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# IMPACT OF DROUGHT ON DESERT SHRUBS: EFFECTS OF SEASONALITY AND DEGREE OF RESOURCE ISLAND DEVELOPMENT

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*Abstract.* Large areas of semiarid grasslands in the southwestern United States have been virtually replaced by shrubs during the past century. Understanding the causes and consequences of such vegetation dynamics requires that we elucidate the interplay between external forces of change (e.g., climate, human impacts) and the internal forces within these ecosystems that foster resilience and/or stability. Several conceptual models of arid ecosystems address this interplay by including the potential role of autogenic shrub effects on ecosystem processes, which lead to the formation of "resource islands" and tend to promote shrub persistence. Specifically, during the process of shrub establishment and maturation, the cycling of nutrients is progressively confined to the zones of litter accumulation beneath shrubs, while bare intershrub spaces become increasingly nutrient poor. As shrub resource islands develop, there is increased interception and stemflow by shrub canopies, confining infiltration of nutrient-enriched rainfall directly beneath the shrubs; the barren intershrub spaces generate overland flow, soil erosion by wind and water, and nutrient losses. These islands are preferred sites for the regeneration of shrubs and herbaceous plants and are correlated with spatial variation in soil microbial populations and soil microfauna that promote nutrient cycling. If further changes in the transition between grassland and shrubland are to be correctly predicted—or if we wish to intervene and redirect transitions—we must develop a greater mechanistic understanding of the structural and functional relationships between shrubs and the resource islands associated with them.

We conducted a 3-yr field study in the Jornada Basin of southern New Mexico to explore the relationships between seasonal manipulations of soil water and its impact on soil nutrient dynamics of resource islands and shrub growth and physiology. At our study site, where total annual precipitation is ~230 mm (~65% falls during the summer period), we simulated seasonal drought in summer (1 June–30 September) and winter/spring (1 October–31 May) by constructing large rainfall-exclusion shelters over shrub resource islands at different stages of development. Our experiment tests two principal hypotheses. The first is that the two major shrub species in the Jornada Basin, creosotebush (*Larrea tridentata*) and mesquite (*Prosopis glandulosa*), have different growth phenologies, rooting patterns, and physiological responses to resource availability (primarily water). The second is that different size classes of shrubs ("small" and "large") represent distinct stages of resource island development (i.e., "young" and "mature," respectively) and, hence, different stabilities—that is, as islands develop, their associated shrubs become less coupled to short-term fluctuations in precipitation and more resistant to long-term drought or climate shifts.

With regard to the first hypothesis, we conclude that the two species are relatively similar in function despite the different phenological "strategies" of *Larrea* (evergreen) and *Prosopis* (winter deciduous). In the absence of drought, both species exhibited maximal rates of shoot and root growth, as well as high photosynthesis and transpiration, in late spring. This remained as the period for maximal growth and physiological activity for *Prosopis* shrubs that experienced drought in either summer or winter/spring. On the other hand, *Larrea* shrubs that experienced drought in winter/spring had maximal growth and activity shifted to the summer period, and in the absence of drought, *Larrea* shrubs also exhibited high physiological activity during the summer (especially following high rainfall). Thus, *Larrea* appears to have a greater capacity for shifting its activity patterns to alternate periods to take advantage of changes in resource availability. Shrubs of both species appeared well adapted to withstand season-long droughts. Mechanisms for survival include the following capacities: (1) to shift growth and physiological activity to utilize different temporal moisture (*Larrea*); (2) to utilize different levels of soil water (both species); (3) to carry out limited physiological activity and growth during drought (especially *Larrea*); and (4) to compensate for some negative impacts of drought through enhanced physiology (especially *Prosopis*) and growth (especially *Larrea*) in the season following drought. With regard to the second hypothesis, we again found more similarities than differences between the different aged (young vs. mature) islands. The stage of maturity of a resource island complex did not seem to be a significant factor to the growth and physiological activity of the shrub.

*Key words: desertification; drought response; Jornada LTER; Larrea tridentata; Prosopis glandulosa; resource island formation; shrub physiology; soil nitrogen; soil water.*

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## Introduction

Many arid regions of the globe have undergone desertification during the last century (Bond et al. 1994, Dodd 1994). In the southwestern United States this is best exemplified by the large areas of semiarid grasslands that have been virtually replaced by arid shrublands (York and Dick-Peddie 1969, Grover and Musick 1990, Bahre and Shelton 1993). The ecological consequences are usually severe, resulting in changes in fundamental processes such as nutrient cycling, primary productivity, and water flux, all of which have important social, economic, and ecological implications (OIES 1991, Le Houérou 1992, Milton et al. 1994).

Understanding processes that initiate and sustain desertification is one of the key objectives of the Jornada Long Term Ecological Research (LTER) program in the Jornada Basin of southern New Mexico. The Jornada LTER conceptual model of desertification (Schlesinger et al. 1990) hypothesizes that undisturbed grasslands are characterized by a relatively uniform spatial distribution of water, nutrients, and other soil resources, and that shrub invasion leads to an increase in the spatial and temporal heterogeneity of soil resources. As grass is replaced by shrubs (causal factors reviewed in Reynolds et al. 1997), the cycling of plant nutrients is progressively confined to the zones of litter accumulation beneath shrubs, while bare intershrub spaces become increasingly nutrient poor, leading to the so-called "islands of fertility" (Charley and West 1975, Virginia and Jarrell 1983, Schlesinger et al. 1996).

These shrub-dominated islands have a number of autogenic effects on other ecosystem processes as well. For example, there is increased interception and stemflow by the canopies of shrubs, which tends to confine the infiltration of rainfall to the soil profile directly beneath the shrubs (Tromble 1988, Navar and Bryan 1990, Mauchamp and Janeau 1993); in addition, this stemflow water is nutrient enriched (Whitford et al. 1997). The barren intershrub spaces generate overland flow, soil erosion by wind and water, and nutrient losses from the ecosystem (Rostagno 1989, Stockton and Gillette 1990, Takar et al. 1990). These islands are preferred sites for the regeneration of shrubs (McAuliffe 1988, Franco-Pizaña et al. 1995) and herbaceous plants (Ludwig et al. 1988), and are highly correlated with spatial variation in soil microbial populations and soil microfauna that promote nutrient cycling in shrub deserts (Freckman and Mankau 1986, Gallardo and Schlesinger 1995, Herman et al. 1995). Consequently, we prefer to view these shrubs and their associated abiotic environment as "resource islands."

In the classical view, grassland-to-shrubland transition involves a shift in water and nutrient availability from surface to deeper soils (Walter 1971, Walker and Noy-Meir 1982). These vertical gradients in resource distribution may be due to external factors, such as timing and duration of moisture inputs, or internal factors, such as vegetation composition and succession. The Jornada desertification model proposes that there are numerous potential interactions among these external forces of change (e.g., climate, human impacts) and the internal forces associated with the vegetation-induced changes. In particular, the model emphasizes feedbacks that could augment the persistence and regeneration of shrubs in desertified habitats, which may be important in controlling the multiple quasi-stable states that can be found in arid ecosystems (Westoby et al. 1989, Laycock 1991). If further changes in the transition between grassland and shrubland are to be correctly predicted, or if we wish to intervene and redirect transitions, we must develop a greater understanding of the structural and functional relationships between shrubs and the resource islands associated with them.

Toward this end, we conducted a field study in the Jornada Basin of southern New Mexico to test two general hypotheses about relationships between seasonal soil water availability and its impact on soil nutrient dynamics of resource islands and shrub growth and physiology. Our first hypothesis is that the two major shrub species in the Jornada Basin, creosotebush (*Larrea tridentata*) and mesquite (*Prosopis glandulosa*), have different growth phenologies, rooting patterns, and physiological responses to resource availability (primarily water). Our second hypothesis is that different stages of resource island development, i.e., "young" vs. "mature" islands, have different stabilities—that is, as islands develop, their associated shrubs become less coupled to short-term fluctuations in precipitation and more resistant to long-term drought or climate shifts. To test these hypotheses, we conducted a 3-yr field experiment where we simulated seasonal (winter/spring vs. summer) drought by using large rainfall exclusion shelters constructed over different size classes of shrubs ("small" and "large") selected to represent distinct stages of resource island development (i.e., "young" and "mature," respectively). We had the following objectives: (1) to characterize the physical characteristics of the islands (soil texture, nitrogen concentration, shrub size, litter accumulation, etc.); (2) to quantify the availability of water and nutrients in the soil profile of islands over time; and (3) to elucidate above- and belowground growth, physiology, and resource-use patterns of the shrubs *Larrea* and *Prosopis*.

## Study Site and Experimental Design

### *Jornada Basin*

The study was carried out in conjunction with the Jornada LTER, which is located at the southern end of the Jornada del Muerto Basin of south-central New Mexico, USA (Doña Ana County). The Jornada Basin

is part of the Mexican Highlands Section of the Basin and Range Physiographic Province within the extreme northern portion of the Chihuahuan Desert (MacMahon and Wagner 1985). Historical records indicate that the Jornada Basin was dominated by warm-season $C_4$ perennial grasses (e.g., *Bouteloua eriopoda, Sporobolus flexuosus*) at the time of European settlement, but much of the area has become dominated by shrubs, especially creosotebush (*Larrea tridentata*) and mesquite (*Prosopis glandulosa*). This transition was initiated in the late 1800s or early 1900s (Humphrey 1958, Buffington and Herbel 1965, Pieper et al. 1983, Gibbens and Beck 1988) and has continued in some areas to the present (Gibbens and Beck 1988). The basin now contains few remnant grassland communities, and most areas are dominated by shrubs or codominated by shrubs, subshrubs, succulents, and/or grasses (Wierenga et al. 1987, Cornelius et al. 1991).

Elevation varies from 1300 to 1400 m over the study site. Soils range from fine-textured, clay soils (vertisols) within the lowest parts of the basin, which are occasionally flooded by runoff from surrounding slopes, to coarse-textured gravelly, sandy soils (haplargids and calciorthids) on the basin slopes. Aeolian sand deposits occur in patchy locations throughout the basin (Hennessy et al. 1985). The soils and geomorphology of the study area have been described in detail by Gile et al. (1981), Hennessy et al. (1985), and Nash and Daugherty (1990).

Climate details for the Jornada are provided in Conley et al. (1992) and Pieper et al. (1983). The mean monthly maximum temperature is highest in June (36°C) and lowest in January (13°C). Nighttime freezing temperatures occur on average from late October through early April (165 d). Conley et al. (1992) characterized the semiarid climate of the Jornada as having three distinct seasons: hot, dry springs (April–June); hot, moist summers (July–October); and cold, moderately dry winters (November–March). Total annual precipitation is ~230 mm, of which nearly 65% falls during the summer period as localized showers associated with thunderstorms; ~25% falls in winter as rain and snow associated with frontal storms over the region; and ~10% occurs in the spring. For the purposes of this drought study, we divided precipitation into two seasonal components: summer (1 June–30 September) and winter/spring (1 October–31 May) (see *Microclimate, soil water, and nutrient analyses*).

### *Study sites*

We selected three shrub communities to study, hereafter referred to as the upper bajada, lower bajada, and dune. The upper bajada site is dominated by *Larrea,* the lower bajada site is codominated by a mixture of *Larrea* and *Prosopis,* and the dune site is dominated by *Prosopis* (Fig. 1). The general soil characteristics are given in Table 1. Details of the vegetation at the upper and lower bajada are given in Cornelius et al. (1991) and for the dunes by Hennessy et al. (1985). A brief summary is given below.

1) The upper bajada community (1370 m elevation) is located on the upper end of a gentle alluvial slope that spans ~3 km from the base of Mt. Summerford to a dry lake bed (playa). The highly eroded, coarse-textured soils and near absence of perennial grasses suggest that this site was invaded by shrubs many decades earlier. *Larrea* is the dominant shrub, with plants of various sizes and cover ranging from 10 to 35%. There is low cover (<10%) of subshrubs (e.g., *Zinnia acerosa* and *Xanthocephalum microcephalum*), forbs (e.g., *Croton pottsii* and *Bahia absinthifolia*), perennial grasses (primarily *Erioneuron pulchellum*), and occasional low densities of ephemeral species in the intershrub areas.

2) The lower bajada community (1318 m elevation) is located at the lower end of the alluvial slope, ~1.4 km from the upper bajada site. This site is codominated by small *Larrea* and *Prosopis* shrubs and is characteristic of a more recent shrub invasion (R. Gibbons, *personal communication*). The cover of perennial grass is high (e.g., *Muhlenbergia porteri, Aristida longesita, Sporobolus cryptandrus, E. pulchellum*), although subshrub (e.g., *Xanthocephalum sarothrae*) and forb species (e.g., *Bahia absinthifolia, C. pottsii, Sphaeralcea subhastata*) codominate. Shrubs (e.g., *Prosopis, Larrea, Ephedra trifurca, Yucca elata*) are scattered throughout. Shrub and subshrub cover is generally <20%. Ephemerals can be abundant, both under shrubs and in the intershrub spaces.

3) The mesquite dune community (1333 m elevation) is located ~20 km northwest of the bajada sites in a broad, flat subsidiary basin characterized by aeolian deposits. The degree of development of the sand dunes suggest that this site was invaded by shrubs 80 yr ago, following intensive grazing and drought (Buffington and Herbel 1965, Hennessy et al. 1985). Vegetation at this site is dominated by shrubs of *P. glandulosa* of various sizes. *Prosopis* occurs here as a multistemmed plant, often a single plant associated with a dune. Cover is generally <20%. Important subordinates include the subshrub *X. sarothrae,* grasses *S. flexuosus* and *E. pulchellum,* with occasional forbs and ephemerals.

The two bajada sites are located on the New Mexico State University Rangeland Research Center (established in 1927) and the mesquite dunes site is on the adjacent Jornada Experimental Range (U.S. Department of Agriculture, established in 1912). Although the specific intensity of grazing on our sites is unknown, none are located near wells or stocking tanks, and can be considered to have been grazed at average levels for the area. Records for the Rangeland Research Center indicate that the area was moderately grazed (~40 ha/animal-unit) from 1920 to 1967 (Fusco et al. 1995). Stocking of the Jornada Experimental Range was slightly greater. This level of grazing, coupled with

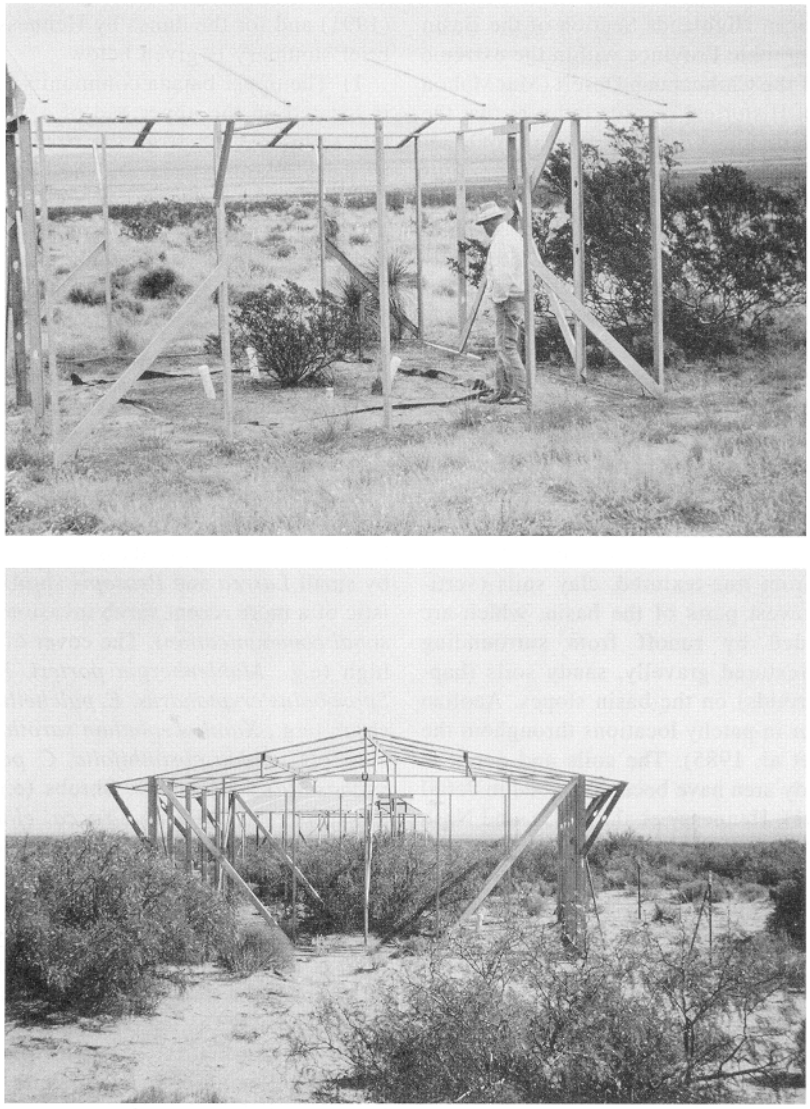


FIG. 1. Upper bajada and dune study sites at the Jornada LTER site, showing relative sizes of rainout shelters. The upper bajada site (upper panel) is dominated by *Larrea tridentata* and the dune site by *Prosopis glandulosa*.

a severe drought in the mid-1950s, resulted in a great reduction of grass cover (Gibbens and Beck 1988). In 1967, the stocking rate of the Rangeland Research Center was reduced to 67 ha/animal-unit and the quality of the range (including grass cover) increased substantially, even with small increases in stocking later on (Fusco et al. 1995). The mesquite dunes site has remained largely as stabilized dunes with sparse grass cover. The upper bajada area was excluded from grazing in 1970 and the lower bajada area was excluded in 1981; the dune area remains a lightly grazed pasture, so fences were installed around all selected shrubs.

### *Size class criteria*

We define two size classes of shrubs—small and large—based on our observations of plant height, stem diameter, average crown volume (based on canopy diameter and plant height, see Ludwig et al. 1975), and litter accumulation under the plant canopy; factors that we found to be generally correlated. Hence, we assume that shrub size is a good indicator of resource island development, that is, a small shrub constitutes a "young" resource island and a large shrub is indicative of a "mature" island. Individual shrubs along with soils directly under, as well as just outside the canopy edge (dripline), are hereafter referred to as (shrub) resource islands. At each site, we selected a number of shrubs for study based on these criteria. Furthermore, we required that the nearest neighbors were >6 m distant to minimize potential shrub–shrub interactions.

At the upper bajada site, 16 small (=young islands) and 16 large (=mature islands) shrubs of *Larrea* were chosen based on the above criteria. Average height and crown volume of the shrubs are summarized in Table 2.

Height varied from 0.3 to 0.6 m for small shrubs and 1 to 2.2 m for the large shrubs, some of which had multiple main stems with individual diameters >20 mm. At the lower bajada, most of the *Larrea* and *Prosopis* plants were small relative to the size variation we observed across the study area. Thus, we only have small size classes for each species at this site (=young islands). We selected 24 shrubs each for *Larrea* and *Prosopis*. Heights of *Larrea* shrubs ranged from 0.2 to 0.6 m (average 0.36 m). *Prosopis* shrubs were generally larger than *Larrea,* with heights varying from 0.4 to 0.8 m (average 0.63 m) and approximately four times greater canopy volume than *Larrea* (Table 2). The dunes site is dominated by *Prosopis* shrubs and, as in the case of *Larrea* at the upper bajada, we also selected small shrubs that were indicative of young islands (average crown volume and height of these plants chosen so as to match those of the small *Prosopis* shrubs at the lower bajada site). Of the many large shrubs, we selected a subset, representative of mature islands, with an average height 1.06 m and crown volume of 2.60 $m^3$ (Table 2). Individual shrubs were identified as clumps of the multistemmed shrubs that formed discrete canopies.

### *Rainout shelters and experimental design*

At each site, sampling plots for the resource islands were created so as to minimize lateral soil water movement and the effects of neighboring plants. This was done by digging a narrow trench (1.5 m depth) around an individual shrub, ~0.5 m from the outer edge of the shrub canopy. For example, for a shrub with a canopy diameter of ~1 m, the plot was 2 m on a side. The soil sidewall of the trench was lined with heavy-gauge black polyethylene and backfilled. This procedure was done several months before the study commenced in July 1991, and no shrub appeared to be adversely affected based on a comparison of predawn water potentials and stomatal conductances of study and nonstudy shrubs in the area (see Franco et al. 1994).

These resource island plots were randomly assigned to treatments or controls. At the upper bajada and dune sites, eight mature and eight young plots were subjected to a summer drought treatment; eight young and eight mature plots were treated as controls (Table 3). At the lower bajada, eight young plots for each species (*Larrea* and *Prosopis*) were subjected to summer drought, eight to winter/spring drought, and eight served as controls.

To simulate seasonal drought, shelters were constructed to exclude rainfall on selected resource island plots. A shelter consisted of a metal frame with a clear polyethylene (0.15 mm; 6 mil) plastic roof (see Fig. 1) and varied in size depending on the size of the shrub resource island. During the off-season, the plastic on the roofs was removed. A typical shelter covering the small shrubs (young islands) was about 3 × 4 m (2 m tall), whereas a typical shelter covering the large shrubs (mature islands) was about 4 × 5 m (3 m tall). The extension of the shelters to >1 m beyond the edge of the trench assured that rainfall was excluded. To examine the magnitude of potential shelter effects, we made a series of paired measurements inside and outside shelters at different times of the year (data not shown). Midday air temperatures differed by approximately ±1°C; peak midday soil temperatures were as much as ±6°C different at 2.5 cm depth and ±1°C different at 30 cm depth, depending on soil moisture and radiation loads; and total integrated daily solar radiation was ~20–35% lower under the shelters. In the latter instance, a 35% reduction in solar radiation on a sunny day is still above the light levels for saturated leaf photosynthesis in these shrub species (Franco et al. 1994).

We simulated summer drought at the upper bajada and dune sites and both summer and winter/spring drought at the lower bajada sites. (It was impossible to conduct winter/spring drought at all three sites due to logistics and costs.) To simulate summer drought, rainout shelters were deployed on 1 June and removed on 1 October except for the first year of study, when they were removed at the end of October. To simulate winter/spring drought, rainout shelters were deployed on 1 October and removed on 1 June. Once a shrub resource island was chosen to receive a particular treatment, it received that treatment for the entire 3-yr duration of the study, except for some changes that were made after the first year. We initially considered October rainfall to be part of the summer's complement (as per Conley et al. 1992), but in 1991 we felt that October rainfall was more characteristic of winter precipitation and could be important in initiating soil moisture recharge associated with winter, while having negligible impact on summer plant activity. Thus, after the first year, October rainfall was considered as part of winter/spring rainfall. For the purposes of this study, measurements made after the start of a new season, but prior to significant rainfall, were considered to be associated with the prior season.

### *Microclimate, soil water, and nutrient analyses*

At the initiation of the study in the summer of 1991, soil physical and nutrient properties (e.g., sand, silt, clay, coarse fragments, $CaCO_3$, organic carbon, total N, and extractable P) were determined. During the course of the study, a number of abiotic factors were monitored at each site at various intervals. Maximum and minimum air temperature and rainfall were monitored daily throughout the study. Soil water content of resource islands was determined approximately biweekly in 1991 and 1993, and less frequently during 1992, with the neutron attenuation technique using a CPN 503DR hydroprobe (CPN Corporation, Santa Barbara, California), field-calibrated (gravimetrically) in soils adjacent to the experimental plots. Access tubes for the hydroprobe were installed into the soil on the

TABLE 1. Soil characteristics ($\bar{X} \pm 1$ SE) from the three study sites at the beginning of the study (except for total nitrogen and extractable $PO_4^-$-P, which were sampled in June 1992).

| Site | Species | Island age | Depth (cm) | Bulk density ($g/cm^3$) | Sand (%) | Silt (%) | Clay (%) |
|---|---|---|---|---|---|---|---|
| Upper bajada | *Larrea* | Young | 5 | 1.55 | ... | ... | ... |
| | | | 15 | 2.05 | 76.6 ± 0.18 | 16.6 ± 0.53 | 6.8 ± 0.71 |
| | | | 30 | 1.48 | 79.9 ± 0.88 | 14.1 ± 2.30 | 6.0 ± 1.41 |
| | | Mature | 5 | 1.50 | | | |
| | | | 15 | 1.76 | 74.4 ± 2.65 | 20.3 ± 3.18 | 5.4 ± 0.53 |
| | | | 30 | 1.48 | 79.0 ± 1.41 | 13.8 ± 2.47 | 7.3 ± 1.06 |
| Lower bajada | *Larrea* | Young | 5 | 1.34 | ... | ... | ... |
| | | | 15 | 1.76 | 66.0 ± 5.66 | 22.9 ± 1.24 | 11.1 ± 4.42 |
| | | | 30 | 1.58 | 61.3 ± 8.84 | 23.8 ± 1.77 | 15.0 ± 7.07 |
| | *Prosopis* | Young | 5 | 1.22 | ... | ... | ... |
| | | | 15 | 1.50 | 79.3 ± 11.31 | 13.3 ± 10.61 | 7.5 ± 0.71 |
| | | | 30 | 1.66 | 74.6 ± 9.37 | 15.4 ± 5.83 | 10.0 ± 3.54 |
| Dunes | *Prosopis* | Young | 5 | 1.26 | ... | ... | ... |
| | | | 15 | 1.58 | 87.8 ± 3.18 | 6.9 ± 3.01 | 5.4 ± 0.18 |
| | | | 30 | 1.47 | 88.8 ± 0.71 | 6.1 ± 0.53 | 5.1 ± 0.18 |
| | | Mature | 5 | 1.15 | ... | ... | ... |
| | | | 15 | 1.58 | 91.4 ± 1.59 | 3.8 ± 1.77 | 4.9 ± 0.18 |
| | | | 30 | 1.59 | 90.1 ± 0.18 | 5.1 ± 0.53 | 4.8 ± 0.35 |

*Note:* Bulk densities and sand, silt, and clay percent averages were based on samples taken from soils adjacent to the plots ($N = 2$); soil pH ($N = 8$), TKN ($N = 4$), and extractable $PO_4^-$-P ($N = 4$) were measured just inside the canopy dripline.

south side of each plant near the edge of its canopy. Water content was measured at 30, 60, and 90 cm depths. Several nutrient attributes of soils were measured during the study. Since our objective was to determine the impact of the seasonal moisture (or lack thereof) on nutrient dynamics and capacity of the soils, we measured these attributes at the end of the winter/spring season in June, and after the summer season in October. Total soil N ($N_{TKN}$) was estimated using Kjeldahl extraction. Soil extractable N ($N_{ext}$) was estimated using KCl extractable $NO_3^-$-N and $NH_4^+$-N. Total capacity for soil N-mineralization ($N_{min}$) was assayed at the end of each season. We also analyzed soils for extractable $PO_4^-$-P. We measured these nutrient attributes over three depths (0–10, 10–20, and 20–30 cm) and two positions: just inside the dripline of the canopy and just outside in each resource island plot. We restricted the majority of the sampling to outside the dripline to avoid disturbing the root systems, especially of the small shrubs.

