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FIELD WATER RELATIONS OF SONORAN DESERT ANNUALS¹

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Abstract. Field water relations were examined in winter and summer annuals of the Sonoran Desert. Both groups were characterized by low belowground biomass allocation. Winter annuals had large interspecific variation in water relations parameters, but their leaves generally had high conductances of water vapor and high water potentials during early growth periods. These high values were very short-lived and were reduced by peak flowering periods. Summer annuals were measured midway through the growing season; their leaves showed less interspecific variability in water vapor conductances and had values similar to the winter annuals for this stage of the growing season. Midday and diurnal courses of photosynthesis in the winter annuals exhibited lower rates than values previously reported for plants grown under unlimited water and nutrient regimes in glasshouses. This was probably due to the decreased leaf water potentials and increased vapor pressure deficits present in field situations. Both the winter and the summer annuals showed a dichotomy among species in leaf water potentials, associated with either variations in soil water availability or the ability of leaves to adjust osmotically to decreased soil water availability. Although winter and summer annuals are ephemeral, some species are capable of tolerating low leaf water potentials and therefore are not drought evading in the traditional sense.

Key words: *annuals; ecophysiology; ephemerals; leaf conductance; leaf water potential; Sonoran Desert; water relations.*

INTRODUCTION

The vegetation of the warm deserts of southwestern North America is characterized by a diverse flora that has evolved in response to the harsh physical regime imposed by the unpredictable, low precipitation and the variable air and soil temperatures of this region (Shreve and Wiggins 1964, Sellers and Hill 1974). This annual flora can be divided into two distinct groups, winter and summer annuals, each associated with one season of the bimodal precipitation patterns (November–April, July–September). They are separated temporally by their strict temperature and water requirements for germination (Went and Westergaard 1949, Juhren et al. 1956). These annuals tend to be ephemeral and to die during the drought period.

Recent investigations indicate that there are large variations in the photosynthetic characteristics (both morphological and physiological) of these annuals. Winter annuals possess the C₃ photosynthetic pathway, whereas the majority of summer annuals possess the C₄ photosynthetic pathway (Mulroy and Rundel 1977, Ehleringer 1984). Several characteristics of winter annuals may be of potential adaptive value, including photosynthetic temperature acclimation (Seemann et al. 1980a, Forseth and Ehleringer 1982a), high leaf photosynthesis and leaf conductance values (Mooney et al. 1976, Monson and Szarek 1979, Wallace and Szarek 1981, Toft and Pearcy 1982, Forseth and Eh-

leringer 1983a, Werk et al. 1983), leaf diaheliotropic movement or solar tracking (Ehleringer and Forseth 1980), and osmotic adjustment to long-term drought (Seemann et al. 1979, Forseth and Ehleringer 1982b). Much less is known about the summer annuals. However, high photosynthetic capacities and osmotic adjustment abilities, traits that characterize several winter annuals, are also present in at least two summer annuals (Toft and Pearcy 1982, Ehleringer 1983).

The purpose of this study was to add base-line information on aspects of the comparative water relations of winter and summer desert annuals, which could be related to the data available on photosynthetic characteristics. Specifically, we were interested in determining (1) if high root : shoot ratios occurred in these annuals or were correlated with those species having high rates of photosynthesis and transpiration, (2) how rooting distributions differed between annuals growing in the two different thermal periods, and (3) what diurnal courses of leaf water loss and leaf water potentials were characteristic of the flora in different seasons.

MATERIALS AND METHODS

Field measurements were collected primarily in two areas. The measurements on winter annuals were made in the southern portion of the Death Valley National Monument, California, between Ashford Mills (elevation, 0 m) and Confidence Wash (elevation, 750 m). In this area, the dominant perennial vegetation is sparsely distributed and consists of *Larrea divaricata*, *Atriplex hymenelytra*, *Ambrosia dumosa*, and *Encelia farinosa* (Hunt 1966). Soils in the area are predominantly stony and coarse sands associated with the grav-

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elly bajadas and washes. There are occasional small sand-dune systems near Ashford Mills. Although there was overlap in the distributions of the winter annuals, some species were found only on the dunes. These included *Abronia villosa* Wats., *Palafoxia linearis* (Cov.) Lag., and *Polygonum aviculare* L. Dune sites were likely to have had more soil water available than did gravelly bajada sites (Pavlik 1980). The species found only on the gravelly bajadas included *Astragalus lentiginosus* Dougl., *Atrichoseris platyphylla* Gray, *Chorizanthe rigida* (Torr.) T. & G., *Eschscholtzia glyptosperma* Greene, *Lupinus arizonicus* Wats., *Mohavea breviflora* Cov., *Plantago insularis* Eastw., *Salvia columbariae* Benth., *Camissonia boothii* Raven, and *Eriogonum deflexum* Torr. The remaining winter annuals that were measured occurred both on and off the sand dunes. These included *Camissonia claviformis* Raven, *Chaenactis carphoclinia* Gray, *Cryptantha utahensis* (Gray) Greene, *Geraea canescens* T. & G., *Malvastrum rotundifolium* Gray, *Phacelia calthafolia* Brand., and *P. crenulata* Torr.

