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PLANT PHENOLOGY AND WATER RELATIONS IN A SALINE PAN-DUNE MOSAIC IN THE WESTERN MOJAVE DESERT

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ABSTRACT

An extensive mosaic of small clay pans and low stable dunes exists within Edwards Air Force Base in the western Mojave Desert of California. This pan-dune ecosystem, positioned between the large Rosamond and Rogers dry lakes on the old Pleistocene lakebed of Lake Thompson, provides an opportunity to study the seasonal patterns in growth and flowering phenology and water relations in a saltbush scrub community dominated by a mix of C₃ and C₄ species. C₃ shrubs initiated vegetative growth in February, with current shoot and leaf production largely ceasing in most species by mid-April. The deeply rooted *Tetradymia stenolepis* and *Ericameria nauseosa* continued vegetative growth through May. C₄ species including *Atriplex* and the grass *Distichilis spicata* typically began vegetative growth in mid- to late March, 2–6 weeks later than the first group and continued this growth in most cases through June and July. Reproductive growth commonly did not begin until June and continued into July and/or August. Shrub species showed a general pattern of slowly declining water potentials (increased stress) through the late spring and summer months reflecting more limited soil water availability. Smaller changes in predawn water potential over this period were seen in the deeply rooted species. Soil moisture availability in the widespread *Atriplex confertifolia* showed a pattern of variation between pan, dune and open flat microhabitats.

Key words: C₄ metabolism, desert plant phenology, Edwards Air Force Base, plant water relations, saltbush scrub.

INTRODUCTION

Saline shrublands communities dominated by shadscale (*Atriplex confertifolia* (Torr. & Frém.) S. Wats.) and saltbush (*Atriplex* spp.) scrub are widespread across the Great Basin in areas of endorheic drainage associated with dry playa lakes and topographic sinks (Billings 1949; West 1983; Caldwell 1985). Extensive studies of these plant communities in these cold desert ecosystems have been carried out in northern Utah, with a focus on plant growth dynamics and ecophysiology (Caldwell 1985; Smith and Nowak 1990). More poorly studied are superficially similar ecosystems that occur in lower elevation playas across the warm Mojave and lower Sonoran Deserts in California, as well as flood plains of the Mojave, Amargosa and Colorado Rivers. Poor drainage and subsequent evaporation rather than elevation are the key elements affecting these saline habitats.

A good example of a characteristic Great Basin saltbush community growing in winter rainfall warm desert climatic conditions can be seen in the Antelope Valley on the western margin of the Mojave Desert in Los Angeles County, California. The Antelope Valley, a low-lying area at about 700 m elevation, is roughly triangular in shape and bordered on the southwest by the San Gabriel Mountains and on the northwest by the Tehachapi Mountains (Charlton and Rundel 2017). The valley is a closed endorheic basin which was the site of the large Pleistocene Lake Thompson. Surface-water runoff in most of the basin ultimately

terminates in topographical depressions, most notably Rogers Dry Lake and the smaller Rosamond Dry Lake, both located entirely within the boundaries of Edwards Air Force Base (EAFB) (Charlton and Rundel 2017).

Our broad objectives in this study have been to expand on baseline studies of plant community structure and demography for the study site (Sharifi et al. 2017) to understand how ecophysiological traits associated with C₃ and C₄ metabolism (Keeley and Rundel 2003) impact the phenology and water relations of dominant plant species. These ecological data are relevant to the resource management of the unusual geomorphic pan-dune ecosystem on EAFB and provide baseline data on the community structure and biodiversity of this area. The fragility of this ecosystem was of paramount concern to the resource management of the base as it includes listed rare and endangered species as well as extensive ground cover of environmentally significant but fragile biotic crusts (Brostoff et al. 2005).

MATERIALS AND METHODS

Study Site

Field studies were carried out in an area of a mosaic of small salt pans and low stable dunes on Edwards Air Force Base between Rogers and Rosamond dry lakes. This site is located about 1 km west of Lancaster Boulevard and 2.5 km north of Branch Memorial Park at an elevation of about 700 m in the western Mojave Desert on the old lakebed of Pleistocene Lake Thompson (34°50'N, 117°55'W). The community structure and demography of the site's vegetation has been described in more detail by Sharifi et al. (2017). Mean annual precipitation at the study site is about 125 mm (EAFB 2008), but was 200 mm in

1996, the year of this study, providing good conditions for plant growth. Seasonal temperature variation at the site is high, with mean summer high temperatures of 36°C and record extremes up to 45°C. Winter lows at night average -1°C, but record lows are -15°C. The small dunes of the pan-dune system are comprised of windblown sands interbedded with fine silts from the lakebeds. Small clay pans develop in the interdune areas where the fine texture and compacted surfaces provide ponding of winter rains and increased deposition of fine evaporites. Patterns of differential establishment of microbial crusts and vascular plants on dune, flats and pan soils help to reinforce distinct vegetation zonation around the clay pans. However, the geomorphic surface of pans and small dunes appears to be a young dynamic one rather than representing a paleo-landscape of the old Lake Thompson lakebed (Lichvar et al. 2004; Orme 2008).

We selected several small areas representing distinct physiographic habitats within the primary study plot for intensive study. Low flat areas adjacent to two small pans were termed Flat 1 and Flat 2. These were relatively small in area with little vegetation cover. Two low dunes in the southeastern half of the plot near these flats were termed Dune 1 and Dune 2. These two dunes appeared to be relatively well cemented and stable and presented no more than 2–3 m of topography above the surrounding flats and pans. A large dune of wind-blown sand at the northwestern margin of the plot was termed Dune 3. This dune, with a sandy structure suggesting a young age and aeolian movement of sediments, showed distinctive plant cover that differed markedly in amount and composition from that on the lower dunes. A flat area immediately to the southeast of Dune 3 with inhomogeneous vegetation was termed Flat 3. The southeastern margin of this area was bounded by a wash habitat termed Wash.