Procedures for soil nutrient analyses were as follows. Soil samples (~35 g) were obtained with a 1.5 cm diameter soil coring device (0–10, 10–20, 20–40 cm depth) and placed in watertight polyethylene bags at the time of collection to maintain field moisture content. On return to the laboratory, each soil sample was sieved through a 2-mm mesh and replaced in the polyethylene bag. A subsample was removed and air dried for analysis of Kjeldahl N (some sample dates). The remaining sample was stored in the collection bag at 6°C until analysis for extractable N and P (some sample dates) and the start of mineralization incubations (8–10 d after collection). Soil $NO_3^-$-N and $NH_4^+$-N were extracted from 5-g soil subsamples in a 2 mol/L KCl solution shaken for 1 h (Keeney and Nelson 1982). Soil $PO_4^-$-P was extracted from 5-g subsamples in a 1 mol/L $NaHCO_3$ solution shaken for one-half hour (Olsen and Sommers 1982). Kjeldahl N (Bremner and Mulvaney 1982) was determined by digestion procedure using a Technicon BD-40 digestor block. Kjeldahl N, extracted $NO_3^-$-N and $NH_4^+$-N, and extracted $PO_4^-$-P amounts were measured colorimetrically with a Technicon Autoanalyser II system (Technicon Industrial Methods Numbers 329-74W/B, March 1977; 158-71W/A, June 1977; 154-71W, February 1973; and 155-71W, January 1973 respectively; Technicon Industrial Systems, Tarrytown, New York).

Laboratory mineralization incubations were carried out using 25 g of soil placed in 75-mL plastic vials and incubated at 30°C for 28 d (Fisher et al. 1987). Moisture content was maintained at 0.1 g/g soil (approximately field capacity) by weekly adjustment. The bottles were covered with air-permeable polyethylene film to reduce water loss between moisture adjustments. Maximum water loss between adjustments was <10% of adjusted moisture contents. At the end of the incubation period, soils were mixed in the vials and an 8-g subsample was extracted and analyzed for $NO_3^-$-N and $NH_4^+$-N by the same procedure used in the field-soil analysis. Incubations were begun at the time of field-soil N determination and mineralization was calculated as the net change in inorganic N over the 28-d interval. Two replicate incubations were performed for each soil sample.

### *Growth, reproduction, and physiology*

Stem growth and leaf, flower, and fruit production were measured at several times over the 3-yr period of

TABLE 1. Extended.

| Soil pH | Total N (TKN) (mg/g) | Extractable $PO_4^-$-P ($\mu$g/g) |
|---|---|---|
| 8.05 ± 0.28 | 0.43 ± 0.07 | 3.33 ± 0.84 |
| 8.90 ± 0.14 | 0.40 ± 0.07 | 2.89 ± 1.14 |
| 8.88 ± 0.04 | ... | 2.42 ± 0.78 |
| 8.17 ± 0.22 | 0.53 ± 0.06 | 5.02 ± 0.61 |
| 8.90 ± 0.21 | 0.43 ± 0.04 | 3.17 ± 0.05 |
| 8.87 ± 0.03 | ... | 3.81 ± 1.09 |
| 8.69 ± 0.07 | 0.44 ± 0.13 | 6.00 ± 0.91 |
| 8.70 ± 0.05 | 0.44 ± 0.05 | 3.93 ± 1.16 |
| 8.45 ± 0.11 | ... | 2.91 ± 0.11 |
| 8.71 ± 0.09 | 0.39 ± 0.12 | 6.22 ± 0.07 |
| 8.70 ± 0.07 | 0.35 ± 0.08 | 2.11 ± 0.14 |
| 8.50 ± 0.05 | ... | 2.19 ± 0.69 |
| 7.11 ± 0.22 | 0.18 ± 0.02 | 3.33 ± 0.86 |
| 7.98 ± 0.35 | 0.18 ± 0.02 | 3.32 ± 0.65 |
| 8.02 ± 0.31 | ... | 2.41 ± 0.42 |
| 7.39 ± 0.48 | 0.23 ± 0.09 | 4.02 ± 0.88 |
| 8.18 ± 0.43 | 0.19 ± 0.02 | 2.87 ± 0.10 |
| 8.05 ± 0.35 | ... | 2.76 ± 0.30 |

the study: four times in 1991, four times in 1992, and 11 times in 1993. On each study plant at each site, three stems were tagged with colored yarn and marked with a permanent paint line or a wire band ~25–50 mm from the tip, so as to include ~10–20 nodes and secondary stems. The length of the primary stem was measured along with the number and total length of secondary stems (nodes). Total number of leaves and any flowers or fruits on the marked stems were recorded. Stem growth was summarized in two ways: first, as the elongation increment of the main stem per unit time, and second, as the increment of secondary stem length per number of nodes per unit time.

The marked stems were changed irregularly throughout the course of the study for several reasons. Some of the marked stems were damaged by herbivores or other factors. The colored markers also occasionally were removed by birds or weathering. Also, stems that elongated substantially during one interval were remarked closer to the tip, in order to keep the number of nodes and stem length roughly similar during each measurement interval. Thus, incremental growth and flower production were based on similarly sized, healthy stems among all plants.

Diurnal leaf gas exchange, including $CO_2$ assimilation ($A$) and transpiration ($E$) were measured using a LI 6200 portable photosynthesis system (LI-COR Incorporated, Lincoln, Nebraska) at several times each year. Measurements were made throughout the year for *Larrea* (evergreen) and from late spring through late summer for *Prosopis* (winter deciduous). Leaf gas exchange was measured every 1–2 h on two samples of each of 3–4 plants of each treatment and size class that were randomly selected for repeated measurements during that day. For *Larrea,* a sample consisted of a single apical branch segment with ~20–40 leaves; for *Prosopis,* the sample was a single bipinnate compound leaf (20–40 leaflets). Leaf samples were sealed into a sample cuvette, and gas exchange measurements were completed within 20 s. Measurements of shaded air temperature and humidity were taken at the start and finish of each measurement cycle. These measurements showed that air temperatures in the cuvette changed little during the measurement. Temperature and humidity values were calculated as the mean of the initial and final readings. Because of the small leaf size, low-to-moderate transpiration rates, and very short enclosure in the curette, we assumed that leaf temperature was equal to air temperature. Thus, the leaf-to-air vapor pressure gradient was obtained as the difference between ambient vapor pressure and saturation of the air. From the diurnal measurements, we estimated daily values of $A$ and $E$ ($A_d$ and $E_d$) by integrating (trapezoidal) from the first measurement to the last (~0830 to 1630 Mountain Daylight Time [MDT]), occasionally using linear extrapolation to estimate missing data points at the start or end of days. We calculated water use efficiency (WUE) as the ratio of $A_d$ to $E_d$.

Plant water status was determined on days of gas exchange measurements from predawn measurements of xylem pressure potential (using a pressure chamber) of one or two small terminal branches from the plants on which gas exchange measurements were made. Only one measurement was made on small plants to minimize plant damage.

### *Root growth*

When plots were established, three minirhizotron tubes with a viewing area 1.2 m in length were installed

TABLE 2. Average (± 1 SE) sizes (height and crown volume) of individual shrubs selected to represent "small" and "large" shrubs at the three study sites.

| Site | Shrub size class | *Larrea* | | *Prosopis* | |
|---|---|---|---|---|---|
| | | Height (m) | Crown volume ($m^3$) | Height (m) | Crown volume ($m^3$) |
| Upper bajada | small ($N$ = 16) | 0.36 ± 0.006 | 0.02 ± 0.006 | ... | ... |
| | large ($N$ = 16) | 1.32 ± 0.073 | 1.51 ± 0.26 | ... | ... |
| Lower bajada | small ($N$ = 24) | 0.50 ± 0.19 | 0.036 ± 0.032 | 0.63 ± 0.13 | 0.146 ± 0.085 |
| Dune | small ($N$ = 16) | ... | ... | 0.49 ± 0.06 | 0.079 ± 0.026 |
| | large ($N$ = 16) | ... | ... | 1.06 ± 0.13 | 2.598 ± 0.55 |

TABLE 3. Summary of experimental design, showing number of treatment and control plots for each island type (young, mature) of the two shrubs. Summer drought = 1 June–30 September; winter/spring drought = 1 October–31 May.

| Site | Treatment | Number of plots | | | |
|---|---|---|---|---|---|
| | | *Larrea* | | *Prosopis* | |
| | | Young | Mature | Young | Mature |
| Upper bajada | summer drought | 8 | 8 | ... | ... |
| | control | 8 | 8 | ... | ... |
| Lower bajada | summer drought | 8 | ... | 8 | ... |
| | winter drought | 8 | ... | 8 | ... |
| | control | 8 | ... | 8 | ... |
| Dune | summer drought | ... | ... | 8 | 8 |
| | control | ... | ... | 8 | 8 |

under each large shrub at the upper bajada (*Larrea*) and Dunes (*Prosopis*) sites. (Small shrubs were not included because we were concerned that installing minirhizotron tubes would cause damage to the plants.) The three tubes were spaced equidistantly around the plant with their tops even with the shrub canopy dripline. Each tube was installed at an angle ~30° from vertical, so that the buried portion tilted toward the center of the shrub. We assumed that the plant–soil system would equilibrate after several months (Rutherford 1983).

The tubes were divided into 12 10-cm horizontal segments by lines marked on the tubes, and had a vertical camera guideline oriented towards the center of the shrub. Because of the angle of the tubes, each of these segments represented ~9 cm of soil depth, for a total depth of ~108 cm. Videotapes documenting roots growing along the sides of each tube were recorded several times during the course of the study four times in 1991, six times in 1992, and ten times in 1993, at both sites. Recordings were made using a Bartz Technologies Model 1 minirhizotron camera on Super VHS videotapes (Bartz Technologies, Santa Barbara, California). The soil area visible in each frame recorded by this camera was 18 mm wide × 13 mm high. A small portable television was used in the field so that the camera operator could see the image being recorded. One recording per tube per date was made by inserting the camera into the tube until it reached the bottom, centering the image on the centering line, and slowly moving the camera up the tube along the line.

Data were collected from the videotapes in the laboratory using a computer-based image analysis system, consisting of a Toshiba SV-771 VCR and a Macintosh Quadra 650 computer with a RasterOps 24XLTV video digitizing board and a NEC 6FG 21-inch (53-cm) color monitor. The recorded "movies" or images for each tube were digitized, stored on magneto-optical disks, and viewed using RasterOps MediaGrabber software. Data were collected by simultaneously comparing images for the same tube taken on several (up to five) consecutive dates. By scrolling through these movie files frame by frame, the numbers of new roots, and of roots that died (disappeared), in each 10-cm segment of tube at each date could be accurately counted.

Since there was often no change in root numbers in some of the 10-cm segments of each tube at each date, root data were combined into three depth increments (0–36, 36–72, and 72–108 cm) instead of 12 for presentation and analyses. Root appearance and death rates in each depth increment of each tube were calculated by dividing the number of new roots appearing (or the number of roots that disappeared) in that increment between two successive measurement dates by the number of days between the two measurements.

We did not follow the life-span of individual roots or cohorts of roots, but we calculated a relatively conservative root life-span from the reciprocal of the relative root disappearance rate (turnover rate for number of fine roots):

$$\text{Mean root longevity} = 0.5(\text{Relative root disappearance rate}_t)^{-1}$$

where

$$\text{Relative root disappearance rate}_t = (\text{Disappearance rate}_t)/(\text{Total root number}_{t-1}).$$

### *Data analyses*

Data were analyzed separately for each site and seasonal drought periods in the study: i.e., June–October 1991, November 1991–May 1992, June–September 1992, October 1992–May 1993, and June–September 1993. All analyses were performed using Data Desk (Velleman 1995).

Soil moisture contents were analyzed using repeated measures analysis of variance (RM-ANOVA). We used univariate (nested) models for all RM-ANOVA analyses. For the lower bajada site, rainout treatment and species were used as main effects, with plots as the nested term (nested within the treatment × species interaction), and measurement depth and date as the repeated factors. For upper bajada and dune sites, having small and large shrubs, analogous models were used except that shrub size (young and mature islands) was used as a main effect instead of species.

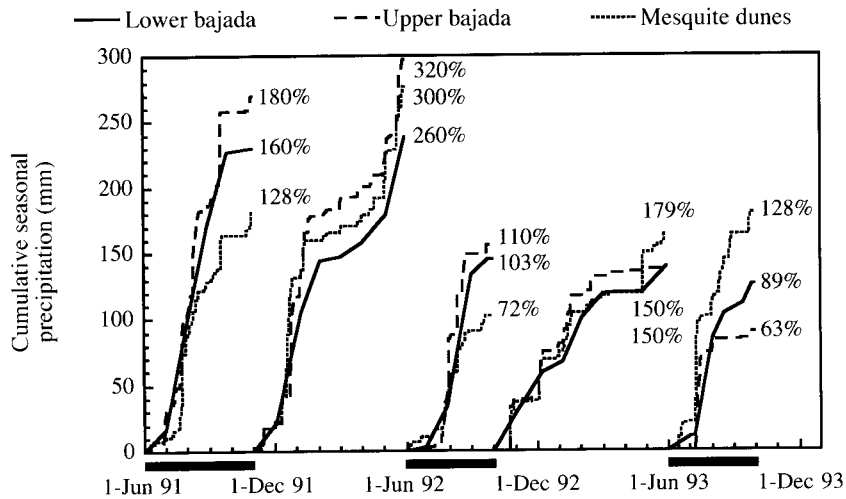



FIG. 2. Rainfall received at the three study sites during 1991–1993. Solid horizontal bars below the $x$ axis represent *summer* rainfall period (June–September); periods without bars represent winter/spring rainfall (October–May). The percentage of average seasonal rainfall amount is shown, based on records from the Jornada Experimental Range in southern New Mexico since 1915.

The effects of drought treatments on plant predawn xylem water potential, integrated $A_d$ and $E_d$, and stem growth were examined separately for each species at the lower bajada site. In cases where measurements were made on all plants (or on the same subset of plants) throughout the entire seasonal drought period, RM-ANOVA was used, with rainout treatment as the main effect, plant number nested within treatment, and date as the repeated factor. Otherwise, two-way ANOVA models were used with treatment and date as main effects. Similar analyses were made of data from the other two sites, except that island size was included as a main effect, either in RM-ANOVA models (with plant number nested within the treatment × island size interaction) or in three-way ANOVA models. Root appearance rates from the upper bajada and dunes sites were analyzed using RM-ANOVA models analogous to those used for soil moisture content data at these sites. We could not carry out an ANOVA to test for differences in root disappearance among treatments or depths, since the large number of zero values for samples invalidated the assumptions of normality.

For all analyses, histograms and normal probability plots were used to check for normal distributions of residuals. Scheffé-Box tests (Sokal and Rohlf 1981) were used to test for homogeneity of variances and arcsine or log transformations were made where appropriate. Subsequent comparisons of treatment means were made using the Scheffé test (Day and Quinn 1989). Also note that for any one season of the year, two comparisons are possible for determining the statistical significance of the drought treatments: the *current* drought treatment compared to controls and the *previous* drought treatment compared to controls. In the latter case, these are instances where we compare summer responses of shrubs following winter/spring drought or winter/spring responses of shrubs following summer drought; these are referred to as "postdrought" comparisons. Otherwise, statistically significant differences refer specifically to currently droughted shrubs/plots compared to control shrubs/plots.

## RESULTS

### *Rainfall and soil water*

The three summers (June–September) and two winter/spring periods were characterized by substantially different amounts of rainfall in successive years (Fig. 2). There were also several important differences in rainfall among the three sites. Summer rainfall in 1991 was 128–180% greater than average at the Jornada Basin, and the following winter/spring period (1991/1992) had 260–320% greater precipitation than normal based on records since 1915 at the Jornada Ranch Headquarters, located ~1 km from the lower bajada site (data from National Climatic Data Center, Asheville, North Carolina; see also Conley et al. 1992). The 1991/1992 winter/spring rainfall at upper bajada was greater than three times the standard deviation of Jornada Basin rainfall and exceeded by 90 mm the maximum recorded in 1941. Summer rainfall in 1992 was normal at the two bajada sites, but only 72% of normal at the dunes. The following winter/spring (1992/93) rainfall was 150–179% greater than normal. Summer rainfall of 1993 was substantially different among the sites, varying from 63% of normal at the upper bajada to 128% at the dunes. The differences were primarily the result of differences in August rainfall, since all sites had low (near normal) June rainfall, abundant (above normal) July rainfall, and low (below normal) September rainfall.

The seasonal patterns of soil water content for re-

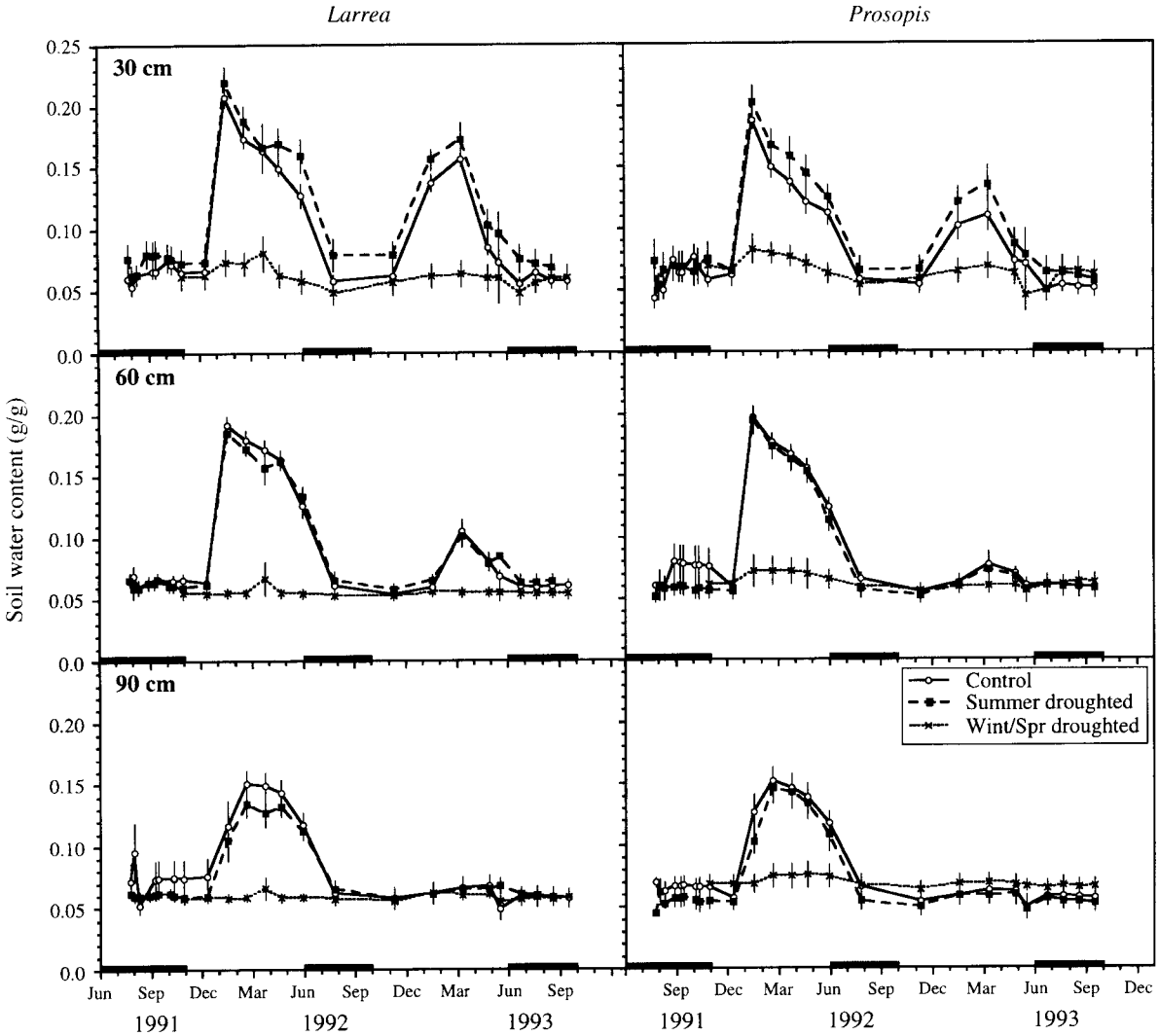



FIG. 3. Soil water content for young resource islands (only) at the lower bajada site (*Larrea* and *Prosopis*). Solid bars are as in Fig. 2.

source islands at the lower and upper bajada sites were similar (Figs. 3 and 4, respectively). At the lower bajada, where there are only young islands, the pattern of seasonal soil water content of the control and summer treatment plots was not significantly different for either species (see Appendix A for summary of statistical tests). In contrast, the winter/spring rainout shelters at the lower bajada had a major impact on soil water content. There were significant differences in recharge of the control and winter-drought treatment plots during the first (1991/1992) winter/spring period at all depths for both species (Fig. 3); during the second winter/spring (1992/1993), this was true only at 30 and 60 cm depths. At the upper bajada, there was a small amount of soil water recharge at 30 cm in summer in undroughted plots of both young and mature islands, resulting in significant differences between drought and control plots at this depth during all three summers (Fig. 4, Appendix A). Winter/spring soil water recharge was substantial at all depths in the first winter/spring (much more than normal precipitation) and at the upper two depths in the second winter/spring (more than normal precipitation) (Fig. 4). There were no significant differences between young and mature islands (there was no winter/spring drought treatment at the upper bajada).