Measurements on summer desert annuals were made on plants growing in and along washes in Arizona between Gila Bend (elevation, 230 m) and Ajo (elevation, 580 m). The terrain is open and flat and occasionally cut by washes. The dominant perennial vegetation of this area is *Larrea divaricata*; in the washes, *Acacia greggii* and *Encelia frutescens* are common. Soils are fine to coarse sand in the washes and fine silt to silt underlain by caliche on the level areas. As with the winter annuals, not all summer annuals occurred in all places. *Cucurbita digitata* Gray, *Datura meteloides* A. DC., and *Proboscidea louisianica* (Mill.) Thell. were found only in washes; annuals found both in the washes and on the level areas were *Allionia incarnata* L., *Amaranthus palmeri* Wats., *A. fimbriatus* (Torr.) Benth., *Boerhaavia wrightii* Gray, *Euphorbia abramsiana* Wheeler, *Kallstroemia grandiflora* Torr., *Pectis papposa* Harv. & Gray, and *Tidestromia lanuginosa* (Nutt.) Standl. The washes appeared to have greater soil water availability than the level areas had.

Leaf conductances of water vapor were measured by using a null-balance porometer (Forseth and Ehleringer 1980) whenever possible. Leaves of *Datura meteloides* and *Proboscidea louisianica* were too large for the null-balance porometer and were therefore measured with a transit-time porometer (Delta-T Instruments, Cambridge, England). Leaf water potentials were measured with a Scholander-type pressure chamber. Sample sizes for leaf conductances and water potentials were three to eight leaves, one each from different plants, except for water potentials in *D. meteloides* and *P. louisianica*, where the sample size was limited to a single leaf. In all cases, the data presented are means of these readings. Midday standard errors are presented on the figures as a measure of within-species variation.

Net rates of photosynthesis on single leaves of winter annuals were measured by using a CO₂ depletion tech-

nique as described by Ehleringer and Cook (1980). Sample sizes were six leaves, one each from different plants.

Root distributions were determined by manually excavating roots. Individual plants were far enough apart so that there was no apparent root overlap. Care was taken to include all roots, but some of the finest roots may have been lost during excavation. Sample sizes were usually five to ten individual plants. In all cases, a single representative root distribution pattern is presented.

RESULTS

Summer annuals differed distinctly from winter annuals in that their roots penetrated deeper and were more fibrous (Figs. 1 and 2). In the summer annuals, the roots tended to be fibrous in two zones: one close to the surface and a second much deeper. This may be the consequence of two distinct types of convective rainstorms: a heavy initial storm that may have charged the soil profile, and additional storms of lower intensity. The root systems of winter annuals tended to be linear and unbranched; there were no obvious major differences in gross structure among the winter annual species. *Geraea canescens*, perhaps the most common of all species, exhibited the least amount of branching. Root excavations made at different times of the season did not show any deviation in this pattern among winter annuals. Root/shoot biomass ratios were very low, averaging 0.134 and 0.131 for winter and summer annuals, respectively (Table 1). The one exception to this pattern was *Atrichoseris platyphylla*, which had a root/shoot ratio two to three times larger than those of the other winter annuals. There appeared to be no correlation between the photosynthetic pathway of a species and either the rooting distribution or the root/shoot ratio. The distribution of root biomass in the soil profile for both types suggested that the upper 0.25–0.50 m of soil was the primary source of water for these life forms.

Midday water relations parameters of winter annuals collected in Death Valley in March 1979, a period of peak vegetative biomass, indicated a wide range of leaf conductances of water vapor among species (Table 2). *Astragalus lentiginosus* had the minimum leaf conductance of 4.7 mm/s; *Plantago insularis* had the maximum value of 18.8 mm/s. The minimum leaf water potential measured in March was -1.70 MPa (for *Chaenactis carphoclinia*); and the maximum value occurred in *Lupinus arizonicus* (-0.58 MPa). There were no clear differences between the leaf water potentials of annuals growing in washes and those growing in sand dunes. Although there were large ranges in both leaf water potentials and leaf conductances among plants of different species growing essentially next to each other, there was no significant relationship between the average values of the two parameters ($r^2 = 0.03$, $n = 17$, $P \gg .5$).