Seasonal Growth and Phenology Measurements

Seasonal growth phenology and water relations were studied for 11 shrub species and three perennial grasses within the study plot. More intensive studies on seasonal patterns in plant water relations were carried out on six of the shrub species. These included *Atriplex confertifolia* (shadscale), *A. torreyi* (S. Watson) S. Watson (Torrey's saltbush), *A. parryi* S. Watson (Parry's saltbush) and *A. canescens* (Pursh) Nutt. (four-wing saltbush) in the Chenopodiaceae, all species with C₄ metabolism, and *Tetradymia stenolepis* Greene (Mojave cottonthorn) and *Eriocameria nauseosa* (Pall. ex Pursh) G.L. Nesom & G.I. Baird subsp. *mohavensis* (Greene) G.L. Nesom & G.I. Baird (rabbitbrush) in the Asteraceae with C₃ metabolism. Less intensive studies of phenology and water relations were carried out on an additional group of C₃ species: *Acamptopappus sphaerocephalus* (A. Gray) A. Gray (goldenhead, Asteraceae), *Allerrolfea occidentalis* (S. Watson) Kuntze (iodine bush, Chenopodiaceae), *Artemisia spinescens* D.C. Eaton (bud sage, Asteraceae), *Krascheninnikovia lanata* (Pursh) A. Meeuse & A. Smit (winterfat, Chenopodiaceae), *Forestiera pubescens* Nutt. (desert olive, Oleaceae), *Isocoma acradenia* (Greene) Greene (alkali goldenbush, Asteraceae), *Lepidium fremontii* S. Watson (desert pepperweed, Brassicaceae) and *Yucca brevifolia* Engelm. (Joshua tree, Agavaceae). Phenological observations were also made on three perennial grass species that were common on the study site: *Distichlis spicata* (L.) Greene (salt grass) with C₄ metabolism and *Stipa hymenoides* Roem. & Schult. (sand grass) and *Sporobo-*

lus airoides (Torr.) Torr. (alkali sacaton) with C₃ metabolism. All plant names and family classification follow Baldwin et al. (2012).

Qualitative phenological observations were made for all study species to monitor activities of current shoot growth, leaf production and reproductive tissue production. Additionally, 10 individuals of each of the five primary study species were selected for quantitative phenological monitoring. Samples of 5–10 actively growing mature branches of each marked species (with similar diameter and length) were cut and brought to UCLA monthly from March to September 1996. In the lab, mature branch basal diameter and branch length were measured and current shoots were separated. Between 15 and 25 current shoots were randomly selected and measurements taken for total branch length, basal diameter and oven dry weight of leaves, flowers and fruits. We used these data to estimate relative growth rates for each tissue component through the seasonal growth period.

Water Relations

Predawn and midday leaf water potential measured monthly from April through August 1996 with a Scholander-type pressure chamber (PMS Instrument Corp., Corvallis, OR) is an indicator of available soil moisture in the rooting profile of the plant at a time when soil and plant moisture are in equilibrium. Midday plant water potentials show water stress at a time when evapotranspirational water losses are at their greatest level during the day. More negative values of water potential indicate greater xylem tensions and thus greater water stress in the plant. Values reported below are means of 3–5 replicated measurements per species.

RESULTS

Growth Phenology

Qualitative phenological observations established two broad groups separated on the timing of their seasonal growth activities. The first group included those species which initiated and completed their growth in the spring months. They began their vegetative growth (leaf production and shoot elongation) in February or early March and continued this growth through April into May. Their reproductive growth (flower and fruit production) was largely restricted to April and May. This group of species, all of which possess typical C₃ metabolism, included *Acamptopappus sphaerocephalus*, *Artemisia spinescens*, *Isocoma acradenia*, *Krascheninnikovia lanata*, *Lepidium fremontii*, *Sporobolus airoides*, *Stipa hymenoides* and *Tetradymia stenolepis*.

The second group of species included those with phenological activity centered on warmer late spring and summer growth. These species typically began vegetative growth in mid- to late March, 2–6 weeks later than the first group, and continued this growth in most cases through June and July. Reproductive growth commonly did not begin until June and continued into July and/or August. This group was largely made up of four species of *Atriplex* (*A. canescens*, *A. confertifolia*, *A. parryi* and *A. torreyi*) and the rhizomatous grass *Distichlis spicata*. All of these species possess C₄ metabolism. One additional species in this phenological group with late season growth was *Forestiera pubescens*, a C₃ shrub.