Soil water dynamics at the dune site were different from the bajada sites. There was a highly significant effect of summer drought, and there were some differences in the patterns of soil water content between the young and mature islands (Fig. 5). In the young islands, there was a significant difference in soil water content (controls vs. summer drought) at all depths during 1991 and 1993 summers, but not in 1992; in the mature islands, there was a significant difference only at 30 cm depth in the summer of 1991. Young

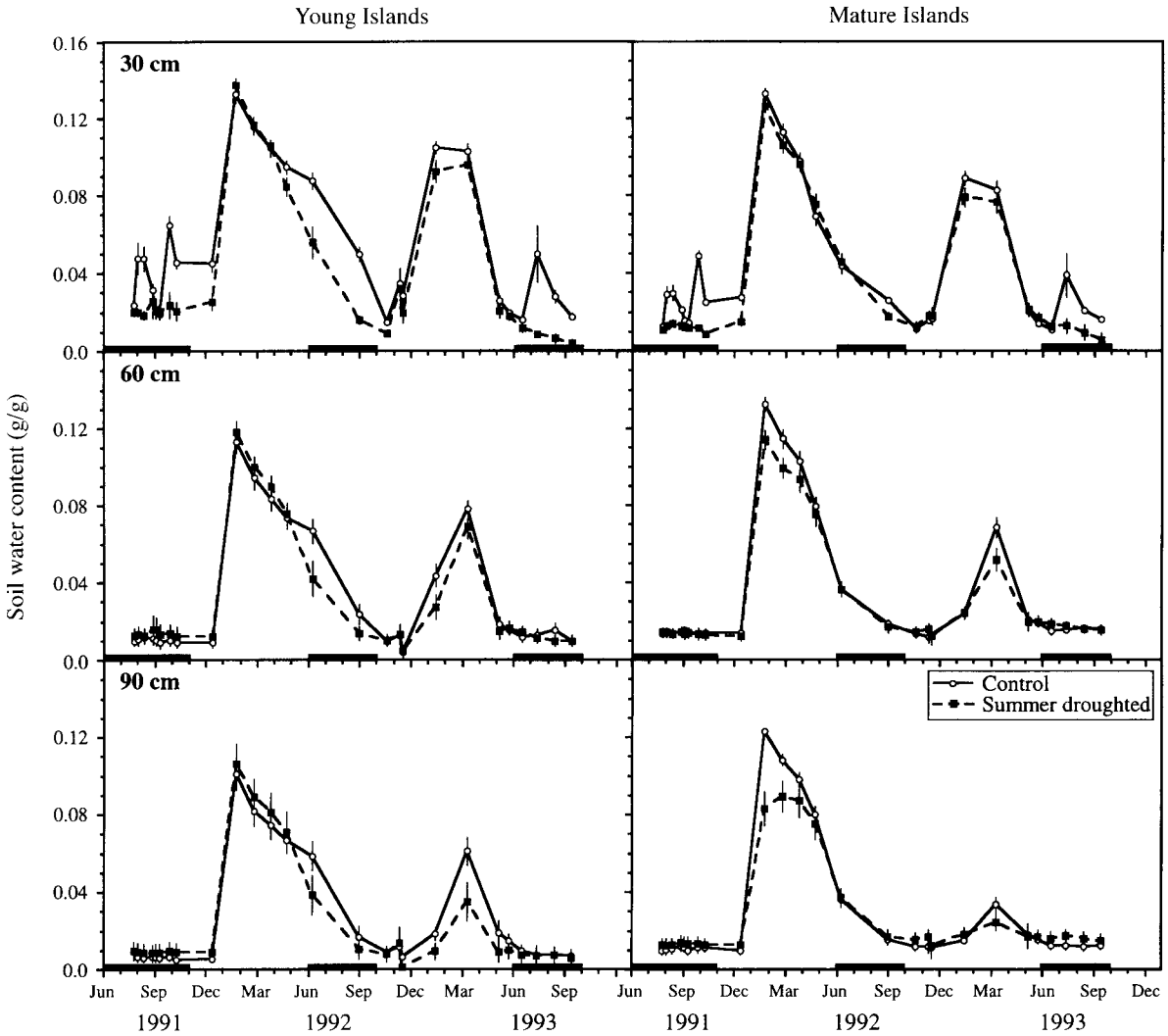



FIG. 4. Soil water content for young and mature resource islands at the upper bajada site (*Larrea* only). Solid bars are as in Fig. 2.

*Prosopis* islands had greater soil water content at 60 cm during summer than mature ones.

### *Soil nutrient dynamics*

Results of different N analyses revealed similar temporal patterns at different soil depths as well as between soils under and outside the canopy. We therefore provide details on results of soil N attributes at the 10 cm depth for soil outside of the canopy dripline (for which we had the greatest amount of data), and results with respect to depth and location (under vs. outside of canopy dripline) (see Tables 1, 4, and 5).

Results for extractable N ($N_{ext}$, i.e., $NO_3^-$ and $NH_4^+$) revealed that soils of resource islands "droughted" (i.e., experiencing drought) during summer often had relatively greater amounts of $N_{ext}$ at the end of summer than controls (Fig. 6). This response was due to similar patterns for $NO_3^-$ and $NH_4^+$, with $NH_4^+$ being somewhat more variable than $NO_3^-$ (data not shown). Differences in $N_{ext}$ observed at the end of the summer generally diminished by the end of the following "undroughted" winter/spring (Fig. 6). At the lower bajada, winter/spring drought did not generally result in differences in $N_{ext}$ (Fig. 6). There was much greater variation in $N_{ext}$ from soils under the canopy relative to that outside the canopy (for measurements at any one time and across all measurement times; data not shown). Because of this high variability, we observed no statistically significant differences between islands or treatment with respect to beneath-canopy nutrient attributes (data not shown; but see results for $N_{TKN}$ below).

Nitrogen mineralization ($N_{min}$) potentials varied with time of measurement, but were not generally affected by drought (Fig. 6). Average $N_{min}$ potentials measured at any one time were similar across all *Larrea* islands from both lower and upper bajadas. $N_{min}$ differences

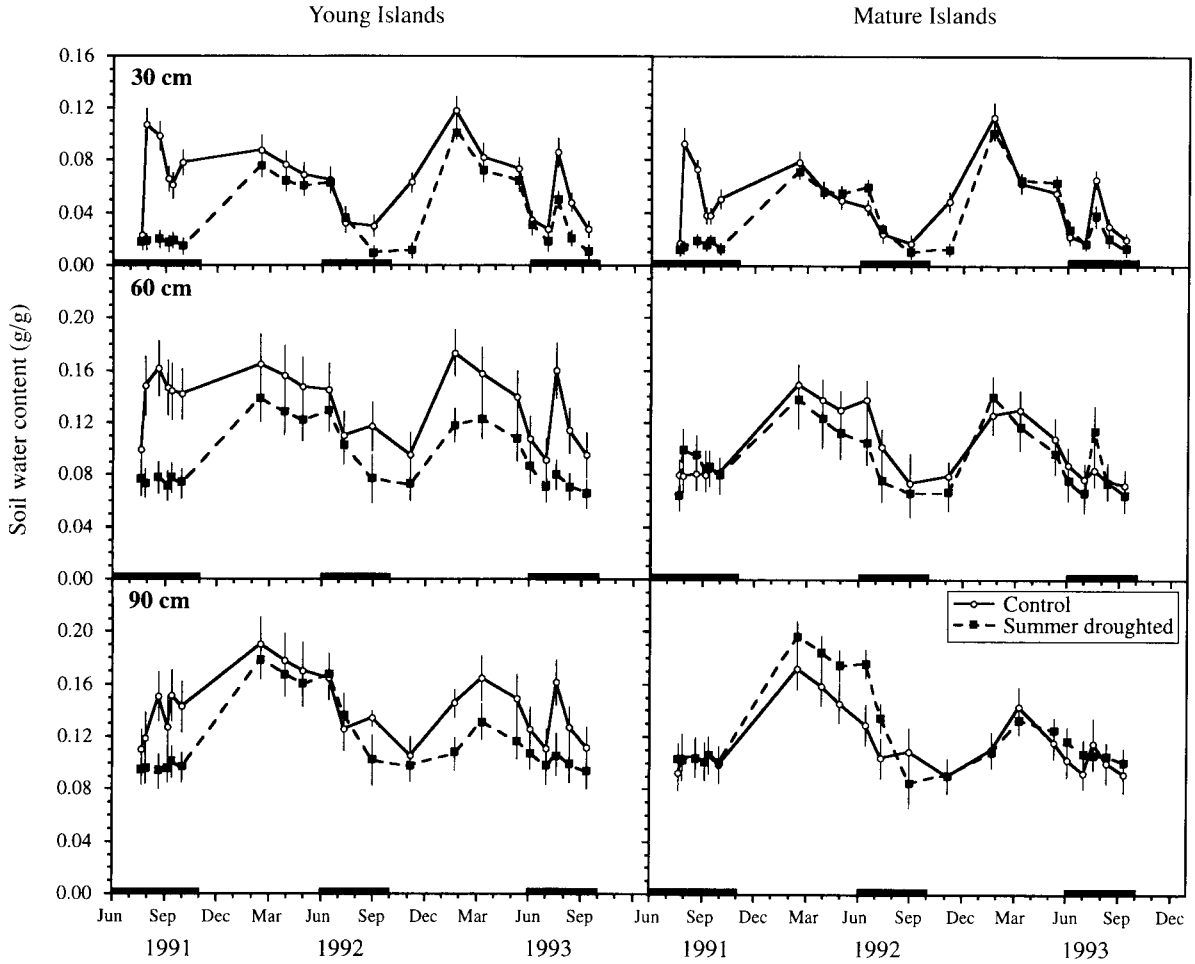



FIG. 5. Soil water content for young and mature resource islands at the dune site (*Prosopis* only). Solid bars are as in Fig. 2.

TABLE 4. Values (μg/g soil) of total extractable N ($N_{ext}$ = $NO_3^-$ and $NH_4^+$), extractable $NO_3^-$-N, and N mineralization ($N_{min}$) potentials at the lower bajada site.

| Species | Soil nutrients | Young resource islands | | | | | |
|---|---|---|---|---|---|---|---|
| | | June | | | October | | |
| | | Control | Summer drought† | Winter drought‡ | Control | Summer drought† | Winter drought‡ |
| *Larrea* | $N_{ext}$ | $3.02^{a} \pm 1.25$ | $3.63^{a} \pm 2.18$ | $3.09^{a} \pm 1.22$ | $4.18^{a} \pm 4.30$ | $8.67^{b} \pm 8.64$ | $5.08^{a} \pm 4.28$ |
| | $NO_3^-$-N | $2.44^{a} \pm 1.19$ | $3.44^{a} \pm 2.72$ | $2.34^{a} \pm 1.24$ | $3.61^{a} \pm 4.33$ | $7.19^{b} \pm 7.46$ | $4.55^{ab} \pm 4.29$ |
| | $N_{min}$ potentials | $7.44^{a} \pm 4.32$ | $6.75^{a} \pm 4.98$ | $7.76^{a} \pm 5.97$ | $5.85^{a} \pm 2.57$ | $7.12^{a} \pm 6.49$ | $6.19^{a} \pm 4.21$ |
| | Ratio of $NO_3^-$ | $2.48 \pm 2.09$ | $2.42 \pm 1.30$ | $1.35 \pm 0.86$ | $0.99 \pm 1.09$ | $0.23 \pm 0.17$ | $0.41 \pm 0.22$ |
| *Prosopis* | $N_{ext}$ | $4.66^{ab} \pm 3.25$ | $3.55^{a} \pm 1.92$ | $2.82^{a} \pm 1.40$ | $4.32^{ab} \pm 4.41$ | $5.65^{b} \pm 3.93$ | $3.34^{a} \pm 2.83$ |
| | $NO_3^-$-N | $4.17^{b} \pm 3.32$ | $3.21^{ab} \pm 1.98$ | $2.24^{a} \pm 1.34$ | $3.99^{ab} \pm 4.38$ | $5.35^{b} \pm 3.99$ | $3.05^{ab} \pm 2.98$ |
| | $N_{min}$ potentials | $7.16^{a} \pm 5.84$ | $8.60^{b} \pm 4.79$ | $5.31^{a} \pm 2.44$ | $6.52^{ab} \pm 3.76$ | $6.46^{ab} \pm 3.68$ | $5.33^{a} \pm 2.82$ |
| | Ratio of $NO_3^-$ | $2.71 \pm 0.85$ | $5.61 \pm 4.20$ | $4.74 \pm 4.80$ | $0.46 \pm 0.21$ | $0.85 \pm 0.62$ | $1.36 \pm 0.97$ |

*Note:* Values are means (± 1 SD) over the three years of the study (1991–1993) taken at 10 cm depth, outside the canopy dripline. The sampling dates represent two critical times: June (immediately following the winter/spring season and at the beginning of the summer season) and October (immediately following the summer season and at the beginning of the winter/spring season). Values having different letters within a row are statistically different ($P < 0.05$). Also shown is the ratio of $NO_3^-$-N (unitless) for values measured under the shrub canopy to outside of the canopy dripline in June and October 1992.

† October–June.

‡ June–October.

between times were not generally significantly different; thus we report mean values over the 3-yr period for treatments vs. controls; values varied from 5.70 to 8.11 μg/g total (mean ± 1 SE, 6.78 ± 0.73 μg/g) (see Tables 4 and 5). Similar values were found for young *Prosopis* islands at the lower bajada (6.56 ± 1.23 μg/g), whereas $N_{min}$ potentials were significantly ($P < 0.01$) lower for the young and mature *Prosopis* islands at the dunes site (2.60 ± 0.60 μg/g) (Table 4). These low values are consistent with the relatively lower values of $N_{ext}$ in *Prosopis* resource islands (Tables 4 and 5, Fig. 6).

Total soil nitrogen ($N_{TKN}$; Kjeldahl N) did not vary significantly over time, nor with drought (data not shown). Therefore, we report only one set of representative values, taken during the middle of the study (June 1992; Table 1). There were also no significant differences between resource islands at the upper and lower bajadas, regardless of age (young vs. mature) or shrub species. However, these values were significantly higher than $N_{TKN}$ for both the young and mature *Prosopis* islands at the dune site. An examination of $NO_3^-$-N ratios (under vs. outside the canopy) suggest that the mature *Prosopis* islands have greater $NO_3^-$-N under the shrubs than outside, relative to young islands; no clear pattern exists for the *Larrea* islands (Table 5).

Total extractable $PO_4^-$-P in soils varied little with time or drought. The amount of $PO_4$ in the soils is summarized in Table 1. There was a significantly greater amount of $PO_4$ in the top soil layer for both *Larrea* and *Prosopis* islands at the lower bajada.

### *Species responses to drought: lower bajada* (Larrea *and* Prosopis)

The responses of the two shrub species to drought at the lower bajada site, measured in terms of xylem water potentials, photosynthesis, transpiration, and stem growth, are shown in Fig. 7. Statistically significant differences indicated in the text are based on the results of the nested ANOVA (Appendices B and C) or on the results of Scheffé tests comparing individual means (not shown). A summary of differences for both the season (summer or winter/spring) during the application of the drought and for the season immediately following drought (a postdrought response) are given in Table 6.

*Xylem water potential (XWP).*—The effects of drought on xylem water potentials varied with season, year, and species (Fig. 7). During summer 1991 (more than normal rainfall, see Fig. 2), drought resulted in lower XWP (compared to controls) in both species. This difference was eliminated following release from drought the following winter/spring (measured in late spring in *Prosopis*). However, during the second (1992) and third (1993) summers (normal and slightly below normal rainfall), drought had no significant impact on XWP in either species. During the first winter/spring period (1991/1992) (much more than normal rainfall) drought resulted in decreased XWP (compared to control plants) during the winter/spring period in both species (measured in late spring in *Prosopis*). This difference was eliminated in *Larrea* following abundant summer 1992 rainfall, while in *Prosopis,* release from winter/spring drought resulted in XWPs that were significantly higher in the previously droughted plants compared to controls (Table 6, Fig. 7). During the second winter/spring period (much more than normal rainfall) drought reduced XWP in *Larrea* but not *Prosopis.* Release from winter/spring drought in the summer resulted in higher XWP between previously droughted plants, and controls in both *Larrea* and *Prosopis.*

*Daily integrated photosynthesis ($A_d$).*—$A_d$ was measured throughout the year in *Larrea,* but only during the summer for *Prosopis* (a winter-deciduous species) (Fig. 7). During the first summer, $A_d$ was relatively high and significantly reduced by summer drought in both species (Table 6). For *Larrea* in the following winter/spring, $A_d$ was similar in controls and summer droughted plants, but greatly reduced in winter/spring-droughted ones. During the following summer $A_d$ was relatively low in both species, compared to the first summer (or spring periods in *Larrea*) and unaffected by summer drought. The second winter/spring revealed a pattern in $A_d$ for *Larrea* similar to the previous winter/spring, in which there was again a significant reduction for winter/spring droughted plants. During the last summer there was no significant effect of current drought on $A_d$ in either species, but in *Prosopis,* plants were observed to have a postdrought response of $A_d$ in which previously droughted (winter/spring) shrubs had a higher $A_d$ than currently droughted ones at the end of the summer (Table 6).

*Daily integrated transpiration ($E_d$) and WUE.*—$E_d$ was measured concurrently with $A_d$ in both species (Fig. 7). The pattern of $E_d$ and the impact of drought was similar to that of $A_d$. The first summer $E_d$ was relatively high in both species; however, it was not affected by summer drought. During the second and third summers, $E_d$ was lower than during the first summer and there was no significant effect of summer drought. In *Prosopis* there was a significant postdrought effect in which winter/spring droughted shrubs had significantly higher $E_d$ than the summer droughted ones (Table 6). In *Larrea,* $E_d$ was low during the first half of both winter/spring periods and increased during the latter part, during which time winter/spring drought resulted in a significantly lower rate of $E_d$ in comparison to controls. The only impact of drought on WUE was on *Larrea* during the first season, in which summer drought significantly reduced WUE (Table 6).

*Stem growth.*—The two species differed in seasonal pattern and response to drought. Stem growth in *Larrea* tended to be high in spring and/or summer and was not significantly impacted by summer drought (although growth of droughted shrubs was considerably less than controls during the first summer) (Fig. 7, Table 6).

TABLE 5. Values (μg/g soil) of total extractable N ($N_{ext}$ = $NO_3^-$ and $NH_4^+$), extractable $NO_3$ -N, and N mineralization ($N_{min}$) potentials at the upper bajada and dune sites.

| Site | Soil nutrient | Young resource islands | | | |
|---|---|---|---|---|---|
| | | June | | October | |
| | | Control | Summer drought† | Control | Summer drought† |
| Upper bajada (*Larrea*) | $N_{ext}$ | $1.53^{a} \pm 1.00$ | $1.79^{a} \pm 0.83$ | $1.28^{a} \pm 1.19$ | $3.54^{b} \pm 2.70$ |
| | $NO_3^-$-N | $1.03^{a} \pm 0.84$ | $1.22^{a} \pm 0.76$ | $0.63^{a} \pm 1.05$ | $3.00^{b} \pm 2.57$ |
| | $N_{min}$ potentials | $6.72^{ab} \pm 2.88$ | $5.70^{a} \pm 2.83$ | $6.16^{a} \pm 3.86$ | $6.44^{a} \pm 2.58$ |
| | Ratio $NO_3^-$ | $1.91 \pm 1.24$ | $1.51 \pm 0.80$ | $1.62 \pm 0.91$ | $3.32 \pm 1.44$ |
| Dunes (*Prosopis*) | $N_{ext}$ | $1.08^{a} \pm 0.62$ | $1.23^{a} \pm 0.64$ | $1.67^{b} \pm 0.94$ | $2.38^{bc} \pm 1.26$ |
| | $NO_3^-$-N | $0.92^{bc} \pm 0.75$ | $0.97^{bc} \pm 0.55$ | $0.99^{bc} \pm 0.98$ | $1.54^{d} \pm 1.04$ |
| | $N_{min}$ potentials | $2.83^{ab} \pm 2.41$ | $2.20^{ab} \pm 0.78$ | $3.51^{b} \pm 3.87$ | $2.58^{ab} \pm 1.23$ |
| | Ratio $NO_3^-$ | $1.40 \pm 0.90$ | $1.61 \pm 1.35$ | $2.70 \pm 1.53$ | $1.30 \pm 1.27$ |

*Note:* Values are averages (± 1 SD) over the three years of the study (1991–1993) taken at 10 cm depth, outside the canopy dripline. The sampling dates represent two critical times: June (immediately following the winter/spring season and at the beginning of the summer season) and October (immediately following the summer season and at the beginning of the winter/spring season). Values having different letters within a row are statistically different ($P < 0.05$). Also shown is the ratio of $NO_3^-$-N (unitless) for values measured under the shrub canopy to outside of the canopy dripline in June and October 1992.
† June–October.

Growth was significantly reduced during the first winter/spring period by drought but not during the second winter/spring period. There was also a postdrought effect in the last summer where previously winter/spring droughted shrubs had higher growth compared to controls (Table 6). Stem growth in *Prosopis* was measured only when leaves were present in late spring and summer (and was not reported for the first year due to problems with predation and loss of stem markings). Stem growth was greatest during the late spring period, coinciding with production of new leaves. Growth at this time was unaffected by current (winter/spring) drought. Summer growth was relatively low compared to spring, and was unaffected by summer drought or previous winter/spring drought.

*Postdrought responses.*—Since both winter/spring and summer drought treatments were carried out at this site, we could examine postdrought responses in measured variables for the winter/spring period following summer drought and for the summer period following winter/spring drought. These results are summarized in Table 6. The only postdrought response for *Larrea* was in stem growth during the summers following winter/spring rain: a decrease in 1992 and an increase in 1993 (see Table 6). On the other hand, *Prosopis* had postdrought responses in several physiological variables (XWP, $E_d$, and $A_d$) following both winter/spring drought periods (Table 6).

### *Shrub size response to drought: upper bajada* (Larrea)

The physiological and growth responses of the large and small *Larrea* shrubs at the upper bajada are shown in Fig. 8. Statistically significant differences indicated in the text are based on the results of the nested ANOVA (Appendices D and F) or on the results of a Scheffé test comparing individual means (not shown). These are summarized for both the season of the drought treatment (summer only) and for the winter/spring immediately following drought (postdrought response) in Table 7.

*Xylem water potentials (XWP).*—In the first summer (wettest, 1991; see Fig. 2), XWPs in *Larrea* were similar between shrub sizes and were significantly reduced by summer drought (Fig. 8). The following winter/spring (1991/1992, much more than average rainfall) there were significant differences in XWPs between the size classes (smaller shrubs > large shrubs), but with no effect of previous summer drought. The second summer (1992, average rainfall) there was a significant effect of drought and shrub size, and a significant interaction between drought and size, reflecting the fact that summer drought significantly reduced XWPs of only the small shrubs (Table 7). The second winter/spring (1992/1993, much more than normal rainfall) there was no difference in XWP between size classes, and no significant effect of drought. During summer 1993, there was a significant interaction between treatment and size class, with small shrubs having significantly reduced XWP (Table 7).

*Daily integrated photosynthesis ($A_d$).*—$A_d$ during the first summer was not significantly different between size classes, but was significantly reduced by summer drought (Fig. 8, Table 7). During the next three seasons, winter/spring (1991/1992), summer (1992), and winter/spring (1992/1993), patterns of $A_d$ were similar between shrub size classes and between summer-droughted and nondroughted controls. During the final summer (1993), $A_d$ was significantly reduced in all summer-droughted shrubs.

*Daily integrated transpiration ($E_d$) and WUE.*—The overall pattern of $E_d$ was similar to $A_d$ (Fig. 8). There were no differences between size classes or droughted and control shrubs during the first summer. During the following winter/spring, small shrubs differed from large ones, mainly due to greater $E_d$ for the small plants

TABLE 5. Extended.

| Mature resource islands | | | |
|---|---|---|---|
| June | | October | |
| Control | Summer drought† | Control | Summer drought† |
| 1.48[a] ± 0.63 | 1.68[a] ± 0.65 | 1.17[a] ± 0.43 | 3.03[b] ± 1.51 |
| 0.99[a] ± 0.41 | 1.16[a] ± 0.59 | 0.63[a] ± 0.35 | 2.94[b] ± 2.09 |
| 7.14[ab] ± 3.22 | 8.11[b] ± 3.89 | 6.20[a] ± 2.66 | 7.36[ab] ± 4.35 |
| 0.87 ± 0.68 | 1.06 ± 0.87 | 3.89 ± 2.04 | 0.78 ± 0.73 |
| 0.87[a] ± 0.43 | 1.62[b] ± 0.65 | 1.23[a] ± 0.64 | 3.01[c] ± 1.99 |
| 0.69[ab] ± 0.54 | 1.09[cd] ± 0.62 | 0.77[ab] ± 0.61 | 1.94[d] ± 1.61 |
| 2.38[ab] ± 0.71 | 2.41[ab] ± 1.52 | 1.61[a] ± 0.88 | 3.26[ab] ± 2.03 |
| 3.91 ± 3.36 | 3.25 ± 2.90 | 4.83 ± 5.87 | 2.18 ± 1.75 |

on the final measurement date (3 June 1992). In the second summer, there was an interaction between treatment and size class, whereby small shrubs were significantly affected by drought (Table 7). We found a significant difference in $E_d$ between shrub size classes (small > large) during the second winter/spring period. During summer of 1993 there was a significant effect of drought on transpiration and a significant interaction between size and drought treatment, such that $E_d$ was reduced in the small shrubs (Table 7). WUE significantly decreased in *Larrea* during the first season for both size classes (Table 7).

*Stem growth.*—Growth of stems during the first summer was similar between size classes and significantly reduced by drought (Fig. 8, Table 7). During the following winter/spring (1991/1992) stem growth varied greatly through time, with very low values at the first sample date (7 December 1991) and greater values thereafter (including the 1 July 1992 sample date, which was included as part of the winter/spring period since there was no June rainfall). There were no further measurements of stem growth during summer 1992 and only one during the first half (winter) of the following winter/spring period. During summer 1993, there was a significant interaction between shrub size class and drought treatment: the small, control shrubs had much greater stem growth than droughted ones (Fig. 8).

*Root growth.*—Root growth was estimated as a rate of appearance of new roots (large shrubs only, see *Methods*). Growth during the first summer (1991) varied with depth (upper > lower) and was significantly reduced by drought at the upper two depths (see Fig. 9, Table 8). Root growth for *Larrea* during the following winter/spring period was variable through time with a period of relatively low growth during winter (November–January), especially at the lower two depths, followed by a significant increase during late spring (May–June). During the winter, root growth of droughted shrubs at all three depths was not changed from the low rates of the previous summer and remained significantly less than controls (Fig. 9).

