indicate $\pm 2 \text{ SD}$.

from a single storm in mid-March (DOY 76) of 31.5 mm. Three summer thunder storms (DOY 146, 176 and 209) deposited 12.0, 2.5, and 9.9 mm, respectively, with no differences in precipitation between study sites. Seasonal air temperatures were typical for this region, though warmer than usual early in the year. Midday air temperatures (T_{air}) during the peak season (DOY 60, 94 and 124) showed a steady increase from 14° to 31°C, while the dry season (DOY 179, 213 and 242) T_{air} ranged from 33° to 40°C. Vapor pressure deficits also followed typical patterns for this region, reaching highs of 78 kPa by late summer.

Predawn water potentials (ψ_{pd}) in *Larrea* varied between sites ($F = 75.7$, 4, 20 df, $P \leq 0.05$). Pooled across both seasonal periods, ψ_{pd} were highest in plants growing on the Dune site (-3.2 ± 0.13 MPa > mean ± 1 SE). ψ_{pd} in plants on the Young Alluvial site (-5.1 ± 0.30 MPa) were intermediate between those of the Intermediate Alluvial site (-4.6 ± 0.28 MPa) and the Pavement and Old Alluvial sites (-5.5 ± 0.41 and -5.2 ± 0.26 MPa, respectively). *Larrea* ψ_{pd} showed a soil-by-season interaction ($F = 22.6$, 5, 100 df, $P \leq 0.05$). This was likely due to large declines in ψ_{pd} in the peak season and the lack of response to summer rainfall in *Larrea* at the Pavement site, as well as to invariant ψ_{pd} in plants at the Dune site. ψ_{pd} responses to rain at the Alluvial sites were different between spring peak and summer dry periods (Fig. 6). In the spring, rain resulted in marked differences in ψ_{pd} between the Alluvial sites; the Intermediate Alluvial site had the greatest positive response to rain (compare DOY 64 to DOY 94), and remained at significantly higher levels compared to Young Alluvial and Old Alluvial plants by the last sampling date. In contrast, shortly following summer rain, Alluvial site plants attained similar ψ_{pd} , and showed little between-site differences at the last sampling date (Fig. 6).

Soil-specific effects were also apparent in seasonal midday photosynthetic gas exchange of *Larrea* ($F = 3.69$, 5, 100 df, $P \leq 0.05$, Fig. 6). Pooled across the study, A_{net} was highest at the Dune site (3.0 ± 0.398 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, mean ± 1 SE) followed by the Intermediate Alluvial (2.62 ± 0.533 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) and the Pavement sites (2.69 ± 0.662 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$), which were higher than the Young Alluvial (1.81 ± 0.585 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) and Old Alluvial sites (1.93 ± 0.780 $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$). The reduction in A_{net} during the dry season was most prominent in plants with the highest A_{net} during the peak portion of the season: Dune, Pavement, and the Intermediate Alluvial sites (Fig. 6). Indeed, A_{net} of *Larrea* at the Pavement site was rarely above photosynthetic compensation at these times (Fig. 6).

There were no site or site-by-time interactions in ψ_{pd} or A_{net} in the drought-deciduous shrub, *Ambrosia dumosa* (Fig. 6). Predawn water potential decreased from -2.7 MPa on DOY 94 to -5.6 MPa on DOY 124 (Fig. 6). A_{net} in *Ambrosia* significantly declined from 9.9

$\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ to photosynthetic compensation by DOY 124 ($F = 30.6$, 2, 12 df, $P \leq 0.05$).

Soil hydrological responses

SHAW model results suggest that the A_v and B_1 horizons have a strong influence on the spatial and temporal persistence of soil water during relatively wet (1995) and extremely dry (1996) years (Fig. 7). On the Young Alluvial site there was a distinct -4 MPa "wet footprint" from the 1995 wet season, whose upper boundary lowered from 5 to 40 cm during the summer dry season, persisted into the early months of 1996. A similar "footprint" was apparent on the Intermediate Alluvial site, but the boundary was limited to the upper 15 cm of the soil profile, and it persisted only into mid-summer 1995. A -4 MPa isopleth at 40 cm over both years is apparent in both these soils.