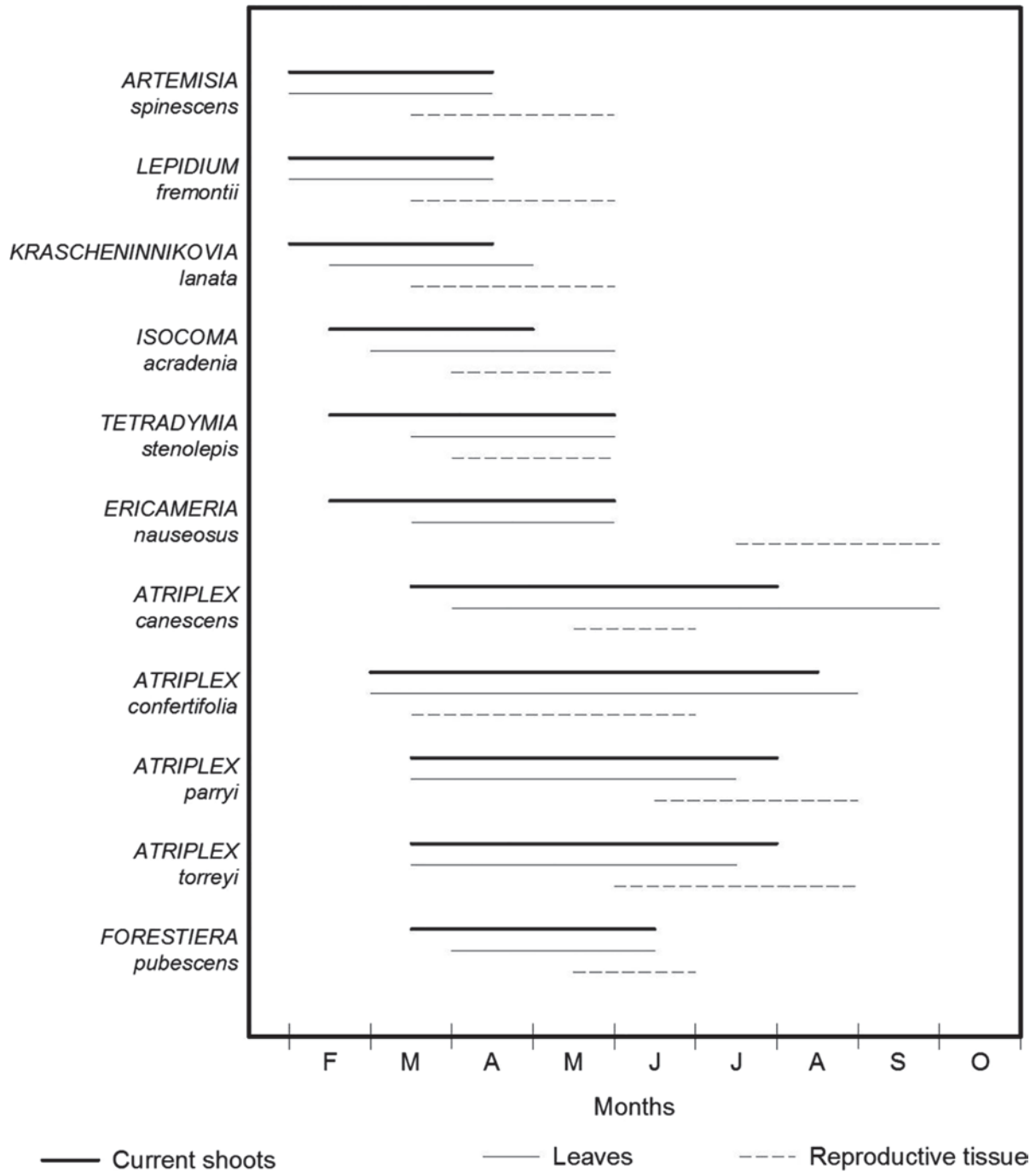


Fig. 1. Phenogram of the dominant woody plants during the 1996 growing season in the pan-dune system at Edwards Air Force Base, California. The beginning of the bars indicates onset of growth, while the bar ends indicate the end of growth activity.

Phenograms with the seasonal cycle of growth for 11 shrub species in the pan-dune study site are shown in Fig 1. Separate lines show the seasonal progression of growth of current shoots, leaves and reproductive tissues for each species. *Artemisia spinescens*, *K. lanata* and *L. fremontii* all initiated vegetative growth early in February, followed by *E. nauseosa*, *I. acradenia* and *T. stenolepis* a few weeks later. The first three of these species also completed their vegetative growth early in the season with current shoot and leaf production largely ceasing

by mid-April. *Tetradymia stenolepis* and *E. nauseosa* continued vegetative growth through May. Reproductive growth began in mid-March in *A. spinescens*, *L. fremontii* and *K. lanata*, two weeks earlier than in *I. acradenia* and *T. stenolepis*. Unlike the other species in this spring group, flower initiation did not begin until late July in *E. nauseosa*, well after vegetative growth had ceased, and continued through September.

Two common species of perennial bunchgrasses, *S. hymenoides* and *S. airoides*, also showed typical spring growth

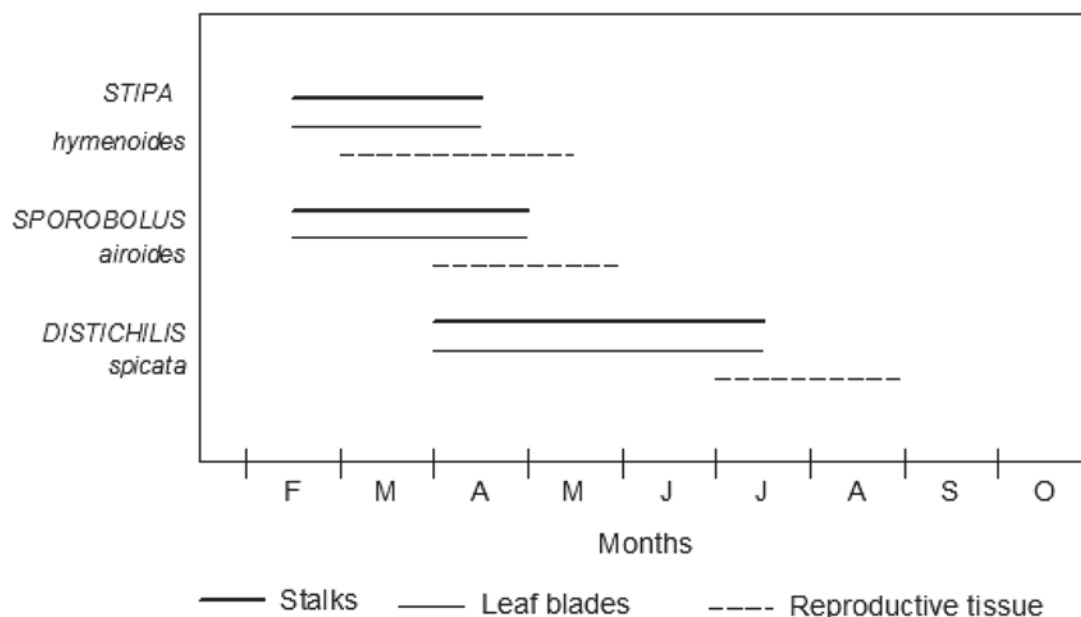


Fig. 2. Phenogram of the perennial native grasses during the 1996 growing season in the pan-dune system at Edwards Air Force Base, California. The beginning of the bars indicates onset of growth, while the bar ends indicate the end of growth activity.

phenology (Fig. 2). Vegetative growth began in mid-February and continued into mid- and late April, respectively, in these two species. Reproductive growth was nearly four weeks earlier in *S. hymenoides* than in *S. airoides*, beginning in early March. Both species had completed their reproductive growth by the end of May.