Root growth increased during late spring (May–June) relative to winter, and there was a treatment × time interaction, i.e., the droughted plants grew more than the controls at the upper two depths (Table 8). Root growth during late summer 1992 (August) declined from the late spring peak at all depths and in both droughted and control plants. Growth was greatest at the upper depth and was significantly reduced by drought at the upper two depths. During the second winter/spring, the pattern of growth was similar to the previous winter/spring: low rates during the winter, followed by a pronounced increase in spring, with previously droughted shrubs having greater rates than nondroughted shrubs at the upper two depths (Table 8). During the final summer (1993), drought significantly reduced growth rates at the upper depth only, and rates for control plants were significantly greater at the upper depth compared to the lower two depths (Fig. 9).

*Root death.*—We estimated root death by the disappearance of roots. Root death in *Larrea* was high during the first summer and early winter/spring period, during which equilibration (soil compacting around the viewing tubes) was apparently occurring (Fig. 9). Recall that we could not test for differences in root death among treatments or depths because of the large number of zero values; see *Methods*.) Thereafter, root death was obvious only during late spring/early summer of each year and only in the upper layer. Maximal root death rates, following this equilibration period, were <0.1 roots/d.

### *Shrub size responses to drought: dunes* (Prosopis)

The physiological and growth responses of large and small *Prosopis* shrubs to summer drought are shown in Fig. 10. Statistically significant differences indicated in the text are based on the results of the nested ANOVA (Appendices E and F) or on the results of a Sheffé tests comparing individual means (not shown). These data are summarized for both the season of the drought treatment (summer only) and for the winter/spring immediately following drought (postdrought response) in Table 7.

*Xylem water potentials (XWP).*—Xylem water potentials during the first summer (1991, 28% above normal rainfall, see Fig. 2) were significantly lower in large shrubs than in small ones, and were significantly reduced in both size classes under summer drought (Fig. 10, Table 7). XWPs were not followed during winter. In the second summer (1992, 28% below normal rainfall) there were no effects due to drought and to shrub size. The third summer (1993, again 28% above normal rainfall) summer droughted small and large shrubs had lower XWPs than the controls.

*Daily integrated photosynthesis ($A_d$).*—During summer 1991, $A_d$ was not significantly different between shrub size classes, but was significantly reduced by summer drought (Fig. 10, Table 7). During the following summer there was no effect of summer drought. However, large shrubs had significantly lower rates of $A_d$ than small ones. In summer of 1993, $A_d$ was again

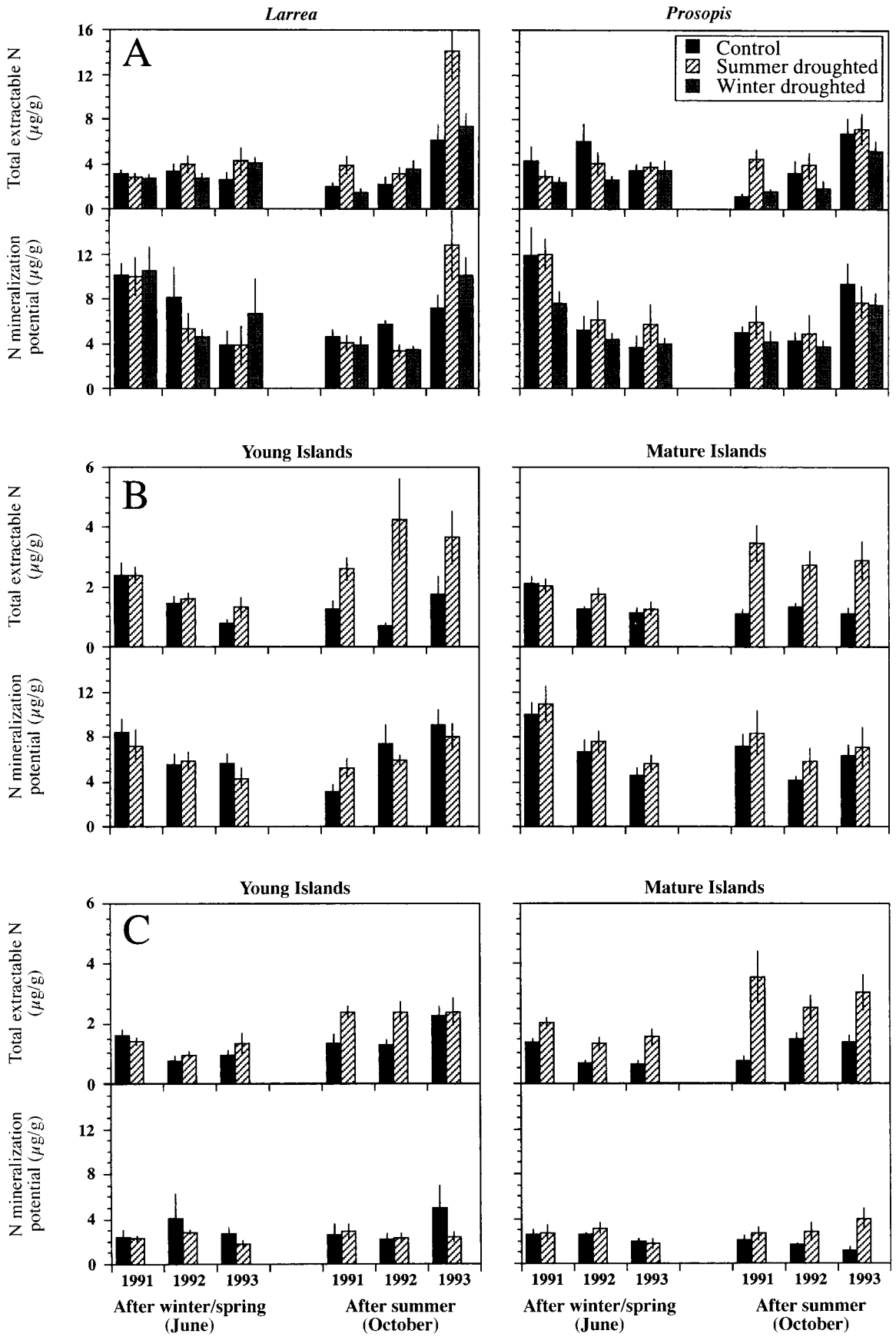

Larrea
Prosopis
A
Control
Summer droughted
Winter droughted
Total extractable N (μg/g)
N mineralization potential (μg/g)
Young Islands
Mature Islands
B
C
1991
1992
1993
After winter/spring (June)
After summer (October)

TABLE 5. Extended.

| Mature resource islands | | | |
|---|---|---|---|
| June | | October | |
| Control | Summer drought† | Control | Summer drought† |
| $1.48^{a} \pm 0.63$ | $1.68^{a} \pm 0.65$ | $1.17^{a} \pm 0.43$ | $3.03^{b} \pm 1.51$ |
| $0.99^{a} \pm 0.41$ | $1.16^{a} \pm 0.59$ | $0.63^{a} \pm 0.35$ | $2.94^{b} \pm 2.09$ |
| $7.14^{ab} \pm 3.22$ | $8.11^{b} \pm 3.89$ | $6.20^{a} \pm 2.66$ | $7.36^{ab} \pm 4.35$ |
| $0.87 \pm 0.68$ | $1.06 \pm 0.87$ | $3.89 \pm 2.04$ | $0.78 \pm 0.73$ |
| $0.87^{a} \pm 0.43$ | $1.62^{b} \pm 0.65$ | $1.23^{a} \pm 0.64$ | $3.01^{c} \pm 1.99$ |
| $0.69^{ab} \pm 0.54$ | $1.09^{cd} \pm 0.62$ | $0.77^{ab} \pm 0.61$ | $1.94^{d} \pm 1.61$ |
| $2.38^{ab} \pm 0.71$ | $2.41^{ab} \pm 1.52$ | $1.61^{a} \pm 0.88$ | $3.26^{ab} \pm 2.03$ |
| $3.91 \pm 3.36$ | $3.25 \pm 2.90$ | $4.83 \pm 5.87$ | $2.18 \pm 1.75$ |

on the final measurement date (3 June 1992). In the second summer, there was an interaction between treatment and size class, whereby small shrubs were significantly affected by drought (Table 7). We found a significant difference in $E_d$ between shrub size classes (small > large) during the second winter/spring period. During summer of 1993 there was a significant effect of drought on transpiration and a significant interaction between size and drought treatment, such that $E_d$ was reduced in the small shrubs (Table 7). WUE significantly decreased in *Larrea* during the first season for both size classes (Table 7).

*Stem growth.*—Growth of stems during the first summer was similar between size classes and significantly reduced by drought (Fig. 8, Table 7). During the following winter/spring (1991/1992) stem growth varied greatly through time, with very low values at the first sample date (7 December 1991) and greater values thereafter (including the 1 July 1992 sample date, which was included as part of the winter/spring period since there was no June rainfall). There were no further measurements of stem growth during summer 1992 and only one during the first half (winter) of the following winter/spring period. During summer 1993, there was a significant interaction between shrub size class and drought treatment: the small, control shrubs had much greater stem growth than droughted ones (Fig. 8).

*Root growth.*—Root growth was estimated as a rate of appearance of new roots (large shrubs only, see *Methods*). Growth during the first summer (1991) varied with depth (upper > lower) and was significantly reduced by drought at the upper two depths (see Fig. 9, Table 8). Root growth for *Larrea* during the following winter/spring period was variable through time with a period of relatively low growth during winter (November–January), especially at the lower two depths, followed by a significant increase during late spring (May–June). During the winter, root growth of droughted shrubs at all three depths was not changed from the low rates of the previous summer and remained significantly less than controls (Fig. 9).

Root growth increased during late spring (May–June) relative to winter, and there was a treatment × time interaction, i.e., the droughted plants grew more than the controls at the upper two depths (Table 8). Root growth during late summer 1992 (August) declined from the late spring peak at all depths and in both droughted and control plants. Growth was greatest at the upper depth and was significantly reduced by drought at the upper two depths. During the second winter/spring, the pattern of growth was similar to the previous winter/spring: low rates during the winter, followed by a pronounced increase in spring, with previously droughted shrubs having greater rates than nondroughted shrubs at the upper two depths (Table 8). During the final summer (1993), drought significantly reduced growth rates at the upper depth only, and rates for control plants were significantly greater at the upper depth compared to the lower two depths (Fig. 9).

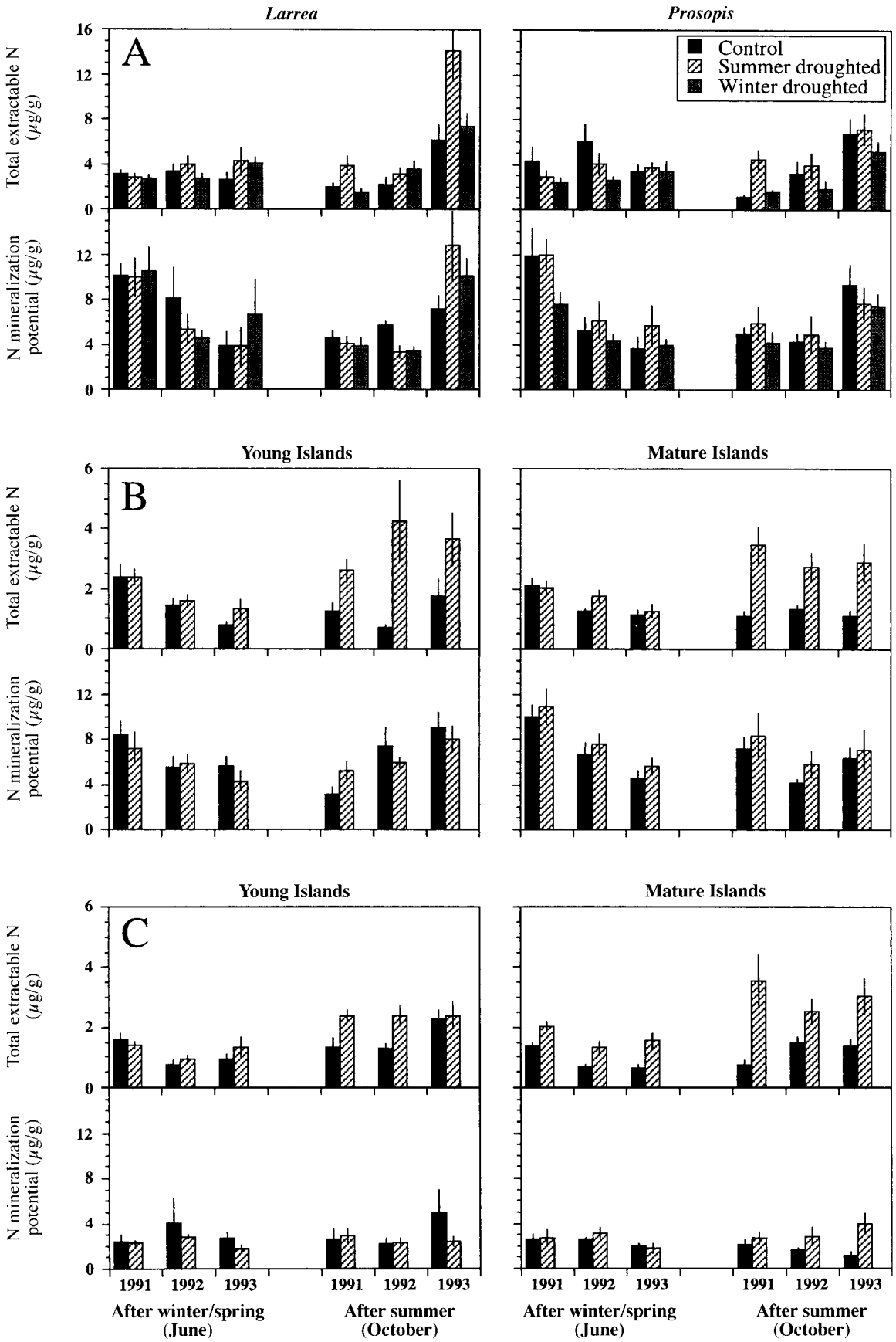
*Root death.*—We estimated root death by the disappearance of roots. Root death in *Larrea* was high during the first summer and early winter/spring period, during which equilibration (soil compacting around the viewing tubes) was apparently occurring (Fig. 9). Recall that we could not test for differences in root death among treatments or depths because of the large number of zero values; see *Methods*.) Thereafter, root death was obvious only during late spring/early summer of each year and only in the upper layer. Maximal root death rates, following this equilibration period, were <0.1 roots/d.

### *Shrub size responses to drought: dunes* (Prosopis)

The physiological and growth responses of large and small *Prosopis* shrubs to summer drought are shown in Fig. 10. Statistically significant differences indicated in the text are based on the results of the nested ANOVA (Appendices E and F) or on the results of a Sheffé tests comparing individual means (not shown). These data are summarized for both the season of the drought treatment (summer only) and for the winter/spring immediately following drought (postdrought response) in Table 7.

*Xylem water potentials (XWP).*—Xylem water potentials during the first summer (1991, 28% above normal rainfall, see Fig. 2) were significantly lower in large shrubs than in small ones, and were significantly reduced in both size classes under summer drought (Fig. 10, Table 7). XWPs were not followed during winter. In the second summer (1992, 28% below normal rainfall) there were no effects due to drought and to shrub size. The third summer (1993, again 28% above normal rainfall) summer droughted small and large shrubs had lower XWPs than the controls.

*Daily integrated photosynthesis ($A_d$).*—During summer 1991, $A_d$ was not significantly different between shrub size classes, but was significantly reduced by summer drought (Fig. 10, Table 7). During the following summer there was no effect of summer drought. However, large shrubs had significantly lower rates of $A_d$ than small ones. In summer of 1993, $A_d$ was again


Larrea
Prosopis
A
Control
Summer droughted
Winter droughted
Total extractable N (μg/g)
N mineralization potential (μg/g)
Young Islands
Mature Islands
B
C
1991
1992
1993
After winter/spring (June)
After summer (October)

significantly reduced by summer drought, although the effect was more pronounced in the smaller shrubs.

*Daily integrated transpiration ($E_d$) and WUE.*—There were differences in $E_d$ between shrub size classes and drought that mirrored the differences in $A_d$ (Fig. 10). During the first summer $E_d$ was similar between size classes and significantly reduced by drought (both size classes) (Table 7). During summer 1992, there was no significant effect of summer drought on either size class, but large shrubs had lower rates of $E_d$ than small ones. We found no drought or size class effects on WUE.

*Stem growth.*—Stem growth in mesquite occurs primarily in late spring/early summer concurrently with new leaf production. During the first two years of the study, measurements were made too late in the summer and at too coarse an interval to capture these dynamics. Hence, growth data for the first two years are omitted. In 1993, stem growth was high in late spring in both sizes of shrubs (Fig. 10) and there were significant postdrought effects (Table 7). Shrubs that had been droughted the previous summer had higher rates of stem growth in spring than did controls. The summer stem growth rates were relatively low in both size classes and were not affected by drought.

*Root growth.*—In *Prosopis,* root growth (i.e., rate of appearance of new roots, large shrubs only, see *Methods*) during summer of 1991 was relatively high in the control shrubs and significantly reduced by summer drought at the first two depths, with very low growth of roots of droughted shrubs (Fig. 9, Table 8). There was also a significant effect of depth, with growth at the uppermost level greater than the two other depths. Root growth was very low during the following winter (December–February) in droughted and nondroughted shrubs at all depths. There was a pronounced increase in growth of nondroughted shrubs in March 1992 (all depths). By late spring (May–June), shrubs that were previously droughted in summer showed increased root growth, achieving values comparable to nondroughted shrubs. Growth during late summer (August 1992) declined relative to late spring peaks for both droughted and control shrubs at all depths. There was also a significant drought × depth interaction, in which control shrubs had similar root growth at all depths but droughted shrubs had greater root growth at the lowest depth and least at the shallowest.

Root growth during the second winter (November–January 1993) was very low in all shrubs, followed by an increase in growth during spring (March) by control shrubs at all upper depths, and by previously summer-droughted (in 1992) shrubs at the two upper depths (Fig. 9). Root growth during summer 1993 varied with depth and was significantly reduced by drought at the two upper depths (Table 8). Root growth was greatest for nondroughted control plants at the uppermost depth where the impact of drought was greatest.

*Root death.*—Patterns of root death (disappearance of roots) in *Prosopis* were similar to those observed in *Larrea.* During the first summer and early winter period there was significant root death during a period of equilibration (Fig. 9; no ANOVA, see *Methods*). Following this period, there were pulses of root death (generally in summer) indicating significant root death, with maximal rates of death <0.1 roots/d.

## Discussion

### *Patterns of soil moisture*

Summer rainfall in the Chihuahuan desert is normally greater (and less variable) than winter precipitation, with 65–80% of the total annual rainfall falling in summer (65% at the Jornada study site) (MacMahon and Wagner 1985, Conley et al. 1992). However, during this study, winter/spring rainfall greatly exceeded normal amounts in both winters. Winter/spring rainfall was similar to the preceding summer rainfall in both 1991 and 1992 at the bajada sites, and greater than summer rainfall at the mesquite dunes site. At the two bajada sites, summer rainfall produced no soil water recharge below 30 cm, and only slight recharge at 30 cm (upper bajada only) (Figs. 3 and 4). However, at the mesquite dune site there was significant soil water recharge in summer at 30 cm and below (Fig. 5).

These differences in recharge can be attributed to differences in soil texture and resulting water-holding capacity (Table 1). The finest textured soils, and thus highest water-holding capacities, were at the lower bajada. At this site there was no penetration of summer rain to 30 cm, even with 160% above normal rainfall in 1991. At the upper bajada, soils were slightly coarser and had some soil moisture recharge at 30 cm during the first (1991) and last (1993) summers (180 and 63% of normal rain, respectively). The dunes site had the most coarse-textured soils and had significant recharge during summer at most depths (and thus a significant impact of drought on soil water). Thus, summer rainfall in the Jornada Basin apparently produces soil water recharge only on sites with relatively coarse-textured soils.

Winter rainfall, on the other hand, led to deep soil moisture recharge at all three sites in both winter/spring periods. The first winter/spring period (1991/1992) cannot be considered representative of normal recharge since the rainfall was so extreme (260–320% of normal). The second winter (1992/1993) had about half as

←

FIG. 6. Patterns of extractable N ($NO_3^-$ and $NH_4^+$) and nitrogen mineralization potentials at (A) lower bajada (*Larrea* and *Prosopis,* young islands only), (B) upper bajada (*Larrea* only), and (C) dune (*Prosopis* only) sites.

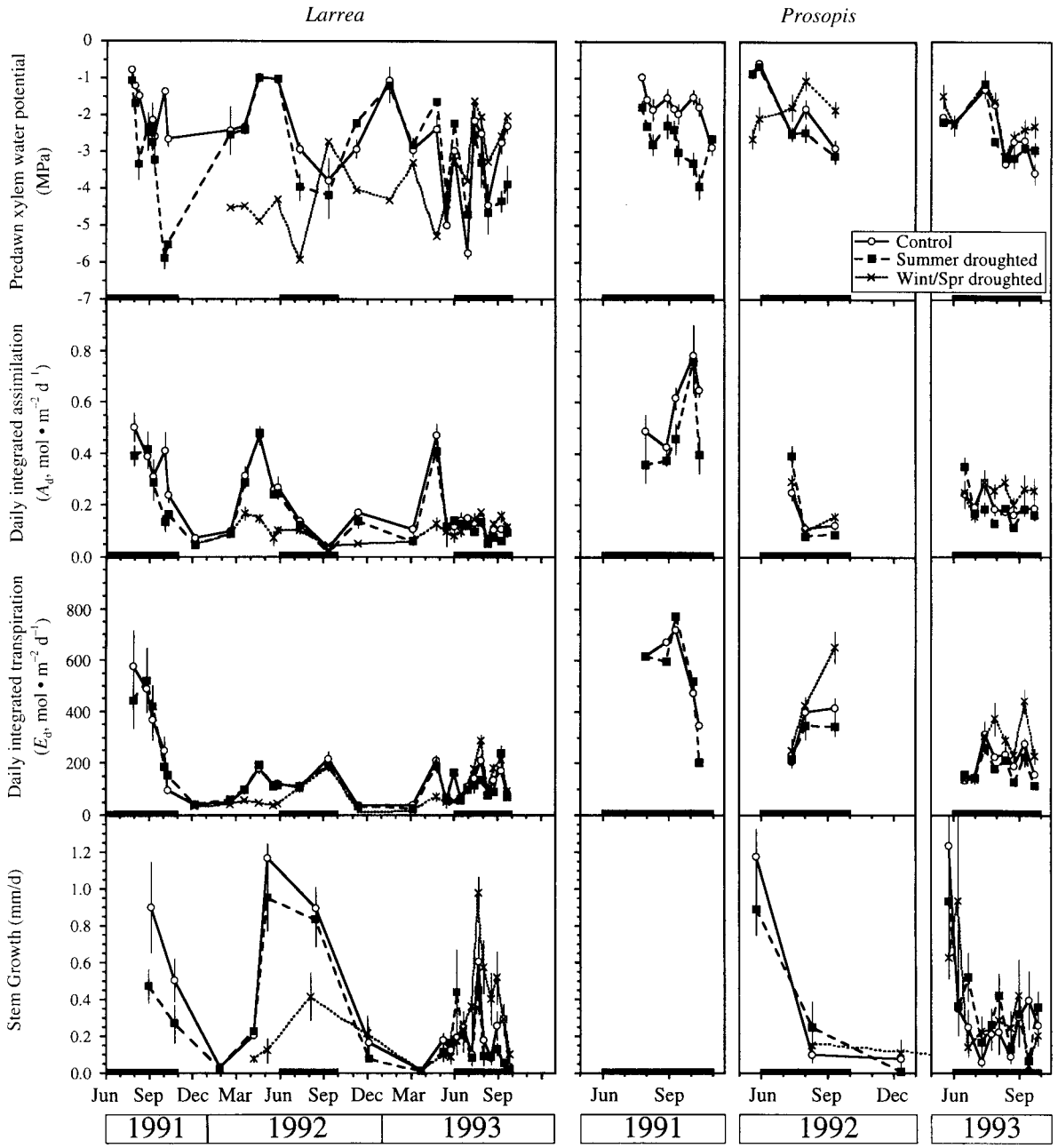



FIG. 7. Response of small (only) *Larrea* and *Prosopis* shrubs to drought at the lower bajada site, measured in terms of xylem water potentials, photosynthesis, transpiration, and stem growth. Solid bars are as in Fig. 2. Note that since no measurements were made on the winter-deciduous *Prosopis* during winter months, summer periods (solid bars) are enlarged relative to that shown for *Larrea*.

much rainfall as the previous (although still 150–179% above normal), and this too resulted in recharge of soil moisture at all sites. This large amount of winter/spring rainfall would be expected to occur <10% of the time (Conley et al. 1992). Wierenga et al. (1987) reported no soil water recharge during a 3-yr period (1982–1984) at a location near (and between) the two bajada sites of the present study; thus, if soil moisture recharge occurs in medium- to fine-textured soils in the Chihuahuan desert, it is likely to occur only in winter, and probably only in some years.