The well-developed surface horizons and lack of B-horizons in the Pavement site soils resulted in a unique soil hydrology. During 1995, the well-developed pavement and A_v horizon at this site did limit infiltration, but the soil remained well hydrated to nearly 35 cm. However, the lack of clay-enriched, subsurface horizons resulted in rapid evaporative loss. Following the scanty precipitation of 1996, soil percolation was extremely shallow, and rapidly lost. In contrast, in the highly developed soils at the Old Alluvial site, the -4 MPa signal was propagated to greater depths (~ 25 cm) compared to the Pavement site, but lasted less than one month (Fig. 7). There also was no high ψ_{mtric} isopleth at 40 cm in these soils. Seasonal drying resulted in "dry footprints," depending on soil horizon development. This is best illustrated by comparing Young and Intermediate Alluvial site soils from July 1995 to March 1996. At the Young Alluvial site, a -16 MPa isopleth initiated in July 1995 persisted between 0 and 20 cm until March 1996, after which propagation of 1996 precipitation inputs raised ψ_{mtric} throughout the profile (Fig. 7). In contrast, at the Intermediate Alluvial site, this -16 MPa isopleth was sustained throughout the 1996 season due to very limited infiltration of the limited rainfall into these soils (Fig. 7). Also, during seasonal drying starting in June for both years, the contour intervals were more widely spaced in Young Alluvial soils, indicating a more gradual transition of soil moisture with depth.

DISCUSSION

Community structure and functional ecology of desert ecosystems have long been assumed to be a consequence of rainfall inputs into the system, such that vegetation structure and primary production vary somewhat predictably along rainfall gradients in space or time (Noy-Meir 1973, Turner and Randall 1989). Spatial patterns, when observed, have largely been attributed to runoff-runon gradients in moisture distribution (Ludwig 1987, Schlesinger et al. 1989, Smith et al. 1995). Here we show that for a chronosequence

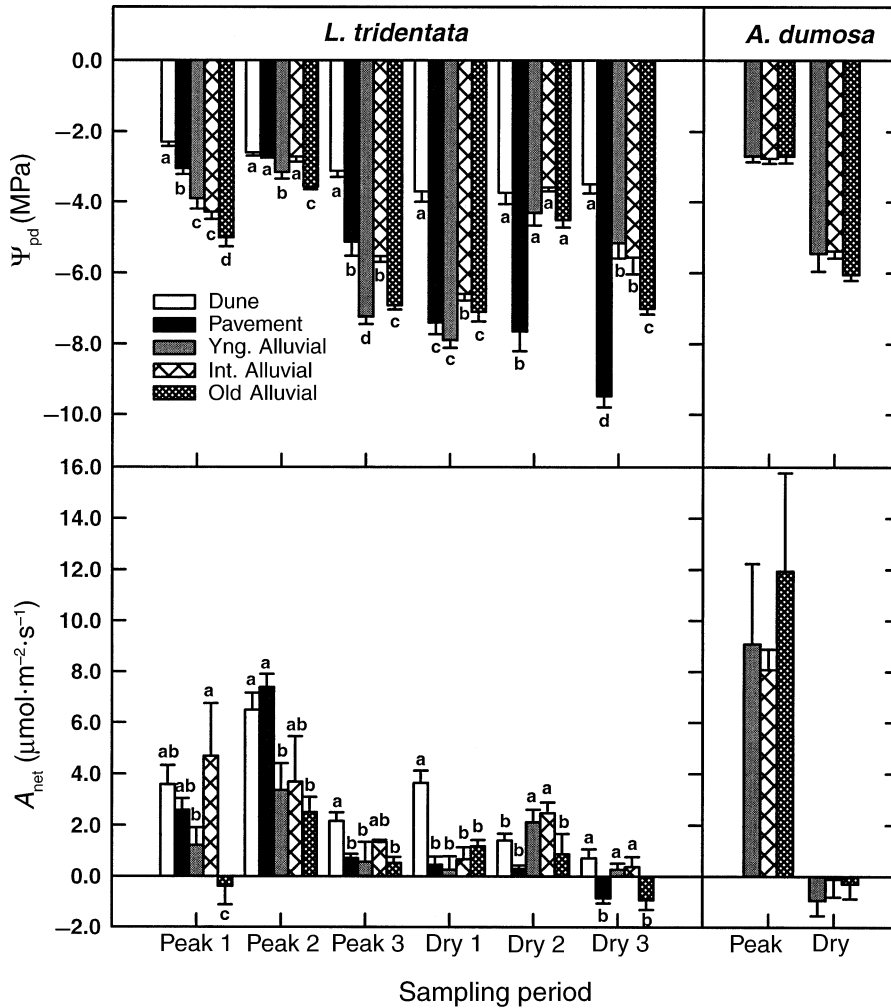


FIG. 6. The 1996 predawn water potential (Ψ_{pd}) and midday photosynthesis (A_{net}) of *Larrea* and *Ambrosia* on the five study sites. For *Larrea*, Peak 2 and dry samples follow rainfall events (31.5 and 9.9 mm, respectively). Each bar is the mean of 15 (*Larrea*) or 5 (*Ambrosia*) measurements; error bars are +1 SE. Different lowercase letters indicate significant ($P < 0.05$) site differences within sampling periods (general linear contrasts).