For the second group of shrubs, *A. confertifolia* was the first to break dormancy, with shoot growth initiating at the beginning of March, two weeks ahead of the other species (Fig. 1). Vegetative growth continued into August in all four species of *Atriplex*, reflecting the adaptive advantage of their C_4 metabolism in allowing efficient use of water and affinity for high growing season temperatures. Reproductive growth in *A. confertifolia* ceased by the end of June, but other species continued their growth into early August (*A. canescens*) or the beginning of September (*A. parryi* and *A. torreyi*).

By the end of May, 95% of leaves of both *A. confertifolia* and *A. parryi* had abscised and the photosynthetic activity was carried out by the green seed wings. These seed wings, resembling leaves at a distance, had a photosynthetic surface area at least three times larger than that of the leaves by early summer. The C_4 rhizomatous grass *D. spicata* also showed a typical pattern of warm season growth. Vegetative growth was not evident until the beginning of April in this species and continued until mid-July (Fig. 2). Reproductive growth did not begin until early July and continued through August. Much of the spread of this species, however, is not by seed dispersal but rather through vegetative reproduction by rhizomes.

The final shrub species, *F. pubescens*, differed somewhat in its adaptive strategies in comparison to other species in this group. It began vegetative shoot growth in mid-March, four weeks later than other C_3 shrubs, and continued vegetative growth until mid-June. This point, marking the end of shoot growth, was two weeks later than that observed in *T. stenolepis* and *I. acradenia* and two months beyond the point when vegetative growth

ceased in the shallow-rooted *A. spinescens*, *L. fremontii* and *K. lanata*.

Quantitative analyses of phenology in five primary study species provided a more detailed view of the seasonal progression of growth activity in the dominant shrub species. Seasonal clipping production of new tissues (leaves, current shoots and reproductive tissues) and rate of shoot elongation occurred with similar patterns within each of these species (Fig. 3). The earliest peak of growth activity among these five species was present in *T. stenolepis* with a broad early peak of growth rate reaching its highest point in mid-April. This pattern of activity was followed four weeks later in *E. nauseosa* with a growth rate peak in mid-May.

The three C_4 species of *Atriplex* followed next in quantitative growth activity, with *A. confertifolia* beginning growth early and peaking broadly with a high point in mid-June. *Atriplex torreyi* began significant growth four weeks later than *A. confertifolia* but continued its high rates of growth for longer with a peak in mid-July (Fig. 3). Growth rate in *A. canescens* also peaked in mid-July, but its seasonal pattern of growth was much more sharply correlated with the summer months than that of *A. torreyi*.

Seasonal Water Relations

Predawn plant water potentials (Table 1) in the early growing season during April were modest, reflecting good soil moisture availability from the earlier rains in the rooting zone of all shrub species. These potentials ranged from a high of -0.82 MPa in *T. stenolepis* to a more negative -1.71 MPa in *A. torreyi*. April midday minimum water potentials were also modest, ranging from -1.51 MPa in *E. nauseosa* to -2.22 MPa in *A. confertifolia* (Table 2).

As the growing season progressed, most species showed a general pattern of slowly declining water potentials (increased