### *Impact of drought on nutrient dynamics*

While there was little change in the total N ($N_{TKN}$) of soils at any of the sites over time or because of drought treatment, there were significant changes in the extractable N ($N_{ext}$; i.e., $NO_3^-$ and $NH_4^+$). The most notable and consistent result was that summer-drought-

TABLE 6. The responses of small *Larrea* and *Prosopis* shrubs to drought at the lower bajada study site, summarized for the season during the application of the drought (summer or winter/spring) and for the season immediately following drought (postdrought response).

| Species | Plant response | Response during drought | | | | | Postdrought response | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | | Summer drought | | | Winter/spring drought | | Winter/spring following summer drought | | Summer following winter/spring drought | |
| | | 1991 | 1992 | 1993 | 1991/1992 | 1992/1993 | 1991/1992 | 1992/1993 | 1992 | 1993 |
| *Larrea* | Water potential (XWP) | ↓ | 0 | 0 | ↓ | ↓ | 0 | 0 | 0 | ↑ |
| | Photosynthesis ($A_d$) | ↓ | 0 | 0 | ↓ | ↓ | 0 | 0 | 0 | 0 |
| | Transpiration ($E_d$) | 0 | 0 | 0 | ↓ | ↓ | 0 | 0 | 0 | 0 |
| | Water use efficiency (WUE) | ↓ | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | Stem growth | 0 | 0 | 0 | ↓ | 0 | 0 | 0 | ↓ | ↑ |
| *Prosopis* | Water potential (XWP) | ↓ | 0 | 0 | ↓ | 0 | 0 | 0 | ↑ | ↑ |
| | Photosynthesis ($A_d$) | ↓ | 0 | 0 | ... | ... | ... | ... | 0 | ↑ |
| | Transpiration ($E_d$) | 0 | 0 | 0 | ... | ... | ... | ... | ↑ | ↑ |
| | Water use efficiency (WUE) | 0 | 0 | 0 | ... | ... | ... | ... | 0 | 0 |
| | Stem growth | 0 | 0 | 0 | ... | 0 | 0 | 0 | 0 | 0 |

*Note:* Statistically significant differences (see Appendices B and C) between treatment and control plants are expressed as: 0 = none; ↓ = lower than control; ↑ = higher than control; ... = insufficient data (or data not available because of plant phenology).

ed resource islands generally had increased $N_{ext}$ at the end of the summer, relative to controls and relative to the start of summer. Although single measurements of $N_{ext}$ do not capture the cumulative N dynamics during the preceding period, they should provide a conservative contrast between the continuously droughted resource islands and the relatively moist control islands of this study.

The differences in $N_{ext}$ at the end of the summer could be the result of effects of drought upon plant activities, e.g., decreased N uptake or decreased root production and exudation (resulting in decreased microbial activities), or effects on soil microbial activities, e.g., increased microbial death (with subsequent release of N or changes in ammonification, nitrification or denitrification activity). The differences in $N_{ext}$ were not associated with changes in $N_{min}$ potentials of soils, except in mature *Prosopis* resource islands (dunes), where there was an increase in $N_{min}$ potentials at the end of the summer drought periods ($P = 0.06$). Since neither $N_{TKN}$ nor mineralizable N were impacted by drought, the differences in $N_{ext}$ must be related to differences in relatively transient soil N pools, most likely associated with microbial processes or plant biomass pools. This conclusion is also supported by the fact that the accumulation of $N_{ext}$ was completely eliminated the following season after release from drought (with the exception of the mature *Prosopis* resource islands at the dune site). Charley (1972) has also shown that mineral N accumulated in an arid shrubland during dry periods when plants were inactive, and attributed this accumulation to short bursts of mineralization activity of microbes responding to small rainfall events that were insufficient to induce plant activity and nutrient uptake.

There is considerable uncertainty regarding the role of moisture in microbial mineralization and the resulting inorganic N availability in arid ecosystems. Whitford et al. (1981, 1986) concluded that decomposition, in general, was not strongly related to actual rainfall, but rather was greatest during the season of most likely rainfall (late summer in the Chihuahuan desert) even during temporarily dry conditions. In the Chaco region of Argentina, Mazzarino (1991) also found strong seasonality in rates of N mineralization, which varied somewhat independently of soil moisture. Fisher et al. (1987) concluded that decomposition and mineralization in the Jornada Basin were directly increased by rainfall, which in turn led to decreased levels of extractable N ($NO_3^-$ and $NH_4^+$) because of increased microbial immobilization and/or increased leaching of N. However, Fisher and Whitford (1995) later reported that extractable N was greatest during the wet season at the Jornada Basin and was significantly reduced by drought. Our results showing that $N_{ext}$ accumulated during summer drought do not support the findings of Fisher and Whitford (1995).

Our single sampling time at the end of the drought period does not allow us to address questions of how accumulation of $N_{ext}$ may occur. For example, $N_{ext}$ accumulation could occur early during soil drying as a result of differential sensitivity of various microbial processes to soil moisture. However, there does not seem to be a greater impact of drought on nitrification compared to mineralization (see Wetselaar 1968), since

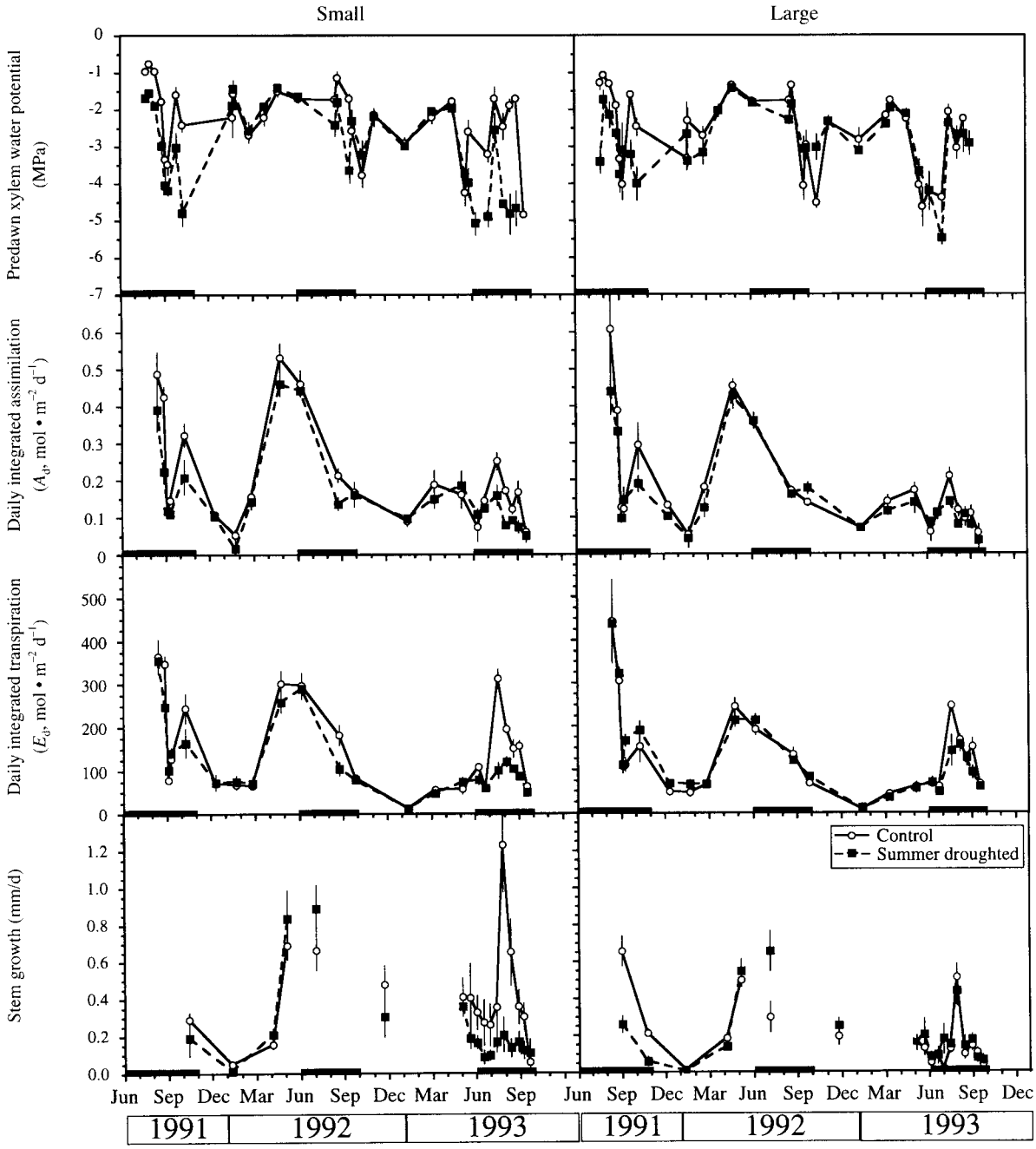



FIG. 8. Response of small and large *Larrea* shrubs to drought at the upper bajada site, measured in terms of xylem water potentials, photosynthesis, transpiration, and stem growth. Solid bars are as in Fig. 2.

$NO_3^-$ accumulated as much or more than $NH_4^+$ (Tables 4 and 5). The simplest explanation we can offer for increased $N_{ext}$ following drought is that it is a result of released labile N from dead microbial biomass, which was not compensated for by microbial or plant uptake.

In the case of the mature *Prosopis* resource islands at the dune site, both $N_{ext}$ and mineralizable N were increased by drought (potential $N_{min}$ was twice that of the control shrub islands; 1.6 vs. 3.3 mg/g). At the end of the following winter/spring, the shrub resource islands that were previously droughted still had significantly higher $N_{ext}$ than nondroughted islands, suggesting that the N equilibrium of these soils was shifted by the drought. This may be related (at least partially) to the effects of drought on plant activity, which could, in turn, affect total levels of soil nitrogen. It would also seem to be related to changes in the pool of nondecomposed organic mass, since changes in the extract-

TABLE 7. Response to drought treatment of small and large shrubs of *Larrea* (upper bajada site) and *Prosopis* (dune site) summarized for the season during the application of the drought (summer) and for the winter/spring season immediately following (a postdrought response).

| Site | Plant response | Small shrubs | | | | | Large shrubs | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | Summer drought | | | Winter/spring following summer drought | | Summer drought | | | Winter/spring following summer drought | |
| | | 1991 | 1992 | 1993 | 1991/1992 | 1992/1993 | 1991 | 1992 | 1993 | 1991/1992 | 1992/1993 |
| Upper bajada (*Larrea*) | Xylem water potential (XWP) | ↓ | ↓ | ↓ | 0 | 0 | ↓ | 0 | 0 | 0 | 0 |
| | Photosynthesis ($A_d$) | ↓ | 0 | ↓ | 0 | 0 | ↓ | 0 | ↓ | 0 | 0 |
| | Transpiration ($E_d$) | 0 | ↓ | ↓ | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| | Water use efficiency (WUE) | ↓ | 0 | 0 | 0 | 0 | ↓ | 0 | 0 | 0 | 0 |
| | Stem growth | ↓ | ··· | ↓ | 0 | 0 | ↓ | ··· | 0 | 0 | 0 |
| Dunes (*Prosopis*) | Xylem water potential (XWP) | ↓ | 0 | ↓ | ··· | 0 | ↓ | 0 | ↓ | ··· | 0 |
| | Photosynthesis ($A_d$) | ↓ | 0 | ↓ | ··· | ··· | ↓ | 0 | ↓ | ··· | ··· |
| | Transpiration ($E_d$) | ↓ | 0 | ↓ | ··· | ··· | ↓ | 0 | ↓ | ··· | ··· |
| | Water use efficiency (WUE) | 0 | 0 | 0 | ··· | ··· | 0 | 0 | 0 | ··· | ··· |
| | Stem growth | 0 | 0 | 0 | 0 | ↑ | 0 | 0 | 0 | ··· | ↑ |

*Note:* See Appendix D (*Larrea*) and Appendix E (*Prosopis*) for statistics about significant differences between size classes. Statistically significant differences between treatment and control plants are expressed as: 0 = none; ↓ = lower; ↑ = higher; ··· = insufficient data (or data not available because of plant phenology).

able pool itself, such as by decreased plant N uptake during drought, should be relatively quickly adjusted through microbial activity following drought. One explanation is that *Prosopis* shrubs undergo leaf abscission during drought, which could lead to increased litter input to soil, particularly in larger shrubs with bigger canopies. An alternative explanation is that drought may impact the symbiotic N relations of *Prosopis* shrubs (especially larger ones), leading to greater N fixation following drought (see *Compensatory responses to drought*).

In contrast to the effects of summer drought on soil nitrogen, winter/spring drought appeared to have little effect. This may be related to the fact that microbial activity is generally greater in summer than winter and the effects of drought on microbial activity would thus be more apparent during summer (e.g., Whitford et al. 1986). Plant activities (e.g., transpiration, root growth) are also lower during the winter, and therefore have less opportunity to effect a difference in the soil N dynamics.

### *Impact of seasonal drought: species differences*

In other desert regions with greater winter/spring rainfall, deep soil water recharge may be significant for shrubs by providing an "exclusive" source of moisture that is not readily available to shallow-rooted herbaceous competitors, nor lost to evaporation (Walter 1971, Walker and Noy-Meir 1982, Sala et al. 1989, Peláez et al. 1994). Donovan and Ehleringer (1994) found that some species of shrubs (particularly deep-rooted, mature individuals) in the winter-moist Great Basin desert are apparently restricted to the use of deep soil moisture. However, we found that both *Larrea* and *Prosopis* were able use soil water of upper layers under some circumstances. For example, during summer 1991, both *Larrea* and *Prosopis* at the lower bajada site had high xylem water potentials, high photosynthetic activity, and, most importantly, high rates of water use (Fig. 7), indicating their use of near-surface soil water, since there was little or no soil water available at 30 cm or below during this period (Fig. 3). We previously reported that surface-applied tracers of strontium and rubidium were readily taken up by both species of shrubs (Ho et al. 1996). Donovan and Ehleringer (1994) also found that for some species in which mature plants did not use shallow water, juvenile or small shrubs did. In this study, utilization of shallow water in *Larrea* appears to be accomplished by both small and large shrubs, since both had high rates of water use during summer 1991 at the upper bajada (Fig. 8) even though there was very little recharge of soil water below 30 cm during this period (Fig. 4). For *Prosopis,* we have insufficient information to determine if large shrubs are able to utilize shallow soil moisture, since at the dunes site where large shrubs occurred, there was nearly always soil moisture available in the soil below 30 cm (Fig. 5). The two shrub species in this study are considered as having somewhat different mechanisms for surviving aridity, namely, drought tolerance in the case of *Larrea* and drought avoidance (phreatophytic) in the case of *Prosopis* (Smith and No-

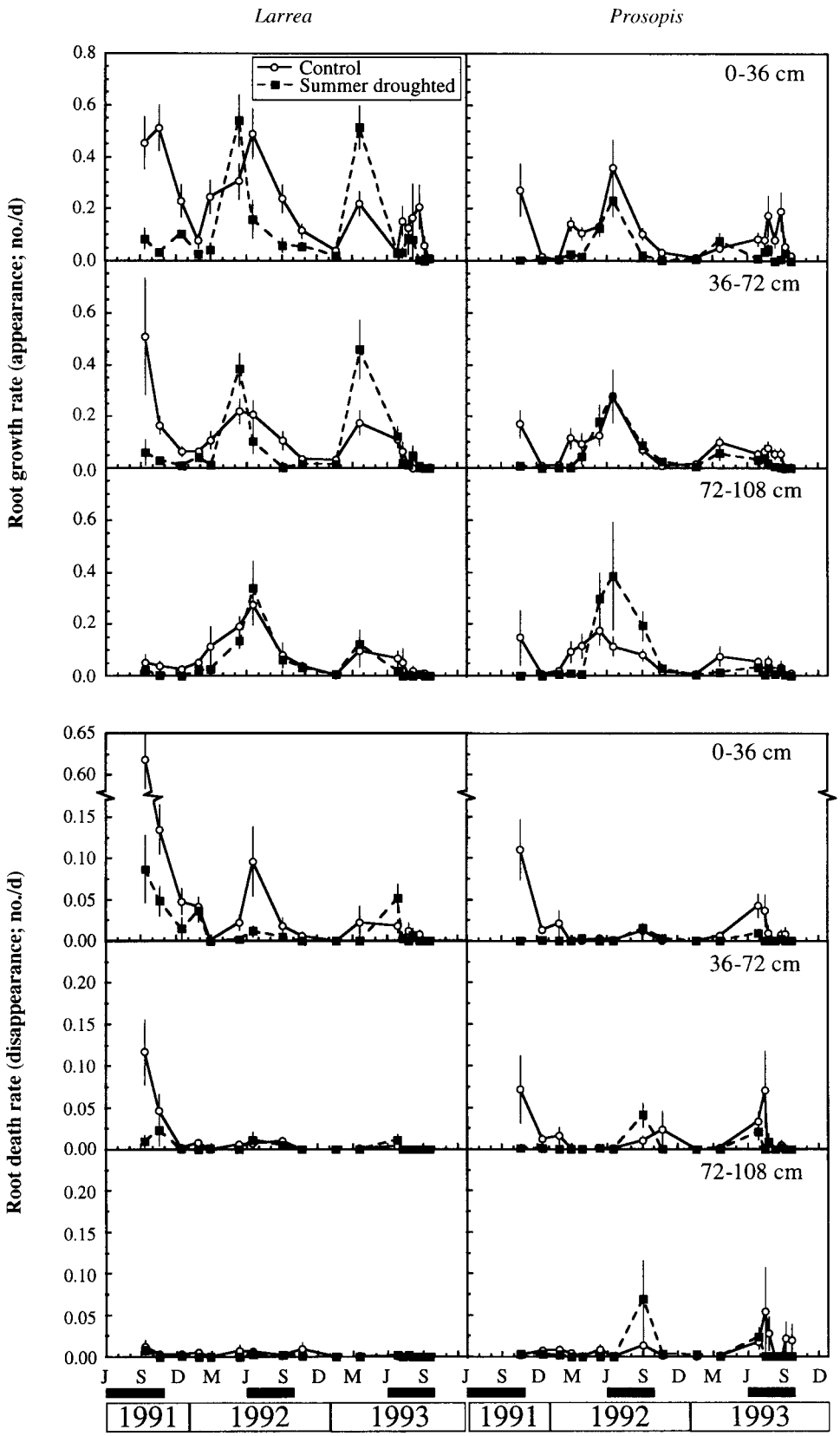



FIG. 9. Root growth and death rates for large (only) shrubs of *Larrea* (upper bajada site) and *Prosopis* (dune site). Note that the ordinate is different for root death rates compared to growth rates. Solid bars are as in Fig. 2.

TABLE 8. Root growth rates of *Larrea* (upper bajada site) and *Prosopis* (dune site) shrubs summarized for the season during the application of the drought (summer) and for the winter/spring season immediately following (a postdrought response); and mean fine root longevity of summer-droughted and control plants over the course of study.

| | | Growth rates | | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | Summer drought | | | Winter/spring following summer drought | | Longevity (yr) | |
| Species | Soil depth (cm) | 1991 | 1992 | 1993 | 1991/1992 | 1992/1993 | Controls | Droughted |
| *Larrea* | 0–36 | ↓ | ↓ | ↓ | ↑ | ↑ | 5.5 | 3.1 |
| | 36–72 | ↓ | ↓ | 0 | ↑ | ↑ | 7.6 | 7.8 |
| | 72–108 | 0 | 0 | 0 | 0 | 0 | 5.5 | 3.4 |
| *Prosopis* | 0–36 | ↓ | 0 | ↓ | 0 | 0 | 4.0 | 2.6 |
| | 36–72 | ↓ | 0 | ↓ | 0 | 0 | 4.0 | 2.4 |
| | 72–108 | 0 | 0 | 0 | ↑ | 0 | 1.4 | 4.7 |

*Notes:* Only large shrubs are included in this analysis. Statistically significant differences (see Appendix F) between treatment and control plants are expressed as: 0 = none; ↓ = lower; ↑ = higher.

bel 1986). Drought tolerance in *Larrea* is attributed to the capacity for seasonal acclimation and adjustment of leaf water relations and gas exchange capacity, and for maintaining growth, gas exchange, and positive leaf turgor at very low soil water availability (Odening et al. 1974, Mooney et al. 1978, Meinzer et al. 1986). Drought avoidance in *Prosopis* is attributed to the capacity for acquisition of stored soil water at depth or in microsites, and maintaining relatively high plant hydration (Mooney et al. 1977, Nilsen et al. 1983, Virginia and Jarrell 1987). However, in the Jornada Basin such a classification does not seem to adequately characterize their dynamics (in particular, their plasticity of responses to variable soil moisture), nor does it reflect the similarities between them in responses (see also Westoby 1979/80). *Prosopis,* for example, is unlikely to act as a true phreatophyte at the dunes site, since the water table is so deep (Hennessy et al. 1985). In fact, the greatest differences between the species in the Jornada Basin appear to be related more to phenology than to intrinsic mechanisms of drought tolerance vs. avoidance.

*Prosopis* exhibited a very regular pattern of deciduousness, with a leafless period of about 5 mo during winter. Leaf initiation and expansion occurred in late spring at approximately the same time among all shrubs, regardless of drought treatment, and at about the same time each year. Leaf abscission in winter was somewhat more variable between years and treatments. We did not observe the leaf dimorphism or dual leaf flushes seen in this species at lower elevations in the Sonoran Desert (Nilsen et al. 1986). Stem growth in *Prosopis* is closely related to leaf phenology, with maximal growth occurring in late spring concurrent with new leaf production, and declining in summer. The amount of stem growth was independent of drought treatment. In this respect, growth of *Prosopis* was different than the growth of many other shrubs in seasonal climates in which the degree of shoot elongation is related to soil moisture and plant water status (Aljaro et al. 1972, Adams and Radosevich 1978, Nilsen and Muller 1981). The marked seasonal phenology, independent of current soil moisture, would be expected of a deep-rooted phreatophyte, but as indicated previously, *Prosopis* in the Jornada Basin is unlikely to have access to the water table, and small shrubs exhibit the same phenological patterns as do large shrubs.

Although *Larrea* is evergreen, leaf production tends to occur in a single flush in spring, with a second, more variable flush in summer (see also Lajtha and Whitford 1989). Stem growth was concurrent with the initiation and expansion of leaves in spring. Chew and Chew (1965) concluded that initiation of spring growth was dependent upon soil temperature and relatively independent of rainfall or soil moisture. Our results support this, as growth in the spring was initiated at about the same time in both years, regardless of drought treatment. In this respect, initiation of growth in *Larrea* was similar to *Prosopis.* However, in contrast to *Prosopis,* the amount of stem growth was strongly related to the amount of rainfall and/or soil water during the first spring, as droughted plants had much less growth. Both the timing and amount of summer growth in *Larrea* is controlled by soil moisture and/or rainfall. This is best exemplified during the final summer (1993) when stem growth was intensively sampled. This summer was preceded by a dry April and May (normal) and growth was relatively low at the start of summer (Figs. 7 and 8). Growth peaked in late July, corresponding to abundant rainfall during this month.

In contrast to some differences in growth and phenology, the two shrub species had relatively similar leaf gas exchange capacities, which were related to moisture availability. During the winter *Prosopis* is leafless. However, this is a period of relatively low gas exchange in *Larrea,* even if moisture is high. This is apparently due to two factors. The most important limitation is probably temperature, perhaps associated with almost nightly frosts, since daytime temperatures were normally high enough to promote moderate gas exchange, given *Larrea*'s capacity for temperature acclimation (Mooney et al. 1978). Leaf age may also be a

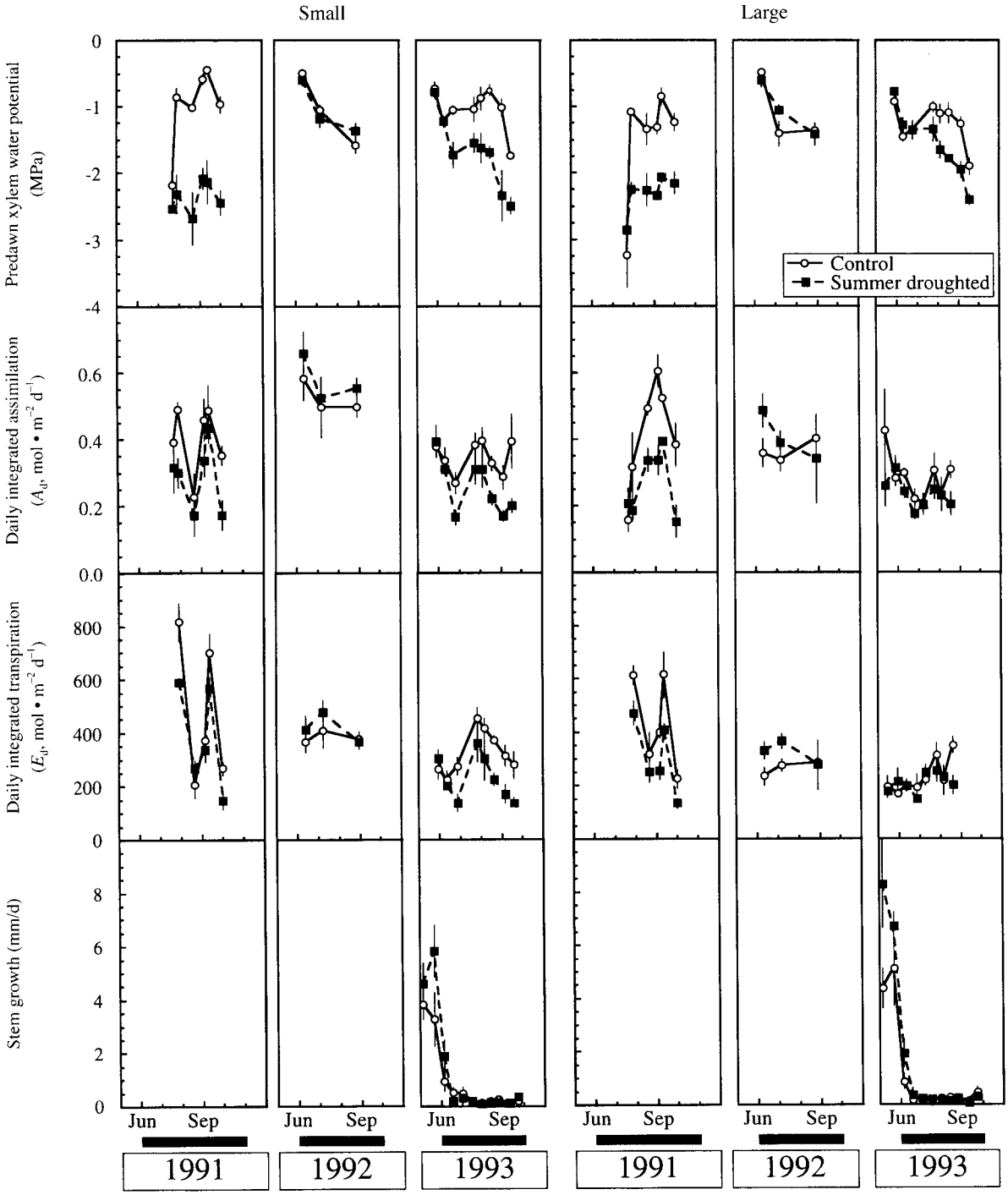



FIG. 10. Response of small and large *Prosopis* shrubs to drought at the dune site, measured in terms of xylem water potentials, photosynthesis, transpiration, and stem growth. Solid bars are as in Fig. 2.

limitation. New leaves were produced in spring with a second, but considerably smaller, cohort produced in late summer. Thus, most of the leaves in winter were ~9 mo old, with lower leaf N and lower photosynthetic capacity than when first produced (Lajtha and Whitford 1989).