of diverse Mojave Desert soils (Figs. 1 and 2) receiving the same rainfall inputs over time, community composition and plant growth attributes vary markedly (Figs. 3–5) between different soils, as do plant ecophysiological performance (Fig. 6).

The observed physiological responses of *Larrea tridentata* and *Ambrosia dumosa* across contrasting geomorphic surfaces differed substantially from our simple prediction that water relations and photosynthesis would mirror whole-plant and vegetation responses. For *Larrea*, our prediction held only for high seasonal performance at the Dune site and low performance at the Old Alluvial site (Fig. 6). The physiological responses of *Larrea* from the Young Alluvial and Pavement sites changed substantially between peak and dry seasons. *Larrea* from the Young Alluvial site had lower xylem pressure potentials than expected during the peak season, but were relatively high during the sum-

mer dry season (Fig. 5). Conversely, plants from the Pavement site performed better than expected during the peak season, but declined steeply during summer drought (Fig. 6). Overall, *Larrea* at the Intermediate Alluvial site performed better than predicted. In marked contrast to the soil-specific responses in *Larrea*, plant performance in *Ambrosia* was identical across the three mixed plutonic (PM) sites (Fig. 6).

Much of the seasonal variability in ecophysiological responses of *Larrea* can be understood in terms of differences in soil hydrology between the sites. Development of strong A_v and B_t horizons in older soils (e.g., Old Alluvial) restricted surface infiltration and subsoil percolation, thereby limiting moisture to relatively shallow depths where its temporal persistence was reduced (Fig. 7). Vertical root distributions of *Larrea* are constrained to shallow depths in soils with strongly developed B_t horizons, but are much deeper in soils

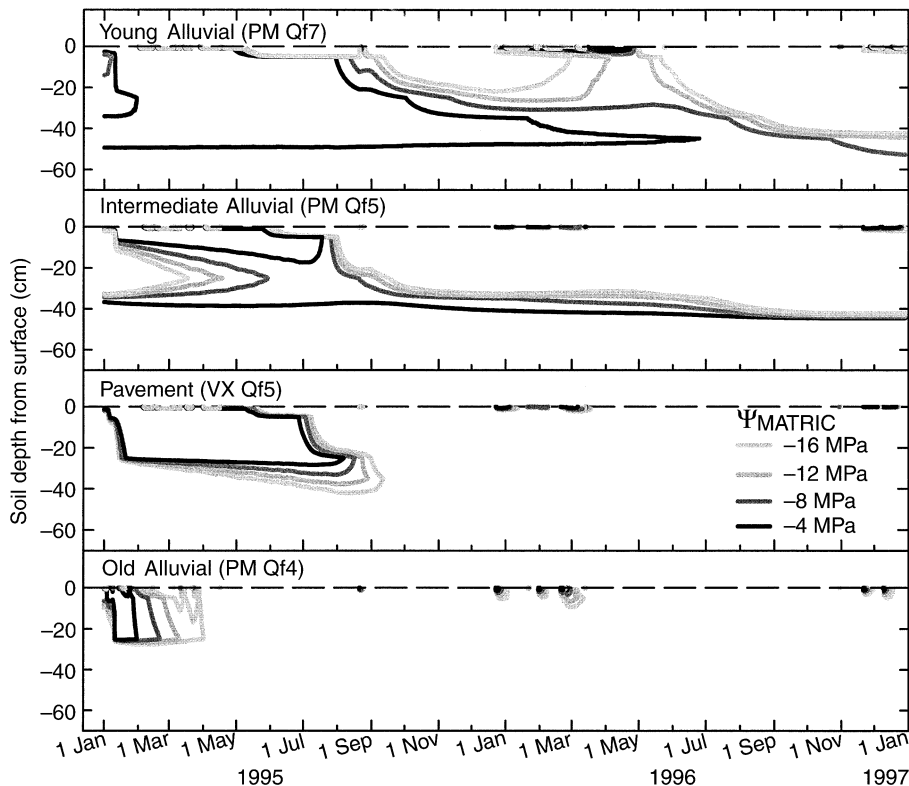


FIG. 7. Contour plots of SHAW model soil matrix potentials for 1995 and 1996 in four Mojave Desert soils with differing degrees of surface and subsurface soil horizon development.