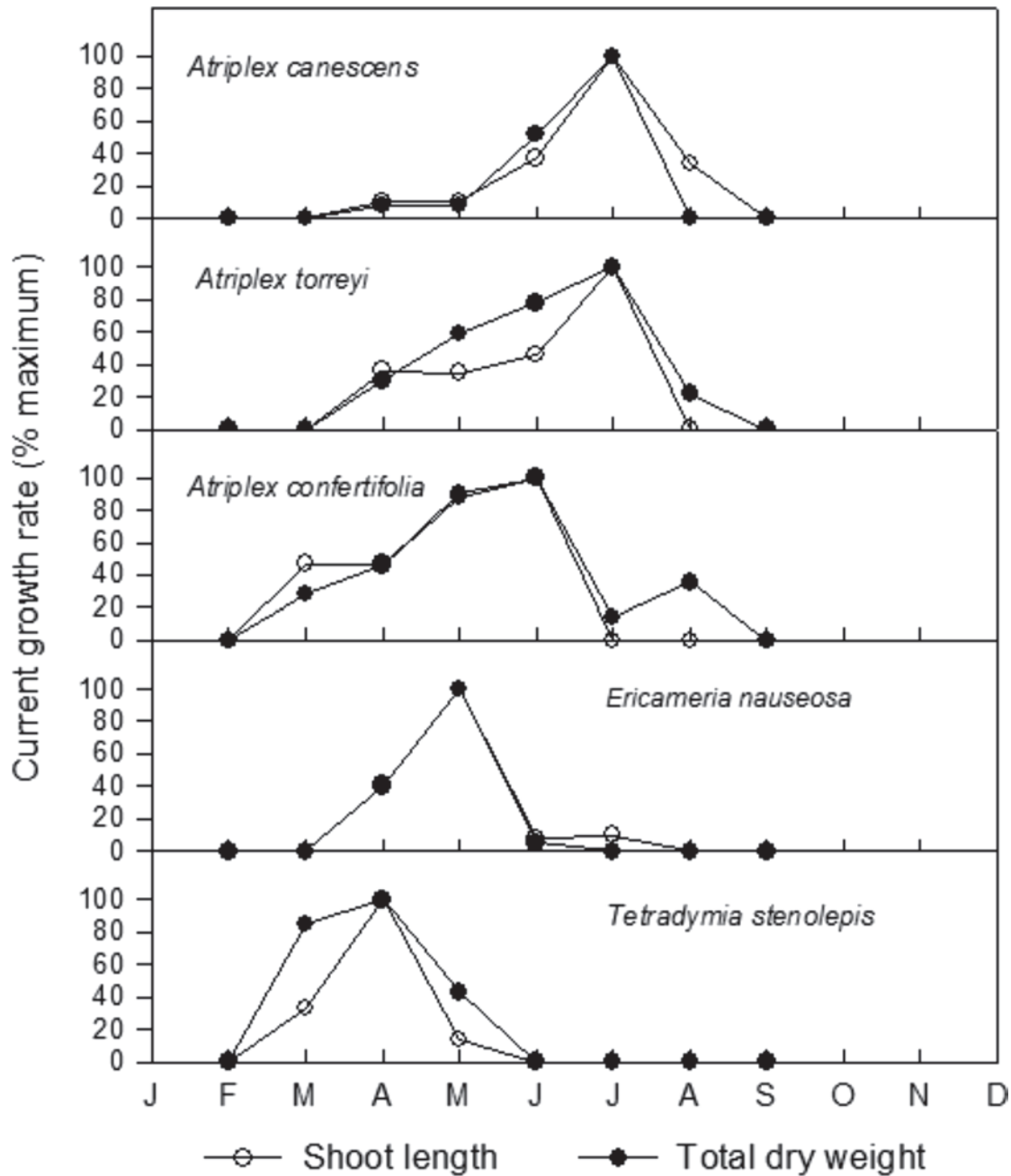


Fig. 3. Seasonal clipping production (leaves, current shoots and reproductive tissue) and shoot elongation rates as a percentage of the yearly maximum in the pan-dune system at Edwards Air Force Base, California.

stress) through the late spring and summer months. Predawn water potentials dropped slowly in May to levels about 1 MPa lower than the April values, reflecting more limited soil water availability. The smallest relative changes in predawn water potential over this period were seen in *T. stenolepis* and *E. nauseosa*, suggesting deeper root systems (Table 1, Fig. 3). Predawn water potential measurements in June showed relatively small further reductions in water potential, with the greatest change observed in *T. stenolepis*. The range of predawn values at this date ranged from -2.11 MPa in *A. canescens* to -3.07 MPa in *A. confertifolia*. By September, predawn water potentials

reached levels that were 1-2 MPa more negative than they had been in spring, reflecting the limited soil moisture availability at this time. Shallow-rooted species such as *A. sphaerocephalus* showed the greatest lowering of predawn water potential, while deep-rooted species such as *T. stenolepis* and *E. nauseosa* exhibited smaller changes. With unusually limited fall rains, about half of the species studied had lower (more negative) predawn water potentials in December than September (Table 1).

The seasonal pattern of midday water potentials showed sharper declines, reflecting the physiological patterns of activity of each shrub species. With good soil moisture availability

Table 1. Seasonal predawn mean water potentials in MPa in the pan-dune system at Edwards Air Force Base, California. The data are the mean of all habitats (flats, dunes and wash). Numbers in parentheses are standard errors of relevant means [nm = not measured].

Species	Apr	May	June	July	Sep	Dec
<i>Acamptopappus sphaerocephalus</i>	-1.10 (0.07)	nm	nm	nm	-3.02 (0.31)	-2.79 (0.05)
<i>Allenrolfea occidentalis</i>	nm	nm	nm	nm	nm	nm
<i>Artemisia spinescens</i>	-1.49 (0.04)	nm	nm	nm	nm	nm
<i>Atriplex canescens</i>	-1.19 (0.38)	-2.31 (0.28)	-2.11 (0.08)	nm	-2.53 (0.08)	-3.17 (0.19)
<i>Atriplex confertifolia</i>	-1.61 (0.10)	-2.68 (0.10)	-3.07 (0.10)	nm	-2.34 (0.18)	-3.07 (0.25)
<i>Atriplex parryi</i>	-1.40 (0.17)	nm	nm	nm	-2.3 (0.07)	nm
<i>Atriplex torreyi</i>	-1.71 (0.19)	-2.69 (0.05)	-2.74 (0.80)	nm	-2.36 (0.09)	-3.55 (0.87)
<i>Ericamerica nauseosa</i>	-1.03 (0.08)	-1.41 (0.06)	nm	nm	-2.14 (0.10)	-1.66 (0.19)
<i>Forestiera pubescens</i>	-1.07 (0.14)	-2.28 (0.01)	-2.81 (0.14)	nm	-3.22 (0.12)	-4.75 (1.40)
<i>Isocoma acradenia</i>	-1.36 (0.08)	nm	nm	nm	nm	nm
<i>Krascheninnikovia lanata</i>	-1.10 (0.14)	nm	nm	nm	nm	nm
<i>Tetradymia stenolepis</i>	-0.82 (0.16)	-1.41 (0.06)	-2.38 (0.21)	nm	-2.00 (1.04)	-1.66 (0.18)

in the spring, most shrub species were found to have only a modest reduction in midday water potentials between April and May (Table 2). An exception, however, was present in the three *Atriplex* species whose midday water potentials dropped sharply from April to May. By June, at the end of the growing season for C₃ shrubs in the Group 1 category, midday water potentials had dropped sharply for all studied species. With sharply reduced metabolic activity in these species in June, midday water potentials were only modestly lower than predawn water potentials.

This was not the case, however, in the C₄ shrubs. In June, the most negative water potentials, indicating reduced water availability, were found in all species of *Atriplex* with values from -4.29 MPa in *A. confertifolia* to -4.88 MPa in *A. torreyi*. These low midday water potentials reflect the photosynthetic activity of these species under conditions of high temperature and high vapor pressure deficit which combine to promote transpirational water loss. The magnitude of the difference between predawn and midday water potentials in these species ranged from 1.2 to 2.2 MPa, far greater than that present at this date in the C₃ shrubs. The four *Atriplex* species studied showed little change in their midday water potentials between June and September when their phenological pattern of growth had ended (Table 2, Fig. 4). Midday water potentials were higher in all these species

in December, reflecting leaf loss and thus reduced transpirational flux.