Following the winter period of low gas exchange activity, *Larrea* exhibits a peak of daily photosynthesis ($A_d$) during spring of each year, the extent of which depends on rainfall and/or soil moisture, since drought greatly reduced $A_d$ (Figs. 7 and 8). We did not measure gas exchange in spring in *Prosopis,* except for very

late in the final year at the dune site (Fig. 10), at which time $A_d$ was moderately high. Both shrubs also had high $A_d$ during some periods each summer. This was apparently related more to rainfall and surface moisture than to soil moisture at 30 cm and below, because there was no summer recharge at depth at either bajada site. Transpiration ($E_d$) in *Larrea* closely paralleled the pattern of $A_d$ during the spring and summer at both sites, but there was not necessarily a strong relationship between the two processes in winter when $A_d$ was apparently temperature limited. Transpiration in *Prosopis* was somewhat independent of $A_d$ in small shrubs at the lower bajada, but was generally highly correlated with water loss in both shrub size classes at the dunes site. This may be related to the difference in soil water availability at the two sites: subsurface soil water was generally available during the entire growing season at the dunes, but virtually never available during the middle and late growing season at the lower bajada.

In summary, there is little evidence from this study that the shrub species differ markedly in their stomatal control of water loss, particularly with increasing drought. Thus, we cannot classify them as either "water spenders" (=drought avoiders), or "water savers" (=drought tolerant) (Noy-Meir 1973, Solbrig and Orians 1977). In fact, both shrubs had nearly identical water-use efficiencies when direct comparisons could be made. Interestingly, WUE was not affected by summer or winter drought in either species, except during summer 1991, when *Larrea* at both bajada sites had improved WUE when droughted (summaries in Tables 6 and 7).

### *Impact of seasonal drought: shrub size and island age*

Resource islands could differ from one another in a number of ways: (1) young vs. mature islands may have different capacities for storage of nutrients and water resources (based on a constant storage rate per unit volume of shrub, see Wallace et al. 1978), although for shrubs themselves, water storage capacity is relatively small and size independent for nonsucculent shrubs (Nobel and Jordan 1983); (2) different-sized shrubs may have access to soil water at different depths (Brown and Archer 1990, Manning and Groeneveld 1990, Donovan and Ehleringer 1992); and (3) shrubs may have different physiological capacities (e.g., Donovan and Ehleringer 1992, Franco et al. 1994, de Soyza et al. 1996). Ontogenetic (size-related) changes in structure and function of shrubs, which we assume are closely associated with different degrees of resource island development, have been hypothesized to be important in allowing shrub species to invade and compete in grassland environments (Reynolds et al. 1997). A corollary to this hypothesis is that size-related changes in structure and function are important in fostering survival in the more variable (extreme) environment of desertified habitats.

There were essentially no differences between young and mature islands of *Larrea* (upper bajada) in their soil moisture storage during summer or winter/spring periods, and the impact of drought (summer only) was similar in both young and mature islands. Furthermore, both size classes of shrubs appeared to utilize water from throughout the profile, when available. In *Prosopis* (dunes site), on the other hand, there were significant differences between young and mature islands in soil water distribution. Young islands had greater summer soil moisture at depths >30 cm than did mature islands. Although this is contrary to our hypothesized difference in soil water recharge associated with island maturity (i.e., that large islands would have greater soil moisture storage), an alternative explanation for the difference is that it is a result of shrub size, with small shrubs not having the root volume to extract moisture from deeper soil. In any case, summer drought significantly reduced soil moisture at depths >30 cm in young islands, resulting in similar soil moisture contents between young and mature islands under drought treatment. Hence, our results provide no indication that mature shrub islands of either species are more effective in soil moisture storage than young islands.

Our previous studies of *Larrea* and *Prosopis* indicate that there are some differences between large and small shrubs (Franco et al. 1994, de Soyza et al. 1996) in response to natural variability in moisture. Thus, it would be expected that greater moisture variation imposed by a season-long drought might elicit even greater differences between shrub size classes. A principal hypothesis in this study was that large shrubs would be less impacted by variation in moisture (drought) than small shrubs. However, the results of this study reveal only small differences between the small and large shrubs of *Larrea,* and essentially no differences between *Prosopis* shrub size classes in response to relatively extreme seasonal drought. The differences in *Larrea* were found in the second and third year of the study, when the small shrubs were, as predicted, more negatively impacted by drought. This suggests that large shrubs are able to draw from a larger pool of reserves in the mature resource islands, which may include water stored within the island from previous seasons/years, and/or carbohydrates associated with larger shrub biomass. However, an alternative that cannot be ruled out is that the large shrubs were able to access water that was outside the rainout plot via root growth under the plot barrier. The lack of differences between shrub size classes of *Prosopis* may be due to the fact that small shrubs chosen for this study had already achieved the capacity to behave primarily like adults. Brown and Archer (1990) showed that within one year, *Prosopis* seedlings quickly developed extensive root systems and had access to relatively deep soil water. It is also possible that the shrubs are able to compensate for loss of a single seasonal component of moisture in the following season. Further studies in-

volving year-long droughts could address this question. Although no shrubs died in this study, the small shrubs of *Larrea* appeared to be the most impacted of either species or size class after three consecutive years of seasonal drought. Compared to similar-sized neighbors that were undroughted, the small, droughted *Larrea* shrubs had much less, as well as more chlorotic, foliage. Thus, it seems likely that multi-season droughts would result in death of small shrubs prior to death of the large ones. Hence, we suggest that while the establishment of shrubs in the Chihuahuan Desert may depend upon a sequence of good years (Neilson 1986, Harrington 1991), the growth and survival of small shrubs depends on a *lack* of a sequence of bad years.

### *Root growth and turnover*

After an initial flurry of root growth (appearance) during equilibration of the minirhizotron tubes, root dynamics were relatively similar between the species over all depths. Growth was low during the early part of winter/spring periods, then increased to a peak during late spring (or early summer), and declined during late summer (Fig. 9). These patterns were strongly correlated with timing of stem growth in *Larrea* in both droughted and control plants: $r = 0.483$ ($P < 0.05$) for 0–36 cm roots, $r = 0.597$ ($P < 0.01$) for 36–72 cm roots, and $r = 0.679$ ($P < 0.001$) for 72–108 cm roots. Although the timing of root growth showed a similar pattern in *Prosopis,* there was not a significant correlation with stem growth, perhaps because of insufficient measurements of stem growth in early season. Root growth through time at a particular depth was not correlated with soil water at that depth for either species, but the magnitude of root growth was, nevertheless, negatively affected by drought at the two upper depths in both species.

Root death (disappearance) rates were also similar for *Larrea* and *Prosopis,* but generally much lower than appearance rates (Fig. 9). The death rates of roots in the uppermost soil layer (0–36 cm) tended to occur in seasonal pulses. In the bottom two soil layers, death rates were extremely low, with a slight seasonal aspect. At all depths the timing of root death was correlated with root growth (*Larrea,* $r = 0.517$, $P < 0.001$; *Prosopis,* $r = 0.223$, $P < 0.05$). Examination of the seasonal patterns suggested that root death peaked somewhat later than growth, and, indeed, there was a much stronger correlation of root growth with root death at the next successive date (lagged-one correlation). The correlation coefficients improved to $r = 0.930$ ($P < 0.001$) for *Larrea* and $r = 0.613$ ($P < 0.001$) for *Prosopis* (see Fig. 9), and lagged-two correlations were not as strong as lagged-one. Since the time between sample dates (mean ± 1 SD) was 38 ± 26 d for *Larrea* and 40 ± 28 d for *Prosopis,* we conclude that peaks in root death tend to succeed peaks in root growth by roughly 40 d.

Although we cannot convert these minirhizotron data for root appearance and disappearance into estimates of root biomass or length, we can nevertheless gain insight into relative root dynamics for these shrubs. Rates of root appearance and disappearance are directly indicative of root growth and root death plus decomposition (or loss from herbivory), respectively. The balance between these two processes is indicative of the rate of change in the size of the root pool (e.g., Joslin and Henderson 1987). If the root pools in the vicinity of the rhizotron tubes were in equilibrium, then the rates of appearance and disappearance of roots would balance on average over a period of time sufficient to account for the seasonal pulses of each. However, over the 2.5 yr of this study, these processes remained greatly out of equilibrium, with root appearance rates roughly 5–10 fold (or more) greater than root disappearance rates. Although this disequilibrium could be due either to slow rates of root death or slow rates of decomposition, relative to root growth, we favor the former as the cause for two reasons.

First, there was little indication of root senescence or death, as most roots exhibited little change in color or appearance during their tenure on the rhizotron window. Wang et al. (1995) has shown that dead roots could be visually distinguished from live roots in a rhizotron with ~85% accuracy for a variety of herbaceous and woody perennial species. Other rhizotron studies have typically shown that a large number of roots undergo color change or otherwise visibly appear to senesce and die (Atkinson 1985, Hendrick and Pregitzer 1992). Second, decomposition of apparently dead fine roots appears to occur very rapidly; therefore, if roots had died without undergoing visible changes, we would still expect fairly rapid decomposition and disappearance (Parker et al. 1984, Distel and Fernandez 1988, Hendrick and Pregitzer 1993).

The disequilibrium between root appearance and disappearance suggests that fine roots of both species have low turnover rates and are thus relatively long lived. Although we did not follow the life-span of individual roots or cohorts of roots, we calculated (see *Methods*) fine-root longevity over the duration of the study. These results showed that the fine roots of *Larrea* lived ~3–8 yr and those of *Prospis* ~2–5 yr (see Table 8). This finding contrasts with many studies in a variety of other ecosystems suggesting that fine roots are relatively short-lived and resulting turnover of the fine-root pool is high (on the order of days to weeks, e.g., Persson 1979, Chapin and Van Cleve 1981, Atkinson 1985, Larsson and Steen 1988). Some studies have reported that turnover time is roughly annual for fine roots (Kummerow et al. 1978, Caldwell 1979, Nadelhoffer et al. 1985, Distel and Fernandez 1988). In these cases the mean life-span of the fine roots would be ~6 mo or less, assuming normally distributed life-spans (Hendrick and Pregitzer 1992). There are few examples of relatively long-lived fine-roots systems. Joslin and Henderson (1987) found that the life-span of fine roots

in a white oak community was ~5 yr, and Rutherford (1983) found no evidence of fine-root mortality for over a year in large woody plants of a South African savanna community. Whether this root longevity is species specific, or a more general phenomenon associated with particular growth forms or ecosystems, remains to be seen. The traditional thinking with regard to root systems of perennials in seasonally dry ecosystems is that root growth occurs with the onset of moisture, and soil drying brings about rapid root death (Lyr and Hoffman 1967, Kummerow et al. 1978, Hayes and Seastedt 1987). Caldwell et al. (1977), for example, found that about three-quarters of the fine root system of two Great Basin cold desert shrubs turned over annually. However, almost nothing is known about root productivity and turnover in warm desert shrubs (Rundel and Nobel 1991), but there are reasons to expect that root productivity and especially root turnover might be different from those in cold desert ecosystems. There are some striking differences in the salient features of the root systems between the cold and warm deserts of North America. First, root biomass is much greater in the cold desert than in warm deserts, in terms of either absolute amount or proportional investment by plants relative to aboveground biomass (Dobrowolski et al. 1990). Second, root growth in the cold desert occurs in a single downward wave each season, driven by a predictable downward pulse of increasing soil temperature and retreating soil moisture reserves that remain from winter precipitation (Fernandez and Caldwell 1975). In contrast, soil water availability in warm desert regions is less reliable in timing and distribution, with moisture occurring in summer or winter and often localized in shallow soils. Consequently, root masses are not as deep or dense as in cold deserts (MacMahon and Wagner 1985).

Our results suggest that the timing of root growth in these warm desert shrubs is a relatively fixed phenological occurrence, much as in cold desert regions. However, in contrast to the cold desert, root growth occurred at a similar time at all depths. In fact, in the Chihuahaun Desert the growth of new roots occurs at a time (late spring) when soils are generally rapidly drying, which would seem to be a costly investment for a very limited period of soil water uptake if they were short-lived. Thus, we would expect these warm-desert shrubs to have relatively long-lived fine ("rain") roots so as to be able to take up moisture quickly after brief recharge periods. Apparently, a small fraction of the new roots die within a short time after appearance (the pulse of root disappearance that was observed ~40 d after appearance), and the remainder become "established," "rain" roots. Orians and Solbrig (1977) and Caldwell (1979) have also argued, using energetics and cost-benefit analysis, that roots of arid-land shrubs ought to be long-lived because production costs take longer to pay off with scarce water and nutrient supplies. Grime et al. (1991), have further suggested that an attribute of the stress-tolerant "strategy" would be long-lived roots to facilitate the utilization of unreliable pulses of moisture. Thus, our finding of relatively long-lived roots for desert shrubs is consistent with these theoretical paradigms.

### *Compensatory responses to drought*

There were several occasions during this study in which shrubs that had been droughted exhibited responses during the following season that were significantly or substantially higher than control plants. We refer to this response as *compensation.* Compensation has been reported for plants in response to several kinds of stress. Compensatory responses may involve shifts in physiology and/or structure concurrently with stress, thereby lessening the impact of the stress, or they may involve shifts in physiology and/or structure that enhance the growth of the plant after release from stress (Geiger and Servaites 1991, Pell et al. 1994). This latter response (poststress compensation) has been observed in a number of species that were subjected to moderately severe, short-term (days or weeks) drought (Brown and Blazer 1970, Corleto and Laude 1974, Horst and Nelson 1979).

Previous studies have attributed the compensatory responses to different mechanisms, depending to some extent upon how the compensation is manifest. Several investigators have shown rapid, relatively transient responses of physiological activity and/or growth following release from drought (e.g., Hsiao and Acevedo 1974, Ludlow and Ng 1974, Lauenroth et al. 1987, BassiriRad and Caldwell 1992). These responses are usually observed during the first 2 wk following release from drought, and have been suggested to be related to conditions created during the drought period, including delay in developmental stages of growth (Ludlow and Ng 1974), increased cell wall extensibility (Hsiao and Acevedo 1974), and the continuation of cell division without expansion (Hsaio 1973). Uptake of water following drought could then lead to rapid growth response as tissues "rebound" to new equilibrium levels. However, the compensatory responses that we observed often occurred more than a month after plants received substantial rainfall following removal of shelters. It does not seem likely that the compensatory responses we observed were fully related to rapid adjustments of tissues to new equilibrium levels.

Our results suggest that postdrought compensation can occur following longer drought periods than reported above: an entire season. Mechanisms for compensation following relatively long-term drought are virtually unknown. In *Larrea,* the compensatory responses were largely related to the production of new shoot and root tissues. Enhanced production of new leaf and stem tissue following release from drought could be directly related to tissue loss during drought. Leaf abscission during drought may lead to formation of buds, which then provides multiple new growth

points following release from drought. This would be analogous to compensatory responses associated with production of new tissues following herbivory (McNaughton 1979). Alternatively, the compensatory growth may be related to accumulation of nonstructural carbohydrates during drought (Horst and Nelson 1979). Compensatory growth of roots in *Larrea* would more likely be related to carbohydrate storage than to bud formation, since we did not observe any greater root death in droughted plants than in controls.

In *Prosopis,* compensatory responses were largely related to improved plant water relations and transpiration following summer or winter/spring drought. Because both water potential and transpiration increased, the compensatory responses must be associated with increased water uptake. This may be the result of a direct plant response, such as increased capacity for water uptake in postdroughted roots (as seen in short-term drought responses cited above), or it may be a secondary response to other drought-induced changes in the shrub island complex, as described in the following paragraphs.

Alternative explanations of compensation in both shrubs are that they result from secondary factors associated with release from drought, such as nutrient availability or interspecific competition. In the case of nutrient availability, Noy-Meir (1973) suggested that there is a pulse of decomposition and nutrient release after rainfall in deserts. In the tallgrass prairie, Seastedt and Knapp (1993) correlated increased growth following drought with "luxury uptake" of nutrients that accumulated during the period of drought. Although our measurements of soil nutrients were not frequent enough to identify any pulses of nutrient availability following release of resource islands from drought, we did observe an accumulation of extractable N ($NO_3^-$ and $NH_4^+$) during summer drought treatment. Thus, N availability was higher in drought-treated plots relative to controls at the start of the winter/spring seasons. Higher N availability could explain the compensatory responses in *Larrea* root and stem growth following summer drought, but would not explain the compensatory responses following winter drought in *Larrea* (stem growth) or *Prosopis* (physiology), since there was not an accumulation of extractable N following winter/spring drought.

Water use by competitors in the plots is another secondary factor that could have affected the responses of shrubs to release from drought. All resource island plots contained annuals and herbaceous/suffrutescent perennials in association with the principal shrub species (*Larrea* or *Prosopis*). The drought treatment may have induced changes in the associated species that made them less competitive for water following release from drought, for example, through leaf loss or root death; the associated species on the droughted plots would then have less total water uptake than those on the control plots, resulting in increased water availability for shrubs on droughted plots. However, the evidence to support or refute such a scenario is lacking. We measured the cover of associated plants at the start and finish of the drought treatment and found little difference from control plots, but we did not follow associated plant cover during the critical transition periods between seasons.

## Conclusions

Our initial hypothesis was that the two major shrub species in the Jornada Basin, creosotebush (*Larrea tridentata*) and mesquite (*Prosopis glandulosa*), have different growth phenologies, rooting patterns, and physiological responses to resource availability (primarily water), which affect the structure and function of resource islands. We conclude, however, that the two species are perhaps more similar than the overall phenological "strategies" (evergreen vs. winter deciduous) of the shrubs would suggest. The patterns of seasonal growth and physiological activity (photosynthesis, transpiration, and water potential) in these two desert shrubs were similar in many respects. In the absence of drought, both species exhibited maximal rates of shoot and root growth, as well as high photosynthesis and transpiration, in late spring. This remained as the period for maximal growth and physiological activity for *Prosopis* shrubs that were droughted in either summer or winter/spring (although we have data only for small shrubs droughted in winter/spring). On the other hand, winter/spring droughted *Larrea* shrubs had maximal growth and activity shifted to the summer period, and undroughted *Larrea* shrubs also exhibited high physiological activity during the summer (especially following high rainfall). Thus, *Larrea* appears to have a greater capacity for shifting its activity patterns to alternate periods to take advantage of changes in resource availability.

Shrubs of both species appeared well adapted to withstand season-long droughts. Mechanisms for survival include the capacity to: (1) shift growth and physiological activity (*Larrea*) to utilize different temporal moisture; (2) utilize different levels of soil water (both species); (3) carry out limited physiological activity and growth during drought (especially *Larrea*); and (4) compensate for some negative impacts of drought through enhanced physiological activity (especially *Prosopis*) and growth (especially *Larrea*) in the season following drought.

With regard to the second hypothesis, that different size classes of shrubs associated with different stages of resource island development should differ in their responses to drought, we again found more similarities than differences between the different-sized shrubs and different-aged (young vs. mature) islands. The maturity of a resource island complex did not generally affect levels of soil water or nutrients under droughted or nondroughted conditions (with some exceptions). In *Larrea* at the upper bajada site, both young and mature

islands had very similar patterns of soil moisture, with deep (>30 cm) recharge restricted to the winter/spring seasons that had much greater than normal rainfall. Both size classes of shrubs utilized water from throughout the profile. Small shrubs associated with young islands were more often negatively impacted by drought (lowered XWPs and transpiration, and reduced stem growth) than were large shrubs (a finding consistent with our hypothesis). In *Prosopis* at the dunes site, coarse soils permitted recharge during both summer and winter/spring seasons. Young islands had greater summer soil moisture at depths >30 cm than did mature islands (inconsistent with our hypothesis, but probably related to shrub size, with small shrubs apparently not using relatively deep soil water). Summer drought significantly reduced soil moisture at depths >30 cm in young islands, resulting in similar soil moisture between young and mature islands under drought treatment. Growth and physiology of both size classes of *Prosopis* shrubs were similarly impacted by drought (inconsistent with our hypothesis).

There were no consistent differences in soil N status between young and mature islands of either species. Drought treatment during summer produced similar effects on extractable N in both species, with both young and mature islands accumulating nitrogen during drought. This accumulated N was depleted during the season following drought, such that droughted and control plots attained similar levels of extractable nitrogen by the end of the post-drought season.

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## Literature Cited

Adams, D. R., and S. R. Radosevich. 1978. Regulation of chamise shoot growth. American Journal of Botany **65**: 320–325.

Aljaro, M. E., G. Avila, A. Hoffman, and J. Kummerow. 1972. The annual rhythm of cambial activity in two woody species of Chilean "matorral." American Journal of Botany **59**:879–885.

Atkinson, D. 1985. Spatial and temporal aspects of root distribution as indicated by the use of a root observation laboratory. Pages 43–65 *in* A. H. Fitter, D. Atkinson, D. J. Read, and M. B. Usher, editors. Ecological interactions in soil, plants, microbes and animals. Special Publication Number 4, British Ecological Society, Blackwell Science, Oxford, UK.

Bahre, C. J., and M. L. Shelton. 1993. Historic vegetation change, mesquite increases, and climate in southeastern Arizona. Journal of Biogeography **20**:489–504.

BassiriRad, H., and M. M. Caldwell. 1992. Temporal changes in root growth and 15N uptake and water relations of two tussock grass species recovering from water stress. Physiologia Plantarum **86**:525–531.

Bond, W. J., W. D. Stock, and M. T. Hoffman. 1994. Has the Karoo spread? A test for desertification using carbon isotopes from soils. South African Journal of Science **90**: 391–397.

Bremner, J. M., and C. S. Mulvaney. 1982. Nitrogen-Total. Pages 595–624 *in* A. L. Page, R. H. Miller, and D. R. Keeny, editors. Methods of soil analysis. Part 2. Chemical and microbiological properties. Second edition. Agronomy Series Number 9. American Society of Agronomy and Soil Science Society of America, Madison, Wisconsin, USA.

Brown, J. R., and S. Archer. 1990. Water relations of a perennial grass and seedling vs. adult woody plants in a subtropical savanna, Texas. Oikos **57**:366–374.

Brown, R. H., and R. E. Blazer. 1970. Soil moisture and temperature effects on growth and soluble carbohydrates of orchardgrass (*Dactylis glomerata*). Crop Science **10**: 213–216.

Buffington, L. C., and C. H. Herbel. 1965. Vegetational changes on a semidesert grassland range from 1858 to 1963. Ecological Monographs **35**:139–164.

Caldwell, M. M. 1979. Root structure: the considerable cost of belowground function. Pages 408–432 *in* O. T. Solbrig, S. Jain, G. B. Johnson, and P. H. Raven, editors. Topics in plant population biology. Columbia University Press, New York, New York, USA.

Caldwell, M. M., R. S. White, R. T. Moore, and L. B. Camp. 1977. Carbon balance, productivity; water use of cold-winter desert shrub communities dominated by C3 and C4 species. Oecologia **29**:275–300.