lacking such horizons (McAuliffe and McDonald 1995, Gile et al. 1998). Restriction of rooting depth by clay-enriched B_t horizons appears to adversely affect physiological function in *Larrea* similar to shallow, cemented calcic horizons or caliche (Shreve and Mallery 1933, Cunningham and Burk 1973, Gile et al. 1998). In addition, A_v and B_t horizon strength seems to affect the persistence of soil moisture from previous years of high rainfall. In the Old Alluvial soils, there was no evidence of carryover of soil moisture derived from the previous season's precipitation, while on the Young and Intermediate Alluvial soils, there was evidence that deeper soil water could persist for extended periods at various depths (Fig. 7).

Most desert perennials, however, completely utilize all annual available soil water to depths well below 1 m (Smith et al. 1995, Yoder and Nowak 1999). Therefore, what might be more important is the propagation and persistence of soil drying. Increasing development of A_v and B_t horizons results in proportionally greater attenuation of precipitation inputs. This could amplify the previous season's or seasons' drying signal, which may persist much longer and across a greater range of depths than periods of available shallow soil moisture (Fig. 7). The Mojave Desert is characterized as an arid climate dominated by cool-season precipitation and dry summers (Smith et al. 1997). However, late summer

and fall precipitation can affect the proportion of vegetative and reproductive springtime growth of *Larrea* (Cunningham et al. 1979). In the Chihuahuan Desert, where most of the annual precipitation is from summer thunderstorms (Smith et al. 1997), infrequent, low-intensity, long-duration winter frontal storms nevertheless have the greatest impact on the ecological responses of long-lived shrubs (Reynolds et al. 1999). Therefore, soil features that modulate the seasonal patterns of the effectiveness of precipitation could be highly important in determining species-specific pulses of recruitment and mortality so important to community dynamics and productivity in deserts (Noy-Meir 1973, Smith and Nowak 1990).

Soil features other than horizon development may also affect the performance of *Larrea*. Within the PM soil chronosequence, *Larrea* from the Intermediate Alluvial site exhibited the highest photosynthesis and water potential (Fig. 6). Given the small volumes of *Larrea* at this site (Fig. 5), this was unexpected. It may be that the large cobble- to boulder-sized clasts on the surface (Fig. 2) and those distributed throughout the soil profile serve to accumulate water and minimize evaporative losses (Abrahams and Parsons 1991, Nobel et al. 1992). In addition, our SHAW model results suggest that intermediate B_t development in these soils could facilitate the persistence of soil moisture avail-

ability at deeper rooting depths (Fig. 7). *Larrea* performance on the similarly aged Pavement site (Fig. 6) supports these assertions. Surface clasts on the Pavement site are smaller and even in size (Fig. 2), and there are few large clasts distributed through the profile and little B_h horizon development (Fig. 1). The uniform cover of small clast sizes and the well-developed A_v horizon could effectively impede infiltration (McDonald et al. 1995), and would evenly distribute the little infiltration that does occur. The shallow, but spatially uniform soil water would be subject to rapid evaporative losses. In contrast, on the Intermediate Alluvial site, larger surface clasts shed much of the precipitation that falls on them, concentrating and augmenting water in areas immediately adjacent to the clasts. Large surface clasts may also subsequently provide a more effective barrier to rapid evaporative depletion of shallow soil moisture. Thus, smaller precipitation events that do not provide plant-available water at the Pavement site, resulting in the markedly lower summertime ψ_{pd} and gas exchange rates noted in *Larrea* at this site (Fig. 6), do so at the Intermediate Alluvial site through localized concentration of precipitation and slowing of evaporative losses.