Among the C₃ shrubs, water relations data demonstrated multiple strategies of below-ground architecture with respect to rooting depth. *Forestiera pubescens*, which is largely restricted to sites on flats immediately adjacent to small pans, clearly used a phreatophytic habit to tap ground water pools which collect belowground in these microsites. These water pools may nevertheless be limited in volume. *Forestiera pubescens* was able to maintain modest midday water potentials through April and May. The midday water potential of this species then dropped abruptly in June to -3.52 MPa at the time when growth activity ceased. This pattern strongly suggests that large shrubs of this species growing adjacent to small pans had exhausted available water pools. Midday water potentials in *F. pubescens* continued to drop over the summer and fall, reaching -4.44 MPa in September and -5.10 MPa in December (Table 2). This latter midday value was the lowest (most negative) water potential measured in any species in December. The quantitative availability of water at various depths on the site is unknown, but may be inferred from the pattern of water potential measurements.

The water potential data also showed strong evidence of deep-rooting architecture in *T. stenolepis* and *E. nauseosa* growing on

Table 2. Seasonal midday mean water potentials (MPa) in the pan-dune system at Edwards Air Force Base, California [nm = not measured].

Species	Apr	May	June	July	Sep	Dec
<i>Acamptopappus sphaerocephalus</i>	-1.72 (0.06)	nm	nm	nm	-3.47 (0.11)	-3.26 (0.08)
<i>Allenrolfea occidentalis</i>	nm	nm	-3.7 (0.16)	nm	-5.38 (0.41)	nm
<i>Artemisia spinescens</i>	-1.70 (0.06)	nm	nm	nm	nm	nm
<i>Atriplex canescens</i>	-2.21 (0.02)	-3.29 (0.11)	-4.37 (0.08)	-3.24 (0.27)	-4.09 (0.39)	-3.31 (0.19)
<i>Atriplex confertifolia</i>	-2.22 (0.06)	-3.41 (0.14)	-4.29 (0.18)	-3.66 (0.10)	-4.13 (0.23)	-3.55 (0.22)
<i>Atriplex parryi</i>	nm	nm	-4.67 (0.26)	nm	nm	nm
<i>Atriplex torreyi</i>	-1.99 (0.08)	-3.65 (0.34)	-4.88 (0.41)	nm	-4.61 (0.11)	-3.99 (0.70)
<i>Ericamerica nauseosa</i>	-1.51 (0.09)	-2.19 (0.08)	-2.47 (0.25)	nm	-2.56 (0.15)	-2.17 (0.28)
<i>Forestiera pubescens</i>	-2.13 (0.06)	-2.68 (0.23)	-3.52 (0.49)	nm	-4.44 (0.03)	-5.10 (0.89)
<i>Isocoma acradenia</i>	-2.08 (0.05)	nm	-3.26 (0.15)	nm	-4.46 (0.08)	-2.79 (0.05)
<i>Krascheninnikovia lanata</i>	-2.14 (0.03)	nm	nm	nm	nm	nm
<i>Tetradymia stenolepis</i>	-1.74 (0.09)	-2.12 (0.05)	-2.99 (0.18)	nm	-2.55 (0.12)	-2.45 (0.34)
<i>Yucca brevifolia</i>	nm	nm	nm	nm	-2.00 (0.67)	nm

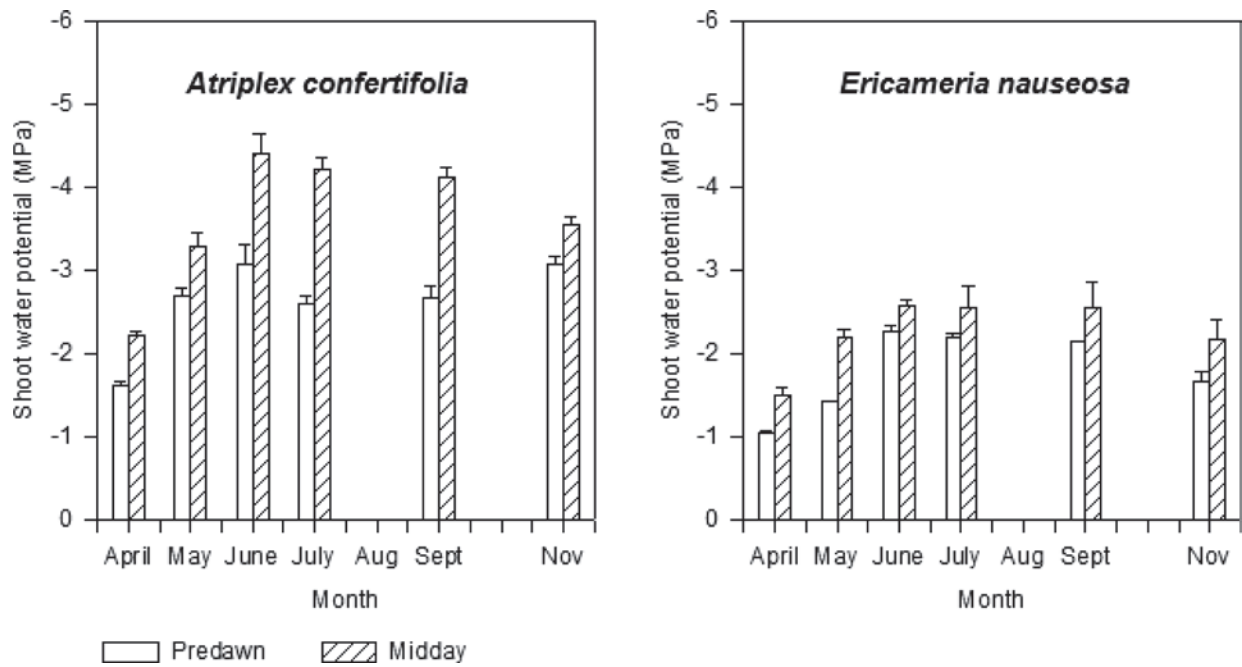


Fig. 4. Seasonal progression of predawn and midday water potential in *Atriplex confertifolia* and *Ericameria nauseosa* in the pan-dune system at Edwards Air Force Base, California.