Chapin, F. S., III, and K. Van Cleve. 1981. Plant nutrient absorption and retention under differing fire regimes. Fire regimes and ecosystem properties, U.S. Forest Service General Technical Report **WO-26**.

Charley, J. L. 1972. The role of shrubs in nutrient cycling. Pages 182–203 *in* C. M. McKell, J. P. Blaisdell, and J. R. Goodin, editors. Wildland shrubs—their biology and utilization. U.S. Forest Service General Technical Report **INT-1**.

Charley, J. L., and N. E. West. 1975. Plant-induced soil chemical patterns in some shrub-dominated semidesert ecosystems of Utah. Journal of Ecology **63**:945–964.

Chew, R. M., and A. E. Chew. 1965. The primary productivity of a desert-shrub (*Larrea tridentata*) community. Ecological Monographs **35**:355–375.

Conley, W., M. R. Conley, and T. R. Karl. 1992. A computational study of episodic events and historical context in long-term ecological processes: climate and grazing in the northern Chihuahuan Desert. Coenoses **7**:55–60.

Corleto, A., and H. M. Laude. 1974. Evaluating growth potential after drought stress. Crop Science **14**:224–227.

Cornelius, J. M., P. R. Kemp, J. A. Ludwig, and G. L. Cunningham. 1991. The distribution of vascular plant species and guilds in space and time along a desert gradient. Journal of Vegetation Science **2**:59–72.

Day, R. W., and G. P. Quinn. 1989. Comparisons of treatments after an analysis of variance in ecology. Ecological Monographs **59**:433–463.

de Soyza, A. G., A. C. Franco, R. A. Virginia, J. F. Reynolds, and W. G. Whitford. 1996. Effects of plant size on photosynthesis and water relations in the desert shrub *Prosopis glandulosa* (Fabaceae). American Journal of Botany **83**:99–105.

Distel, R. A., and O. A. Fernandez. 1988. Dynamics of root

growth and decay in two grasses native to semi-arid Argentina. Australian Journal of Ecology **13**:327–336.

Dobrowolski, J. P., M. M. Caldwell, and J. H. Richards. 1990. Basin hydrology and plant root systems. Pages 243–292 *in* C. B. Osmond, L. F. Pitelka, and G. M. Hidy, editors. Plant biology of the Basin and Range. Ecological Studies 80. Springer-Verlag, Berlin, Germany, USA.

Dodd, J. L. 1994. Desertification and degradation in sub-Saharan Africa—the role of livestock. BioScience **44**:28–34.

Donovan, L. A., and J. R. Ehleringer. 1992. Contrasting water-use patterns among size and life-history classes of a semi-arid shrub. Functional Ecology **6**:482–488.

Donovan, L. A., and J. R. Ehleringer. 1994. Water stress and use of summer precipitation in a Great Basin shrub community. Functional Ecology **8**:289–297.

Fernandez, O. A., and M. M. Caldwell. 1975. Phenology and dynamics of root growth of three cool semi-desert shrubs. Journal of Ecology **63**:703–714.

Fisher, F. M., L. W. Parker, J. P. Anderson, and W. G. Whitford. 1987. Nitrogen mineralization in a desert soil: interacting effects of soil moisture and nitrogen fertilizer. Soil Science Society of America Journal **51**:1033–1041.

Fisher, F. M., and W. G. Whitford. 1995. Field simulation of wet and dry years in the Chihuahuan desert: soil moisture, N mineralization and ion-exchange resin bags. Biology and Fertility of Soils **20**:137–146.

Franco, A. C., A. G. de Soyza, R. A. Virginia, J. F. Reynolds, and W. G. Whitford. 1994. Effects of plant size and water relations on gas exchange and growth of the desert shrub, *Larrea tridentata*. Oecologia **97**:171–178.

Franco-Pizaña, J., T. E. Fulbright, and D. T. Gardiner. 1995. Spatial relations between shrubs and *Prosopis glandulosa* canopies. Journal of Vegetation Science **6**:73–78.

Freckman, D. W., and R. Mankau. 1986. Abundance, distribution, biomass and energetics of soil nematodes in a northern Mojave Desert ecosystem. Pedobiologia **29**:129–142.

Fusco, M., J. Holechek, A. Tembo, A. Daniel, and M. Cardenas. 1995. Grazing influences on watering point vegetation in the Chihuahuan Desert. Journal of Range Management **48**:32–38.

Gallardo, A., and W. H. Schlesinger. 1995. Factors determining soil microbial biomass and nutrient immobilization in desert soils. Biogeochemistry **28**:55–68.

Geiger, D. R., and J. C. Servaites. 1991. Carbon allocation and response to stress. Pages 103–127 *in* H. A. Mooney, W. E. Winner, and E. J. Pell, editors. Response of plants to multiple stresses. Academic Press, New York, New York, USA.

Gibbens, R. P., and R. F. Beck. 1988. Changes in grass basal area and forb densities over a 64-year period on grassland types of the Jornada Experimental Range. Journal of Range Management **41**:186–192.

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.

Grime, J. P., B. D. Campbell, J. M. L. Mackey, and J. C. Crick. 1991. Root plasticity, nitrogen capture and competitive ability. Pages 381–397 *in* D. Atkinson, editor. Plant root growth: an ecological perspective. Special Publication Number 10, British Ecological Society, Blackwell Science, Oxford, UK.

Grover, H. D., and H. B. Musick. 1990. Shrubland encroachment in southern New Mexico, U.S.A.: an analysis of desertification processes in the American Southwest. Climatic Change **17**:305–330.

Harrington, G. N. 1991. Effects of soil moisture on shrub seedling survival in a semi-arid grassland. Ecology **72**: 1138–1149.

Hayes, D. C., and T. R. Seastedt. 1987. Root dynamics of tallgrass prairie in wet and dry years. Canadian Journal of Botany **65**:787–791.

Hendrick, R. L., and K. S. Pregitzer. 1992. The demography of fine roots in a northern hardwood forest. Ecology **73**: 1094–1104.

Hendrick, R. L., and K. S. Pregitzer. 1993. The dynamics of fine root length, biomass, and nitrogen content in two northern hardwood ecosystems. Canadian Journal of Forest Research **23**:2507–2520.

Hennessy, J. T., R. P. Gibbens, J. M. Tromble, and M. Cardenas. 1985. Mesquite (*Prosopis glandulosa* Torr.) dunes and interdunes in southern New Mexico: a study of soil properties and soil water relations. Journal of Arid Environments **9**:27–69.

Herman, R. P., K. R. Provencio, J. Herreramatos, and R. J. Torrez. 1995. Resource islands predict the distribution of heterotrophic bacteria in Chihuahuan Desert soils. Applied and Environmental Microbiology **61**:1816–1821.

Ho, M. C., R. E. Roisman, and R. A. Virginia. 1996. Using strontium and rubidium tracers to characterize nutrient uptake patterns in creosotebush and mesquite. Southwestern Naturalist **41**:239–247.

Horst, G. L., and C. J. Nelson. 1979. Compensatory growth of tall fescue following drought. Agronomy Journal **71**: 559–563.

Hsaio, T. C. 1973. Plant response to water stress. Annual Review of Plant Physiology **24**:519–570.

Hsiao, T. C., and E. Acevedo. 1974. Plant responses to water deficit, water-use efficiency, and drought resistance. Agricultural Meteorology **14**:59–84.

Humphrey, R. R. 1958. The desert grassland: a history of vegetational change and an analysis of causes. Botanical Review **24**:193–252.

Joslin, J. D., and G. S. Henderson. 1987. Organic matter and nutrients associated with fine root turnover in a white oak stand. Forest Science **33**:330–346.

Keeney, D. R., and D. W. Nelson. 1982. Nitrogen—inorganic forms. Pages 643–698 *in* A. L. Page, R. H. Miller, and D. R. Keeny, editors. Methods of soil analysis. Part 2. Chemical and microbiological properties. Second edition. Agronomy Series Number 9. American Society of Agronomy and Soil Science Society of America, Madison, Wisconsin, USA.

Kummerow, J., D. Krause, and W. Jow. 1978. Seasonal changes of fine root density in southern California chaparral. Oecologia **37**:201–212.

Lajtha, K., and W. G. Whitford. 1989. The effect of water and nitrogen amendments on photosynthesis, leaf demography, and resource-use efficiency in *Larrea tridentata*, a desert evergreen shrub. Oecologia **80**:341–348.

Larsson, K., and E. Steen. 1988. Changes in mass and chemical composition of grass roots during decomposition. Grass and Forage Science **43**:173–177.

Lauenroth, W. K., O. E. Sala, D. G. Milchunas, and R. W. Lathrop. 1987. Root dynamics of *Bouteloua gracilis* during short-term recovery from drought. Functional Ecology **1**:117–124.

Laycock, W. A. 1991. Stable states and thresholds of range condition in North American rangelands: a viewpoint. Journal of Range Management **44**:427–433.

Le Houérou, H. N. 1992. An overview of vegetation and land degradation in world arid lands. Pages 127–163 *in* H. E. Dregne, editor. Degradation and restoration of arid lands. International Center for Arid and Semi-Arid Lands Studies, Texas Tech University, Lubbock, Texas, USA.

Ludlow, M. M., and T. T. Ng. 1974. Water stress suspends leaf aging. Plant Science Letters **3**:235–240.

Ludwig, J. A., G. L. Cunningham, and P. D. Whitson. 1988. Distribution of annual plants in North American deserts. Journal of Arid Environments **15**:221–227.

Ludwig, J. A., J. F. Reynolds, and P. D. Whitson. 1975. Size-biomass relations of several Chihuahuan Desert shrubs. American Midland Naturalist **94**:451–461.

Lyr, H., and G. Hoffman. 1967. Growth rates and growth periodicity of tree roots. International Review of Forest Research **2**:181–236.

MacMahon, J. A., and F. H. Wagner. 1985. The Mojave, Sonoran, and Chihuahuan deserts of North America. Pages 105–202 *in* M. Evenari, I. Noy-Meir, and D. W. Goodall, editors. Hot deserts and arid shrublands. Ecosystems of the world. Elsevier Science, New York, New York, USA.

Manning, S. J., and D. P. Groeneveld. 1990. Shrub rooting characteristics and water acquisition on xeric sites in the western Great Basin. Pages 238–244 *in* E. D. McArthur, E. M. Romney, S. D. Smith, and P. T. Teuller, editors. Proceedings of the Symposium on Cheatgrass Invasion, Shrub Dieoff and Other Aspects of Shrub Biology and Management. U.S. Forest Service General Technical Report **INT-276**.

Mauchamp, A., and J. L. Janeau. 1993. Water funnelling by the crown of *Flourensia cernua*, a Chihuahuan desert shrub. Journal of Arid Environments **25**:299–306.

Mazzarino, M. J., L. Oliva, A. Nuñez, G. Nuñez, and E. Buffa. 1991. Nitrogen mineralization and soil fertility in the Dry Chaco ecosystem (Argentina). Soil Science Society of America Journal **55**:515–522.

McAuliffe, J. R. 1988. Markovian dynamics of simple and complex desert communities. American Naturalist **131**: 459–490.

McNaughton, S. J. 1979. Grazing as an optimization process: grass–ungulate relationships in the Serengeti. American Naturalist **113**:691–703.

Meinzer, F. C., P. W. Rundel, M. R. Sharifi, and E. T. Nilsen. 1986. Turgor and osmotic relations of the desert shrub *Larrea tridentata*. Plant, Cell and Environment **9**:467–475.

Milton, S. J., W. R. J. Dean, M. A. Duplessis, and W. R. Siegfried. 1994. A conceptual model of arid rangeland degradation—the escalating cost of declining productivity. BioScience **44**:70–76.

Mooney, H. A., O. Björkman, and G. J. Collatz. 1978. Photosynthetic acclimation to temperature in the desert shrub *Larrea divariacata*. I. Carbon dioxide exchange characteristics of intact leaves. Plant Physiology **61**:406–410.

Mooney, H. A., B. B. Simpson and O. T. Solbrig. 1977. Phenology, morphology and physiology. Pages 26–42 *in* B. B. Simpson, editor. Mesquite: its biology in two desert ecosystems. Dowden, Hutchinson and Ross, Stroudsburg, Pennsylvania, USA.

Nadelhoffer, K. J., J. D. Aber, and J. M. Melillo. 1985. Fine roots, net primary production and nitrogen availability: a new hypothesis. Ecology **66**:1377–1390.

Nash, M. H., and L. A. Daugherty. 1990. Soil–landscape relationships in alluvium sediments in southern New Mexico. New Mexico Agricultural Experiment Station Bulletin Number **746**.

Navar, J., and R. B. Bryan. 1990. Interception loss and rainfall redistribution by three semi-arid growing shrubs in northeastern Mexico. Journal of Hydrology **115**:51–63.

Neilson, R. P. 1986. High-resolution climatic analysis and Southwest biogeography. Science **232**:27–34.

Nilsen, E. T., and W. H. Muller. 1981. Phenology of the drought-deciduous shrub *Lotus scoparius*: climatic controls and adaptive significance. Ecological Monographs **51**:323–341.

Nilsen, E. T., M. R. Sharifi, P. W. Rundel, W. M. Jarrell, and R. A. Virginia. 1983. Diurnal and seasonal water relations of the desert phreatophyte *Prosopis glandulosa* (honey mesquite) in the Sonoran Desert of California. Ecology **64**: 1381–1393.

Nilsen, E. T., M. R. Sharifi, P. W. Rundel, and R. A. Virginia. 1986. Influences of microclimatic conditions and water relations on seasonal leaf dimorphism of *Prosopis glandulosa* var. *Torreyana* in the Sonoran Desert, California. Oecologia **69**:95–100.

Nobel, P. S., and P. W. Jordan. 1983. Transpiration stream of desert species: resistance and capacitance for a C3, a C4, and a CAM plant. Journal of Experimental Botany **34**: 1379–1391.

Noy-Meir, I. 1973. Desert ecosystems: environment and producers. Annual Review of Ecology and Systematics **4**:25–41.

Odening, W. R., B. R. Strain, and W. C. Oechel. 1974. The effect of decreasing water potential on net $CO_2$ exchange of intact desert shrubs. Ecology **55**:1086–1095.

OIES. 1991. Arid ecosystem interactions. Office of Interdisciplinary Earth Studies, Boulder, Colorado, USA.

Olsen, S. R., and L. E. Sommers. 1982. Phosphorus. Pages 403–430 *in* A. L. Page, R. H. Miller, and D. R. Keeny, editors. Methods of soil analysis. Part 2. Chemical and microbiological properties. Second edition. Agronomy Series Number 9. American Society of Agronomy and Soil Science Society of America, Madison, Wisconsin, USA.

Orians, G. H., and O. T. Solbrig. 1977. A cost-income model of leaves and roots with special reference to arid and semi-arid areas. American Naturalist **111**:677–690.

Parker, L. W., P. F. Santos, J. Phillips, and W. G. Whitford. 1984. Carbon and nitrogen dynamics during the decomposition of litter and roots of a Chihuahuan Desert annual *Lepidium lasiocarpum*. Ecological Monographs **54**:339–360.

Peláez, R., R. A. Distel, R. M. Boo, O. R. Elia, and M. D. Mayor. 1994. Water relations between shrubs and grasses in semi-arid Argentina. Journal of Arid Environments **27**: 71–78.

Pell, E. J., P. J. Temple, A. L. Friend, H. A. Mooney, and W. E. Winner. 1994. Compensation as a plant response to ozone and associated stresses—an analysis of ROPIS experiments. Journal of Environmental Quality **23**:429–436.

Persson, H. 1979. Fine-root production, mortality and decomposition in forest ecosystems. Vegetatio **41**:101–109.

Pieper, R. D., J. C. Anway, M. A. Ellstrom, C. H. Herbal, R. L. Packard, S. L. Pimm, R. J. Raitt, E. E. Staffeldt, and J. G. Watts. 1983. Structure and function of North American desert grassland ecosystems. Report Number 39, U.S. Department of Agriculture Agricultural Experiment Station, New Mexico State University, Las Cruces, New Mexico, USA.

Reynolds, J. F., R. A. Virginia, and W. H. Schlesinger. 1997. Defining functional types for models of desertification. Pages 194–214 *in* T. M. Smith, H. H. Shugart, and F. I. Woodward, editors. Plant functional types: their relevance to ecosystem properties and global change. Cambridge University Press, Cambridge, UK.

Rostagno, C. M. 1989. Infiltration and sediment production as affected by soil surface conditions in a shrubland of Patagonia, Argentina. Journal of Range Management **42**: 382–385.

Rundel, P. W., and P. S. Nobel. 1991. Structure and function in desert root systems. Pages 349–377 *in* D. Atkinson, editor. Plant root growth: an ecological perspective. British Ecological Society Special Publication Number 10. Blackwell Scientific, Oxford, UK.

Rutherford, M. C. 1983. Growth rates, biomass and distribution of selected woody plant roots in *Burkea africana–Ochna pulchra* savanna. Vegetatio **52**:45–63.

Sala, O. E., R. A. Golluscio, W. K. Lauenroth, and A. Soriano.

1989. Resource partitioning between shrubs and grasses in the Patagonian steppe. Oecologia **81**:501–505.

Schlesinger, W. H., J. A. Raikes, A. E. Hartley, and A. F. Cross. 1996. On the spatial pattern of soil nutrients in desert ecosystems. Ecology **77**:364–374.

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.

Seastedt, T. R., and A. K. Knapp. 1993. Consequences of non-equilibrium resource availability across multiple time scales: the transient maxima hypothesis. American Naturalist **141**:621–633.

Smith, S. D., and P. S. Nobel. 1986. Deserts. Pages 14–62 *in* N. R. Baker and S. P. Long, editors. Photosynthesis in contrasting environments. Elsevier Science, Amsterdam, The Netherlands.

Sokal, R., and F. J. Rohlf. 1981. Biometry. W. H. Freeman, New York, New York, USA.

Solbrig, O. T., and G. H. Orians. 1977. The adaptive characteristics of desert plants. American Scientist **65**:412–421.

Stockton, P. H., and D. A. Gillette. 1990. Field measurement of the sheltering effect of vegetation on erodible land surfaces. Land Degradation and Rehabilitation **2**:77–85.

Takar, A. A., J. P. Dobrowolski, and T. L. Thurow. 1990. Influence of grazing, vegetation life-form, soil type on infiltration rates and inter-rill erosion on a Somali rangeland. Journal of Range Management **43**:486–490.

Tromble, J. M. 1988. Water interception by two arid land shrubs. Journal of Arid Environments **15**:65–70.

Velleman, P. F. 1995. Data desk handbook. Data Description, Ithaca, New York, USA.

Virginia, R. A., and W. M. Jarrell. 1983. Soil properties in a mesquite-dominated Sonoran desert ecosystem. Soil Science Society of America Journal **47**:138–144.

Virginia, R. A., and W. M. Jarrell. 1987. Approaches for studying the function of deep root systems. Pages 107–127 *in* J. D. Tenhunen, F. M. Catarino, O. L. Lange, and W. C. Oechel, editors. Plant response to stress—functional analysis in Mediterranean ecosystems. Springer-Verlag, Berlin, Germany.

Walker, B. H., and I. Noy-Meir. 1982. Aspects of stability and resilience of savanna ecosystems. Pages 556–590 *in* B. J. Huntley and B. H. Walker, editors. Ecology of tropical savannas. Ecological Studies Volume 42. Springer-Verlag, Berlin, Germany.

Wallace, A., E. M. Romney, G. E. Kleinkopf, and S. M. Soufi. 1978. Uptake of mineral forms of nitrogen by desert plants. Pages 130–151 *in* N. E. West and J. J. Skujins, editors. Nitrogen in desert ecosystems. US/IBP Synthesis Series 9. Dowden, Hutchinson and Ross, Stroudsburg, Pennsylvania, USA.

Walter, H. 1971. Ecology of tropical and subtropical vegetation. Oliver and Boyd, Edinburgh, UK.

Wang, Z., W. H. Burch, P. Mou, R. H. Jones, and R. J. Mitchell. 1995. Accuracy of visible and ultraviolet light for estimating live root proportions with minirhizotrons. Ecology **76**:2330–2334.

Westoby, M. 1979/80. Elements of a theory of vegetation dynamics in arid rangelands. Israeli Journal of Botany **28**: 169–194.

Westoby, M., B. Walker, and I. Noy-Meir. 1989. Opportunistic management for rangelands not at equilibrium. Journal of Range Management **42**:266–274.

Wetselaar, R. 1968. Soil organic nitrogen mineralization as affected by low soil water potentials. Plant and Soil **29**:9–17.

Whitford, W. G., J. Anderson, and P. M. Rice. 1997. Stemflow contribution to the "fertile island" effect in creosotebush, *Larrea tridentata*. Journal of Arid Environments **35**:451–457.

Whitford, W. G., V. Meentemeyer, T. R. Seastedt, K. Cromack, Jr., D. A. Crossley, Jr., P. Santos, R. L. Todd, and J. B. Waide. 1981. Exceptions to the AET model: deserts and clear-cut forest. Ecology **62**:275–277.

Whitford, W. G., Y. Steinberger, W. MacKay, L. W. Parker, D. Freckman, J. A. Wallwork, and D. Weems. 1986. Rainfall and decomposition in the Chihuahuan Desert. Oecologia **68**:512–515.

Wierenga, P. J., J. H. M. Hendricx, N. M. Nash, J. Ludwig, and L. A. Daugherty. 1987. Variation of soil and vegetation with distance along a transect in the Chihuahuan Desert. Journal of Arid Environments **13**:53–63.

York, J. C., and W. A. Dick-Peddie. 1969. Vegetation changes in southern New Mexico during the past hundred years. Pages 157–166 *in* W. G. McGinnies and B. J. Goldman, editors. Arid lands in perspective. University of Arizona Press, Tucson, Arizona, USA.