The poor ecophysiological performance of *Larrea* at the Young Alluvial site was unexpected (Fig. 6), and is not consistent with modeled soil water potentials and distributions (Fig. 7). This site also has the highest total *Larrea* canopy volume on a per-area basis (Fig. 5), with plants having basal diameters commonly exceeding 50 cm (Fig. 3) and a nearly complete lack of recruitment of young individuals. Dominance of large, relatively old individuals of *Larrea* and a general lack of recruitment has been documented on Holocene-aged alluvial surfaces in the Sonoran Desert (McAuliffe 1991, 1994, 1999a) and is attributed to strong intraspecific competitive inhibition of seedling establishment and recruitment. It may be that the soil hydrology of the Young Alluvial site permits rapid growth during favorable years, facilitating long-term persistence of large plants. Such soils could therefore foster the development of highly competitive regimes that could influence ecophysiological status (Fonteyn and Mahall 1981). Thus, the low ψ_{pd} and A_{net} observed during the peak season, when plants from other sites were performing much better, and the lack of significant declines in ψ_{pd} between peak and drought periods (Fig. 6), may reflect the effect of biotic interactions on ecophysiological performance of *Larrea* at this site. Brisson and Reynolds (1994) found that in stands of even-sized *Larrea*, plants had root volumes with little or no root overlap (<15%) between individuals, possibly due to expression of root exudates that minimize root contact between individuals (Mahall and Callaway 1992). Our findings suggest that the soil volumes on the Young Alluvial site may be saturated with roots, and thus strong competition between large established individ-

uals may deplete soil water to the point that plant recruitment is limited.

In contrast, in soil environments characterized by highly seasonal and interannual fluctuations in moisture content, such competitive saturation may never be achieved. At the Old Alluvial and Pavement sites, the higher mortality rates, lack of extremely large clonal individuals (Fig. 5), and the greater proportions of young plants indicate higher population turnover. In such situations, the greater variability and unpredictability of soil moisture supplies could reduce the development of competitive interactions in determining plant performance.

The invariant ecophysiological responses of *Ambrosia* on the three alluvial sites (Fig. 6) indicate this species is relatively unaffected by constraints to water infiltration and rooting depth imposed by well-developed argillic horizons, such as those found on the Old Alluvial site (Fig. 1). Whereas total canopy volume on a per-area basis is lowest at this site for *Larrea*, it is highest for *Ambrosia* (Fig. 5). *Ambrosia* on the Old and Intermediate Alluvial sites have smaller median canopy volumes than those on the Young Alluvial site (Fig. 4), which probably reflects restriction of rooting depth imposed by argillic horizons. This suggests that the soil conditions potentially cause temporal limitations to canopy development by affecting leaf area early in the growing season, but then by limiting photosynthetic activity as soils dry (Comstock and Ehleringer 1986, Comstock et al. 1988). In addition, the invariant physiological performance of *Ambrosia* on the PM sites may be due to phenotypic plasticity in gas exchange and water-use efficiency (Monson et al. 1992, Schuster et al. 1992, Ehleringer 1994), and age-dependent axis splitting in *Ambrosia* that could maintain consistent rooting and canopy volumes (Jones 1984, Ehleringer 1994). Thus, the invariant ψ_{pd} and canopy volume per ground area data indicate that *Ambrosia* varies rooting volumes across contrasting soils such that it experiences similar seasonal soil moisture regimes.

The unique soil hydrology at the Pavement site produced by uniformly small and tightly packed pavement clasts (Fig. 2), coupled with the underlying, fine-textured A_{vk} horizon (Fig. 1), apparently excludes *Ambrosia*. On the Pavement site, only large and very infrequent precipitation events produce infiltration to a depth where moisture is not rapidly lost to evaporation. Whereas such infrequent, deep recharge supports *Larrea*, it apparently cannot support *Ambrosia* at the Pavement site. The shallower root system of *Ambrosia* may require more frequent, relatively shallow wetting of the soil by smaller precipitation events than occur at the Pavement site. *Ambrosia* does occur in small, first-order flumes at the edge of this deposit that collect and concentrate runoff shed by the adjacent pavements, effectively amplifying precipitation inputs (Schlesinger and Jones 1984, Schlesinger et al. 1989). Predawn water potentials and photosynthetic gas exchange for *Am-*

brosia in these fluves (data not shown) were identical to those attained on the PM Alluvial surfaces (Fig. 6), suggesting that runoff augmentation did result in similar seasonal soil water for this deciduous species at this site.

Our findings indicate that desert plant functional responses are strongly dependent on soil characteristics. By extension, our results show that the soil plays an important mediating influence on plant population- and community-level processes. Detailed understanding of the processes underlying landform evolution and soil development in deserts provides a meaningful contextual framework to decipher the effects of current climate regimes and potential impacts of future climate change in aridland systems. Future studies utilizing this synoptic view will provide deeper insight and understanding of a wide range of plant and ecosystem processes in desert landscapes.

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