the low dunes. In May, at the end of their growing season, these two species, like *F. pubescens*, had midday water potentials averaging about -2.1 MPa, compared to values of about -3.4 MPa in *Atriplex* species with shallower root systems. Their predawn water potentials at this time of -1.4 MPa compared to values of -2.3 to -2.7 MPa in the *Atriplex* species clearly establishes the greater water availability in the rooting zones of *T. stenolepis* and *E. nauseosa*. In contrast to these relatively deep-rooted C_3 shrubs, other species which we have studied less intensively clearly lack deep rooting architecture and show early evidence of water stress. Good examples of this can be seen with *A. sphaerocephalus*, *A. spinescens* and *K. lanata* (Tables 1 and 2).

Only very limited water relations studies were carried out with *Yucca brevifolia*, the only woody arboreal species in the plot. *Yucca brevifolia* showed quite specific habitat requirements in the pan-dune ecosystem, occurring only on sandy dunes where soil moisture can accumulate and soil infiltration and aeration are good. The midday water potential of *Y. brevifolia* in September was only a modest -2.0 MPa. Such a modest water potential is expected in large succulents or other plants with a high water storage capacity.

Habitat Variation in Water Relations

The characteristics associated with the geomorphology of site suggested the possibility that soil moisture availability might differ between flat, dune and wash habitats. We therefore examined these patterns using *Atriplex confertifolia* (Fig. 4–5), a species present in almost all habitats within the plot. In April, we found no significant differences in either predawn or midday water potentials of this species within the three flat, three dune and wash habitats sampled (Fig. 5). Predawn water potentials had a mean value of -1.5 MPa, while midday water potentials had a mean of

-2.2 MPa. These modest water potentials in the shallow-rooted *A. confertifolia* indicate good soil moisture availability.

By June, however, clear differences in water availability between habitats were apparent in the water potential measurements of *A. confertifolia*. Predawn water potentials, a measure of soil moisture availability in the rooting zone, averaged -3.8 MPa in Flat 1 and 2, small flats adjacent to pans. The more extensive Flat 3 and Dune 1 and 2 were all similar with a predawn water potential of about -3.1 MPa, indicating greater water availability. Finally, the large and extensive Dune 3 site and wash habitat showed the greatest water availability with a mean water potential of -2.3 MPa.

Midday water potentials in June, which reflected the physiological availability of water under active growth conditions in *A. confertifolia*, were much less variable between habitats (Fig. 5). The most negative water potentials (-5.4 MPa) occurred in the extensive Flat 3 habitat. The other flat and dune habitats had midday water potentials ranging from -3.9 MPa (Dune 2) to -4.4 MPa (Flat 1).

DISCUSSION

Deserts with their low levels of total precipitation and strong seasonal drought would be expected to experience very low water potentials as the dry season develops. For the summer-dry Mojave Desert, differences in minimum water potentials can be related to factors such as rooting depth and leaf phenology (evergreen versus drought deciduous). Shallow-rooted and drought deciduous species typically exhibit more negative water potentials than deep-rooted, evergreen species. For chaparral communities, studies suggest that evergreen species are more resistant to xylem cavitation than drought-deciduous species as they must

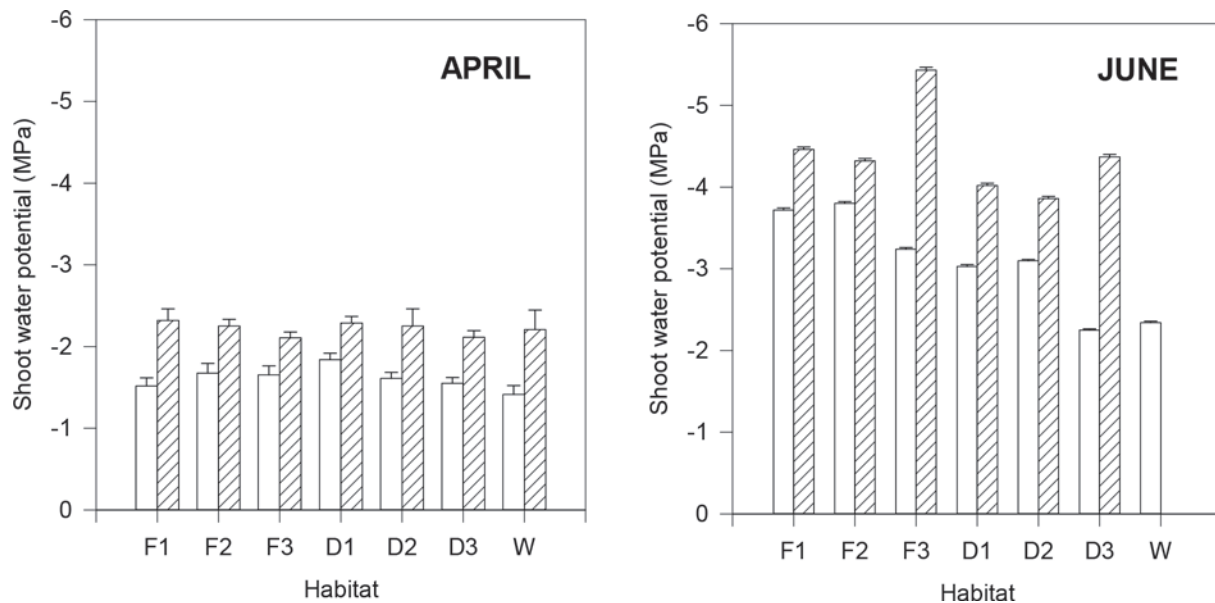


Fig. 5. Predawn and midday water potential in *Atriplex confertifolia* in April and June 1996 for a series of dune, flat and wash habitats in the pan-dune system at Edwards Air Force Base, California. See text for details of sample sites.

preserve water-conducting xylem pathways throughout the year (Jacobsen et al. 2007, 2008).