## APPENDIX A

*F* values for soil water dynamics at the three study sites. Degrees of freedom are in parentheses.

| Source | Summer 1991 | Winter/spring 1992 | Summer 1992 | Winter/spring 1993 | Summer 1993 |
|---|---|---|---|---|---|
| Lower bajada† | | | | | |
| Drought treatment (trt) | 0.03 (1) | 105.97 (2)*** | 1.12 (2) | 7.65 (2)*** | 0.28 (2) |
| Species | 0.02 (1) | 0.15 (1) | 0.02 (1) | 3.53 (1) | 0.11 (1) |
| Trt × species | 0.06 (1) | 1.67 (2) | 1.47 (2) | 2.45 (2) | 0.95 (2) |
| Plot | 16.81 (28)*** | 7.61 (42)*** | 1.63 (40)* | 6.04 (42)*** | 7.62 (42)*** |
| Depth | 0.14 (2) | 55.42 (2)*** | 0.14 (2) | 113.85 (2)*** | 0.09 (2) |
| Trt × depth | 3.47 (2)* | 21.48 (4)*** | 1.58 (4) | 35.26 (4)*** | 3.59 (4)** |
| Species × depth | 0.67 (2) | 8.96 (2)*** | 0.17 (2) | 7.05 (2)*** | 1.38 (2) |
| Trt × species × depth | 0.60 (2) | 0.60 (4) | 0.02 | 0.32 (4) | 0.08 (4) |
| Time | 0.74 (7) | 187.12 (5)*** | ··· | 45.26 (4)*** | 0.40 (3) |
| Trt × time | 0.30 (7) | 37.04 (10)*** | ··· | 7.40 (8)*** | 0.93 (6) |
| Species × time | 0.19 (7) | 0.44 (5) | ··· | 1.93 (4) | 0.01 (3) |
| Trt × species × time | 0.35 (6) | 0.82 (10) | ··· | 0.73 (8) | 0.06 (6) |
| Depth × time | 0.67 (14) | 13.42 (10)*** | ··· | 17.56 (8)*** | 0.34 (6) |
| Trt × depth × time | 0.45 (14) | 2.44 (20)*** | ··· | 3.77 (16)*** | 0.31 (12) |
| Species × depth × time | 0.23 (14) | 0.47 (10) | ··· | 1.23 (8) | 0.02 (6) |
| Trt × species × depth × time | 0.74 (14) | 0.17 (20) | ··· | 0.57 (16) | 0.06 (12) |
| Error mean square | 0.0003 (530) | 0.0006 (713) | 0.0004 (80) | 0.0004 (513) | 0.0003 (462) |
| Upper bajada‡ | | | | | |
| Drought × trt | 1.11 (1) | 2.47 (1) | 8.77 (1)** | 0.65 (1) | 5.07 (1)* |
| Island age | 0.04 (1) | 0.10 (1) | 0.17 (1) | 0.04 (1) | 3.57 (1) |
| Trt × age | 0.02 (1) | 0.11 (12) | 2.52 (1) | 0.83 (1) | 0.73 (1) |
| Plot | 35.06 (28)*** | 19.65 (28)*** | 3.43 (27)*** | 15.98 (28)*** | 9.16 (28)*** |
| Depth | 319.73 (2)*** | 170.06 (2)*** | 17.35 (2)*** | 236.22 (2)*** | 16.73 (2)*** |
| Trt × depth | 48.20 (2)*** | 5.54 (2)** | 0.90 (2) | 0.36 (2) | 19.48 (2)*** |
| Age × depth | 84.27 (2)*** | 50.44 (2)*** | 3.53 (2)* | 20.69 (2)*** | 2.08 (2) |
| Trt × age × depth | 2.97 (2) | 5.07 (2)** | 0.35 (2) | 1.18 (2) | 1.61 (2) |
| Time | 6.88 (6)*** | 1358 (6)*** | ··· | 400.65 (6)*** | 3.02 (2) |
| Trt × time | 6.11 (6)*** | 3.52 (6)** | ··· | 4.56 (6)*** | 0.01 (2) |
| Age × time | 0.59 (6) | 9.94 (6)*** | ··· | 11.43 (6)*** | 0.28 (2) |
| Trt × age × time | 0.42 (6) | 10.08 (6)*** | ··· | 0.61 (6) | 0.27 (2) |
| Depth × time | 7.21 (12)*** | 8.18 (12)** | ··· | 54.81 (12)*** | 1.88 (4) |
| Trt × depth × time | 5.85 (12)*** | 4.69 (12)*** | ··· | 1.12 (12) | 0.77 (4) |
| Age × depth × time | 0.29 (12) | 2.61 (12)** | ··· | 2.06 (12) | 0.14 (4) |
| Trt × age × depth × time | 0.12 (12) | 0.41 (12) | ··· | 0.83 (12) | 0.29 (4) |
| Error mean square | 0.0007 (556) | 0.0006 (557) | 0.2490 (51) | 0.0007 (460) | 0.2880 (201) |
| Dunes | | | | | |
| Drought trt | 12.07 (1)** | 0.08 (1) | 0.03 (1) | 0.61 (1) | 3.14 (1) |
| Island age | 1.29 (1) | 0.47 (1) | 0.58 (1) | 0.32 (1) | 1.02 (1) |
| Trt × age | 3.00 (1) | 1.51 (1) | 0.53 (1) | 1.00 (1) | 1.78 (1) |
| Plot | 31.75 (28)** | 20.45 (28)*** | 5.60 (28)*** | 15.34 (28)*** | 17.45 (28)*** |
| Depth | 735.80 (2)*** | 536.60 (2)*** | 219.02 (2)*** | 464.94 (2)*** | 486.54 (2)*** |
| Trt × depth | 75.31 (2)*** | 2.59 (2) | 0.68 (2) | 3.35 (2)* | 4.21 (2)* |
| Age × depth | 3.29 (2)* | 1.48 (2) | 0.80 (2) | 0.66 (2) | 0.55 (2) |
| Trt × age × depth | 4.51 (2)* | 1.97 (2) | 0.98 (2) | 2.69 (2) | 2.34 (2) |
| Time | 16.48 (5)*** | 14.59 (3)*** | 9.03 (1)** | 1.37 (2) | 52.68 (3)*** |
| Trt × time | 15.55 (5)*** | 2.13 (3) | 3.65 (1) | 0.10 (2) | 8.57 (3)*** |
| Age × time | 0.67 (5) | 0.67 (3) | 0.13 (1) | 0.18 (2) | 1.18 (3) |
| Trt × age × time | 1.88 (5) | 0.36 (3) | 0.00 (1) | 0.10 (2) | 0.18 (3) |
| Depth × time | 5.08 (10)*** | 0.33 (6) | 0.87 (2) | 1.36 (4) | 6.63 (6)*** |
| Trt × depth × time | 4.63 (10)*** | 0.05 (6) | 0.31 (2) | 0.12 (4) | 0.49 (6) |
| Age × depth × time | 0.10 (10) | 0.11 (6) | 0.33 (2) | 0.11 (4) | 0.08 (6) |
| Trt × age × depth × time | 0.15 (10) | 0.01 (6) | 0.39 (2) | 0.09 (4) | 0.26 (6) |
| Error mean square | 0.0021 (472) | 0.0018 (308) | 0.0025 (92) | 0.0022 (217) | 0.0021 (304) |

*Note:* Levels of significance: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

† A single sampling date for summer 1992: 23 July 1992.

‡ A single sampling date for summer 1992: 29 August 1992.

## APPENDIX B

*F* values for growth and physiology of *Larrea* at the lower bajada. Degrees of freedom are in parentheses.

| Source | Summer 1991 | Winter/spring 1992 | Summer 1992 | Winter/spring 1993 | Summer 1993 |
|---|---|---|---|---|---|
| Xylem water potential (XWP) | | | | | |
| Drought treatment (trt) | 99.56 (1)*** | 48.01 (2)*** | 2.04 (2) | 36.84 (2)*** | 16.28 (2)*** |
| Plant | ... | ... | ... | ... | ... |
| Time | 29.16 (7)*** | 9.43 (3)*** | 3.30 (1) | 11.89 (5)*** | 15.62 (5)*** |
| Trt × time | 16.94 (7)*** | 2.37 (6)* | 9.29 (2)*** | 6.92 (10)*** | 1.37 (10) |
| Error mean square | 0.30 (46) | 0.18 (65) | 1.21 (29) | 0.59 (80) | 0.57 (42) |
| Photosynthesis ($A_d$) | | | | | |
| Drought trt | 7.55 (1)** | 31.95 (2)*** | 1.66 (2) | 14.19 (2)*** | 5.24 (2)** |
| Plant | ... | 1.86 (21)* | ... | 3.32 (19)** | ... |
| Time | 7.84 (4)*** | 119.51 (5)*** | ... | 85.43 (3)*** | 8.57*** |
| Trt × time | 2.30 (4) | 7.07 (10)*** | ... | 6.22 (6)*** | 2.52 (16)** |
| Error mean square | 0.012 (46) | 0.078 (77) | 0.001 (15) | 0.071 (28) | 0.0008 (68) |
| Transpiration ($E_d$) | | | | | |
| Drought trt | 0.35 (1) | 28.96 (2)*** | ... | 14.56 (2)*** | 1.57 (2) |
| Plant | 0.91 (20) | 2.49 (21)** | ... | 2.13 (19)* | 5.73 (20)*** |
| Time | 8.19 (4)*** | 56.32 (5)*** | ... | 96.32 (3)*** | 38.39 (7)*** |
| Trt × time | 0.85 (4) | 8.57 (10)*** | ... | 2.54 (6)* | 6.29 (14)*** |
| Error mean square | 33 196 (26) | 0.067 (77) | ... | 0.11 (33) | 0.052 (53) |
| Water use efficiency (WUE) | | | | | |
| Drought trt | 24.16 (1)*** | 0.92 (2) | 2.69 (2) | 1.27 (2) | 0.36 (2) |
| Plant | 1.77 (20) | 3.19 (21)*** | ... | 4.10 (19)*** | 6.37 (20)*** |
| Time | 14.98 (4)*** | 27.87 (5)*** | ... | 141.3 (3)*** | 50.11 (7)*** |
| Trt × time | 6.22 (4)** | 1.68 (10) | ... | 1.69 (6) | 3.07 (14)** |
| Error mean square | 0.045 (24) | 0.23 (77) | 0.012 (15) | 0.008 (28) | 0.037 (50) |
| Stem growth | | | | | |
| Drought trt | 1.94 (1) | 38.01 (2)*** | 5.41 (2)* | 0.11 (2) | 7.52 (2)** |
| Plant | 3.32 (15)* | 2.12 (20) | ... | 2.90 (19)** | 3.94 (20)*** |
| Time | 12.21 (1)** | 114.69 (1)*** | ... | 17.34 (3)*** | 15.89 (8)*** |
| Trt × time | 0.44 (1) | 28.01 (2)*** | ... | 1.53 (6) | 2.22 (16)** |
| Error mean square | 0.078 (13) | 0.014 (20) | 0.054 (20) | 0.017 (46) | 0.036 (144) |

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

## APPENDIX C

*F* values for growth and physiology of *Prosopis* at the lower bajada. Degrees of freedom are in parentheses.

| Source | Summer 1991 | Winter/spring 1992 | Summer 1992 | Winter/spring 1993 | Summer 1993 |
|---|---|---|---|---|---|
| Xylem water potential (XWP) | | | | | |
| Drought treatment (trt) | 64.47 (1)*** | 66.72 (2)*** | 14.59 (2)*** | 1.86 (2) | 6.81 (2)** |
| Plant | ... | ... | ... | ... | ... |
| Time | 7.55 (8)*** | 12.11 (1)** | 8.19 (2)*** | 5.70 (1)* | 31.89 (5)*** |
| Trt × time | 4.11 (8)*** | 0.42 (2) | 0.63 (4) | 2.48 (2) | 2.28 (10)* |
| Error mean square | 0.21 (46) | 0.046 (17) | 0.31 (37) | 0.12 (16) | 0.18 (47) |
| Photosynthesis ($A_d$) | | | | | |
| Drought trt | 8.89 (1)** | ... | 0.92 (2) | ... | 10.81 (2)*** |
| Plant | ... | ... | | ... | ... |
| Time | 5.82 (4)*** | ... | 51.46 (2) | ... | 5.97 (7)*** |
| Trt × time | 0.77 (4) | ... | 3.78 (4)* | ... | 2.30 (14)* |
| Error mean square | 0.90 (35) | ... | 0.10 (39) | ... | 0.066 (69) |
| Transpiration ($E_d$) | | | | | |
| Drought trt | 0.032 (1) | ... | 3.51 (2)* | ... | 6.64 (2)** |
| Plant | 2.71 (15)* | ... | 2.91 (21)* | ... | 3.98 (21)*** |
| Time | 7.14 (4)*** | ... | 33.32 (2)*** | ... | 25.81 (6)*** |
| Trt × time | 0.35 (4) | ... | 5.85 (4)** | ... | 3.30 (12)** |
| Error mean square | 29 648 (20) | ... | 6339 (18) | ... | 0.037 (51) |
| Water use efficiency (WUE) | | | | | |
| Drought trt | 4.20 (1) | ... | 1.41 (2) | ... | 0.16 (2) |
| Plant | 0.86 (15) | ... | 0.95 (21) | ... | 3.73 (21)*** |
| Time | 25.49 (4)*** | ... | 128.5 (2)*** | ... | 33.84 (6)*** |
| Trt × time | 0.42 (4) | ... | 1.82 (4) | ... | 1.65 (12) |
| Error mean square | 0.084 (20) | ... | 0.075 (18) | ... | 0.043 (51) |
| Stem growth | | | | | |
| Drought trt | 2.02 (1) | 1.93 (1) | 1.76 (2) | 1.75 (2) | 0.22 (2) |
| Plant | ... | ... | ... | ... | 1.32 (21) |
| Time | ... | ... | ... | ... | 2.77 (8)** |
| Trt × time | ... | ... | ... | ... | 0.58 (16) |
| Error mean square | 0.005 (13) | 0.16 (13) | 1.95 (19) | 0.29 (16) | 0.83 (121) |

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

## APPENDIX D

*F* values for growth and physiology of *Larrea* at the upper bajada. Degrees of freedom are in parentheses.

| | Summer 1991 | Winter/spring 1992† | Summer 1992 | Winter/spring 1993† | Summer 1993 |
|---|---|---|---|---|---|
| Xylem water potential (XWP) | | | | | |
| Drought treatment (trt) | 90.14 (1)*** | 0.18 (1) | 9.60 (1)** | 0.22 (1) | 65.06 (1)*** |
| Island age | 0.77 (1) | 17.97 (1)*** | 9.92 (1)** | 0.99 (1) | 2.53 (1) |
| Trt × island | 1.23 (1) | 1.85 (1) | 8.39 (1)** | 0.75 (1) | 31.2 (1)*** |
| Plant | ... | ... | ... | ... | ... |
| Time | 39.99 (7)*** | 21.55 (5)*** | 31.34 (3)*** | 24.38 (7)*** | 40.98 (5)*** |
| Trt × time | 4.70 (7)*** | 1.3 (5) | 1.81 (3) | 3.04 (7)** | 5.37 (5)*** |
| Island × time | 2.39 (7)* | 5.10 (5)*** | 3.02 (3)* | 3.00 (4)* | 3.73 (5)** |
| Trt × island × time | 2.14 (7) | 0.87 (5) | 8.95 (3)*** | 2.07 (3) | 2.40 (5) |
| Error mean square | 0.3 (81) | 0.069 (131) | 0.24 (61) | 0.024 (72) | 0.29 (52) |
| Photosynthesis ($A_d$) | | | | | |
| Drought | 16.4 (1)*** | 4.74 (1)* | 0.17 (1) | 0.002 (1) | 17.29 (1)*** |
| Island | 0.72 (1) | 4.94 (1)* | 0 (1) | 2.99 (1) | 4.59 (1)* |
| Trt × island | 0.35 (1) | 0.04 (1) | 1.26 (1) | 0.17 (1) | 2.43 (1) |
| Plant | ... | 1.49 (28) | 7.01 (12)** | 1.93 (12) | 2.2 (28)** |
| Time | 49.58 (4)*** | 324.16 (4)*** | 0.21 (1) | 21.60 (2)*** | 32.93 (4)*** |
| Trt × time | 2.11 (4) | 0.61 (4) | 11.86 (1)** | 2.62 (2) | 0.28 (4) |
| Island × time | 1.00 (4) | 5.17 (4)*** | 1.02 (1) | 0.97 (2) | 0.42 (4) |
| Trt × island × time | 0.96 (4) | 0.76 (4) | 0.004 (1) | 0.40 (2) | 0.73 (4) |
| Error mean square | 0.0059 (46) | 0.0034 (110) | 0.00043 (12) | 0.00091 (21) | 0.00084 (46) |
| Transpiration ($E_d$) | | | | | |
| Drought trt | 0.02 (1) | 1.88 (1) | 1.77 (1) | 1.61 (1) | 53.82 (1)*** |
| Island | 1.35 (1) | 10.99 (1)** | 0.26 (1) | 6.77 (1)* | 0.36 (1) |
| Trt × island | 4.15 | 2.17 (1) | 7.56 (1)* | 1.05 (1) | 5.04 (1)* |
| Plant | ... | ... | ... | 1.64 (12) | ... |
| Time | 68.12 (4)*** | 168.26 (4)*** | 14.92 (1)*** | 124.41 (2)*** | 66.49 (5)*** |
| Trt × time | 1.20 (4) | 1.50 (4) | 4.84 (1)* | 0.74 (2) | 6.51 (5)*** |
| Island × time | 1.44 (4) | 1.18 (4) | 0.02 (1) | 2.41 (2) | 0.46 (5) |
| Trt × island × time | 1.41 (4) | 0.61 (4) | 2.02 (1) | 2.36 (2) | 1.49 (5) |
| Error mean square | 3.08 (46) | 0.11 (38) | 409.0 (24) | 144.0 (22) | 0.055 (69) |
| Water use efficiency (WUE) | | | | | |
| Drought trt | 63.51 (1)*** | 6.57 (1)* | 0.01 (1) | 0.20 (1) | 0.46 (1) |
| Island age | 0.42 (1) | 2.31 (1) | 0.30 (1) | 0.55 (1) | 7.87 (1)** |
| Trt × island | 3.05 (1) | 1.73 (1) | 0.26 (1) | 0.03 (1) | 0.27 (1) |
| Plant | ... | 2.13 (28)** | 2.20 (12) | 4.38 (12)** | 1.42 (28) |
| Time | 10.68 (4)*** | 43.96 (4)*** | 18.98 (1)*** | 364 (2)*** | 31.61 (4)*** |
| Trt × time | 1.32 (4) | 2.36 (4) | 0.22 (1) | 3.10 (2) | 2.05 (4) |
| Island × time | 3.45 (4)* | 0.17 (4) | 0.03 (1) | 0.10 (2) | 0.63 (4) |
| Trt × island × time | 5.39 (4)** | 1.51 (4) | 1.29 (1) | 1.56 (2) | 0.65 (4) |
| Error mean square | 0.029 (46) | 0.27 (110) | 0.10 (1) | 0.32 (20) | 0.10 (45) |
| Stem growth | | | | | |
| Drought trt | 22.58 (1)*** | 4.07 (1) | ... | 0.03 (1) | 2.85 (1) |
| Island age | ... | 8.93 (1)** | ... | 10.30 (1) | 3.12 (1) |
| Trt × island | ... | 0 (1) | ... | 1.09 (1)** | 5.61 (1)* |
| Plant | 3.62 (14)* | 2.48 (27)** | ... | 1.90 (28)* | 6.29 (28)*** |
| Time | 110.59 (1)*** | 78.18 (2)*** | ... | 3.52 (2)* | 23.26 (7)*** |
| Trt × time | 0.91 (1) | 5.50 (2)** | ... | 0.05 (2) | 5.33 (7)*** |
| Island × time | ... | 4.14 (2)* | ... | 0.11 (2) | 1.60 (7) |
| Trt × island × time | ... | 2.49 (2) | ... | 1.45 (2) | 2.97 (7)** |
| Error mean square | 0.0069 (14) | 0.016 (53) | ... | 0.81 (49) | 0.03 (195) |

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

† Significant drought treatment effect reflects differences in previously summer-droughted plants and controls.

## APPENDIX E

*F* values for growth and physiology of *Prosopis* at the dune site. Degrees of freedom are in parentheses.

| | Summer 1991 | Winter/spring 1992† | Summer 1992 | Winter/spring 1993‡ | Summer 1993 |
|---|---|---|---|---|---|
| Xylem water potential (XWP) | | | | | |
| Drought treatment (trt) | 200.03 (1)*** | ... | 0.03 (1) | ... | 21.02 (1)*** |
| Island age | 10.93 (1)** | ... | 0.001 (1) | ... | 0.24 (1) |
| Trt × island | 13.65 (1)*** | ... | 0.20 (1) | ... | 5.29 (1)* |
| Plant | ... | ... | ... | ... | ... |
| Time | 18.78 (5)*** | ... | 86.10 (2)*** | ... | 18.55 (7)*** |
| Trt × time | 7.47 (5)*** | ... | 1.69 (2) | ... | 5.73 (7)*** |
| Island × time | 1.61 (5) | ... | 0.54 (2) | ... | 0.80 (6) |
| Trt × island × time | 0.11 (5) | ... | 2.28 (2) | ... | 0.64 (6) |
| Error mean square | 0.018 (53) | ... | 0.017 (67) | ... | 0.077 (90) |
| Photosynthesis ($A_d$) | | | | | |
| Drought trt | 34.86 (1)*** | ... | 1.79 (1) | 0.72 (1) | 33.64 (1)*** |
| Island age | 0.03 (1) | ... | 22.95 (1)*** | 9.38 (1)* | 9.95 (1)** |
| Trt × island | 0.52 (1) | ... | 0.04 (1) | 0.07 (1) | 3.35 (1)* |
| Plant | ... | ... | ... | ... | ... |
| Time | 9.93 (5)*** | ... | 2.87 (2) | ... | 5.31 (6)*** |
| Trt × time | 1.97 (5) | ... | 0.72 (2) | ... | 0.99 (6) |
| Island × time | 6.86 (5)*** | ... | 0.23 (2) | ... | 1.48 (6) |
| Trt × island × time | 0.93 (5) | ... | 0.46 (2) | ... | 0.65 (6) |
| Error mean square | 0.0084 (49) | ... | 0.021 (67) | 0.0029 (10) | 0.0043 (84) |
| Transpiration ($E_d$) | | | | | |
| Drought trt | 32.02 (1)*** | ... | 3.24 (1) | 0.88 (1) | 34.51 (1)*** |
| Island age | 9.06 (1)** | ... | 15.93 (1)*** | 6.43 (1)* | 10.09 (1)** |
| Trt × island | 1.04 (1) | ... | 0.20 (1) | 0 (1) | 5.87 (1)* |
| Plant | ... | ... | ... | ... | ... |
| Time | 79.06 (4)*** | ... | 1.89 (12) | ... | 9.13 (6)*** |
| Trt × time | 2.69 (4)* | ... | 0.90 (2) | ... | 2.16 (6) |
| Island × time | 3.56 (4)* | ... | 0.12 (2) | ... | 1.63 (6) |
| Trt × island × time | 1.09 (4) | ... | 0.06 (2) | ... | 1.11 (6) |
| Error mean square | 5988.0 (44) | ... | 12 264.0 (67) | 0.097 (11) | 0.089 (84) |
| Water use efficiency (WUE) | | | | | |
| Drought trt | 4.52 (1)* | ... | 0.09 (1) | 2.41 (1) | 2.55 (1) |
| Island age | 5.03 (1)* | ... | 0.93 (1) | 0.23 (1) | 1.32 (1) |
| Trt × island | 0.24 | ... | 1.95 (1) | 0.21 (1) | 2.63 (1) |
| Plant | ... | ... | ... | ... | ... |
| Time | 20.97 (4)*** | ... | 28.46 (2)*** | ... | 16.80 (6)*** |
| Trt × time | 2.03 (4) | ... | 0.89 (2) | ... | 1.15 (6) |
| Island × time | 1.22 (4) | ... | 0.36 (2) | ... | 2.18 (6) |
| Trt × island × time | 1.78 (4) | ... | 0.07 (2) | ... | 1.38 (6) |
| Error mean square | 0.069 (42) | ... | 0.049 (66) | 0.097 (12) | 0.028 (84) |
| Stem growth | | | | | |
| Drought trt | 0.07 (1) | ... | 3.68 (1) | 12.92 (1)*** | 0.03 (1) |
| Island age | 2.13 (1) | ... | 3.59 (1) | 2.77 (1) | 2.94 (1) |
| Trt × island | 0.01 (1) | ... | 2.37 (1) | 0.47 (1) | 0.83 (1) |
| Plant | ... | ... | ... | ... | ... |
| Time | ... | ... | ... | 37.31 (2)*** | 3.21 (7)** |
| Trt × time | ... | ... | ... | 1.28 (2) | 0.57 (7) |
| Island × time | ... | ... | ... | 0.02 (2) | 0.74 (7) |
| Trt × island × time | ... | ... | ... | 0.23 (2) | 0.43 (7) |
| Error mean square | 2.04 (18) | ... | 1.69 (21) | 0.64 (68) | 0.91 (166) |

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

† Samples inadequate for analyses.

‡ Significant drought treatment effects reflect differences in previously summer-droughted plants and controls.

## APPENDIX F

*F* values for root appearance rates for *Larrea* (upper bajada) and *Prosopis* (dune site). Degrees of freedom are in parentheses.

| | Summer 1991 | Winter/spring 1992† | Summer 1992 | Winter/spring 1993† | Summer 1993 |
|---|---|---|---|---|---|
| *Larrea* | | | | | |
| Drought treatment (trt) | 33.00 (1)*** | 4.52 (1) | 11.21 (1)** | 0.27 (1) | 4.68 (1)* |
| Plant | 4.02 (14)*** | 2.04 (14)* | 1.56 (14)* | 2.66 (14)** | 3.27 (14)** |
| Tubes within plants | 1.04 (32) | 1.16 (32) | 1.09 (32) | 1.50 (32)* | 1.14 (32) |
| Depth | 53.71 (2)*** | 31.72 (2)*** | 7.33 (2)*** | 31.22 (2)*** | 17.30 (2)*** |
| Trt × depth | 27.63 (2)*** | 0.52 (2) | 6.78 (2)** | 0.34 (2) | 8.22 (2)*** |
| Time | 0.61 (1) | 78.58 (3)*** | 32.82 (1)*** | 98.38 (2)*** | 12.26 (6)*** |
| Trt × time | 0.87 (1) | 10.73 (3)*** | 0.17 (1) | 18.43 (2)*** | 2.55 (6)* |
| Depth × time | 0.30 (2) | 4.79 (6)*** | 1.64 (2) | 11.69 (4)*** | 5.00 (12)*** |
| Trt × depth × time | 1.43 (2) | 3.78 (6)*** | 0.20 (2) | 2.667 (4)* | 1.86 (12)* |
| Error mean square | 0.247 (229) | 0.253 (502) | 0.477 (230) | 0.215 (354) | 0.139 (892) |
| *Prosopis* | | | | | |
| Drought trt | 18.48 (1)*** | 8.13 (1)** | 1.17 (1) | 2.99 (1) | 32.84 (1)*** |
| Plant | 1.60 (14) | 2.77 (14)** | 2.54 (14)* | 1.58 (14) | 1.99 (14) |
| Tubes within plants | 2.01 (32)** | 1.69 (32)** | 1.39 (32) | 1.82 (32)** | 1.28 (32) |
| Depth | 7.41 (2)*** | 7.94 (2)*** | 0.71 (2) | 4.08 (2)* | 13.72 (2)*** |
| Trt × depth | 3.73 (2)* | 0.36 (2) | 4.86 (2)** | 1.78 (2) | 7.83 (2)*** |
| Time | ... | 77.16 (5)*** | ... | 25.28 (2)*** | 23.11 (6)*** |
| Trt × time | ... | 8.38 (5)*** | ... | 0.09 (2) | 3.57 (6)** |
| Depth × time | ... | 1.58 (10) | ... | 1.67 (4) | 2.12 (12)* |
| Trt × depth × time | ... | 1.01 (10) | ... | 4.22 (4)** | 0.96 (12) |
| Error mean square | 2.860 (92) | 3.282 (701) | 3.719 (701) | 2.906 (365) | 2.994 (885) |

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

† Significant drought treatment effects reflect differences in previously summer-droughted plants and controls.