The seasonal minimum water potentials present in the saltbush scrub communities at Edwards Air Force Base are relatively high (less negative) for what might be expected for such an arid region. However, previous studies comparing season water potential and plant hydraulics in chaparral and Mojave Desert shrublands have reported modest seasonal extremes in water potential for the more arid desert species compared to the less xeric chaparral growing under higher rainfall conditions (Jacobsen et al. 2007, 2008). Similar results of relatively modest minimum water potentials have been reported for cold desert species in Utah (Sperry and Hacke 2002) and arid shrublands in Spain (de Dios Miranda et al. 2010). These findings point to the complexity of morphological, ecophysiological and phenological traits that confer drought avoidance and resistance.

Our studies broadly parallel earlier research on the ecophysiology of saltbush scrub communities carried out at Curlew Valley, Utah, in the early 1970s as part of the Desert Biome program of the National Science Foundation. These included measurements of seasonal patterns of net assimilation, water relations and phenology of *Atriplex confertifolia* and *Krascheninnikovia lanata* (Moore et al. 1972; Fernandez and Caldwell 1975; Caldwell et al. 1977; West and Gasto 1978; Holthausen and Caldwell 1980; Caldwell 1985). These studies clearly established the adaptive significance of C_4 metabolism in *Atriplex* species in allowing these shrubs to maintain a high level of water use efficiency and maintain active growth into early summer well past the time when most C_3 shrubs have become dormant. These metabolic adaptations reduce direct competition for resources between C_3 and C_4 shrubs by separating their seasonal periods of maximal growth activity.

At the community level, studies with saltbush scrub in Utah also provide a means to make a first approximation of the impacts of plant cover on hydrologic budgets. In Curlew Valley

the amount of water that moves through the transpiration stream was about half of precipitation levels (Caldwell 1985). Because these communities generally have internal drainage patterns and little or no subsurface drainage, the other half of precipitation is presumably lost through evaporation from the soil surface.

C_4 metabolism provides two types of advantages that can be extremely useful for desert plants. The first of these is that the highly efficient manner of carbon uptake by the initial C_4 enzymes is not inhibited by high temperatures. Plants with more typical C_3 metabolism have an optimal temperature for photosynthesis, but these rates decline at higher temperatures as the Calvin cycle enzymes become less efficient and release carbon dioxide through photorespiration (Gibson and Rundel 2012). C_4 plants avoid loss of carbon in photorespiration and are thus highly efficient at operating at high temperatures where they can maintain very high rates of photosynthesis. Another potential advantage of C_4 metabolism comes from the highly efficient fixation of carbon by the C_4 enzymes. With this efficiency, C_4 plants need open their stomata very little, yet still achieve the same amount of carbon uptake present in typical C_3 plants that lack this metabolic system. Under these conditions, C_4 plants can exhibit very high rates of efficiency in water use to aid their success in desert environments.

C_4 metabolism represents an important ecological strategy in a number of desert shrubs, most notably species of *Atriplex*, which often are important community dominants in areas of alkaline or saline soils. In these shrubs, the key adaptation of C_4 metabolism is the ability to maintain growth under high summer temperatures and drought conditions at a time when C_3 shrubs are dormant, thus reducing interspecific competition for water (Caldwell et al. 1977). The maximal rates of photosynthesis in these desert C_4 shrubs are moderate and generally no higher than those of co-occurring C_3 shrubs, but their water use efficiency is far greater. Our observations that water potentials of *Artemisia confertifolia* differ between nearby microhabitats is consistent

with previous work on the water relations of this species (Sperry and Hacke 2002).

Unlike the summer-active species, *F. pubescens* lacks the adaptive advantages for summer growth that are associated with C₄ metabolism. This C₃ shrub was able to maintain a late growth season phenology using its deep root system which taps underground pools of water not available to many other species. Plants with differential patterns of rooting depth thus compete for different soil water resources and thereby reduce interspecific competition (Manning and Barbour 1988). We have described this pattern in the studies of comparative shrub water relations on desert dunes (Rundel and Gibson 1996).

Deep rooting architecture has been previously reported in *Ericameria nauseosa* and a congener of *Tetradymia stenolepis* (Donovan and Ehleringer 1992, 1994; Hacke et al. 2000). Unlike *F. pubescens*, however, these two species did not exhibit a sharp decline in midday water potentials in June or a continued decline in such values through the summer and fall. There are two factors that might account for this pattern. Both of these species are drought deciduous, effectively shedding leaf tissues at the end of their growing season. Thus, there is little or no photosynthetic surface area during the months of summer drought from which transpirational water loss may occur. A second factor may be the habitat selection and relatively deep roots of these species. Dunes effectively trap precipitation during rains because of the high infiltration capacity of their sandy soil texture. Water availability below dunes in arid regions is generally large compared to other runoff sites. Relatively deep rooting architecture in *Tetradymia* and *Ericameria* allows these species to utilize such water (Hacke et al. 2000).

Halophytic species of *Atriplex* and *Krascheninnikovia lanata* are tolerant of both low moisture availability and salinity but use differing mechanisms of tolerance to saline soils. *Krascheninnikovia lanata* excludes salt ions at the root/soil interface, behaving thereafter much as a nonhalophytic species (Caldwell 1985; Smith and Nowak 1990). Most *Atriplex* species in contrast accumulate salts and then excrete these ions into bladder hairs on the leaves. These bladder hairs eventually rupture, effectively excreting the salts. In this way *Atriplex* species act to increase salt concentrations under their canopies as we have found (Caldwell 1985; Smith and Nowak 1990). Another group of halophytic species, all extremely salt tolerant, are restricted to habitats around playa margins with accessible soil moisture around the margins of pans, as previously described. Flooding tolerance is known to vary significantly between these species (Groenewald and Crowley 1988), representing another mechanism of episodic disturbance in wet years.

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