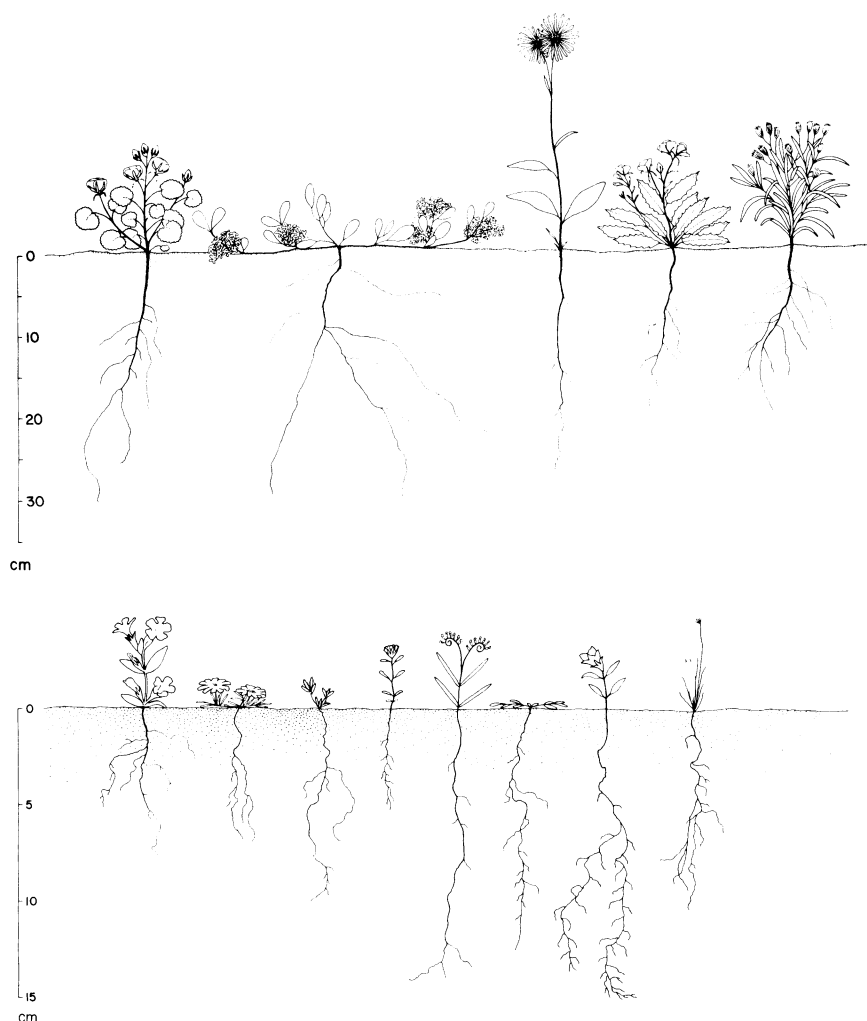


FIG. 1. Rooting distributions for Sonoran Desert winter annuals. Upper plate (left to right): *Malvastrum rotundifolium*, *Abronia villosa*, *Geraea canescens*, *Camissonia brevipes*, and *Palafoxia linearis*. Lower plate (left to right): *Mimulus bigelovii*, *Monoptilon belioides*, *Eriophyllum wallacei*, *Syntrichopappus fremontii*, *Cryptantha utahensis*, *Polygonum aviculare*, *Mohavea breviflora*, and *Plantago insularis*.

The water relations of winter annuals in March were investigated more closely by collecting diurnal measurements of both leaf conductance of water vapor and leaf water potential (Fig. 3). Both 20 March 1980 and 21 March 1982 were clear days and represented similar phenological periods; 20 March 1980 was warmer than 21 March 1982, and daytime air temperatures fluctuated from 18 to 31°C and from 15 to 23°C, respectively. Largely as a consequence of the differences in air temperature, water vapor pressure deficits (VPD) for the two days reached maxima of 4.2 and 2.2 kPa, respectively.

On 20 March 1980, leaf water potentials of *Abronia villosa*, *Malvastrum rotundifolium*, and *Palafoxia linearis* were clustered together and varied 0.3–0.4 MPa over the day, reaching midday minima of ≈ -1.6 MPa

(Fig. 3). Although *L. arizonicus* was growing adjacent to these three species, leaf water potentials measured in *L. arizonicus* were much higher, declining from -0.56 to -0.96 MPa through the day.

Leaf conductances of water vapor were highest in the early morning (0800–1000) and then decreased, except for leaf conductances of *L. arizonicus*, which declined slowly through the day (Fig. 3). Only leaves of *M. rotundifolium* showed any sign of an afternoon recovery, most likely in response to a decline in the VPD, since leaf water potentials had not yet recovered.

Net rates of photosynthesis (as CO_2 uptake) were also measured diurnally on these same species (Fig. 4). To interpret these data, it is important to realize that *L. arizonicus*, *M. rotundifolium*, and *P. linearis* were leaf solar tracking species (diaheliotropic orientation

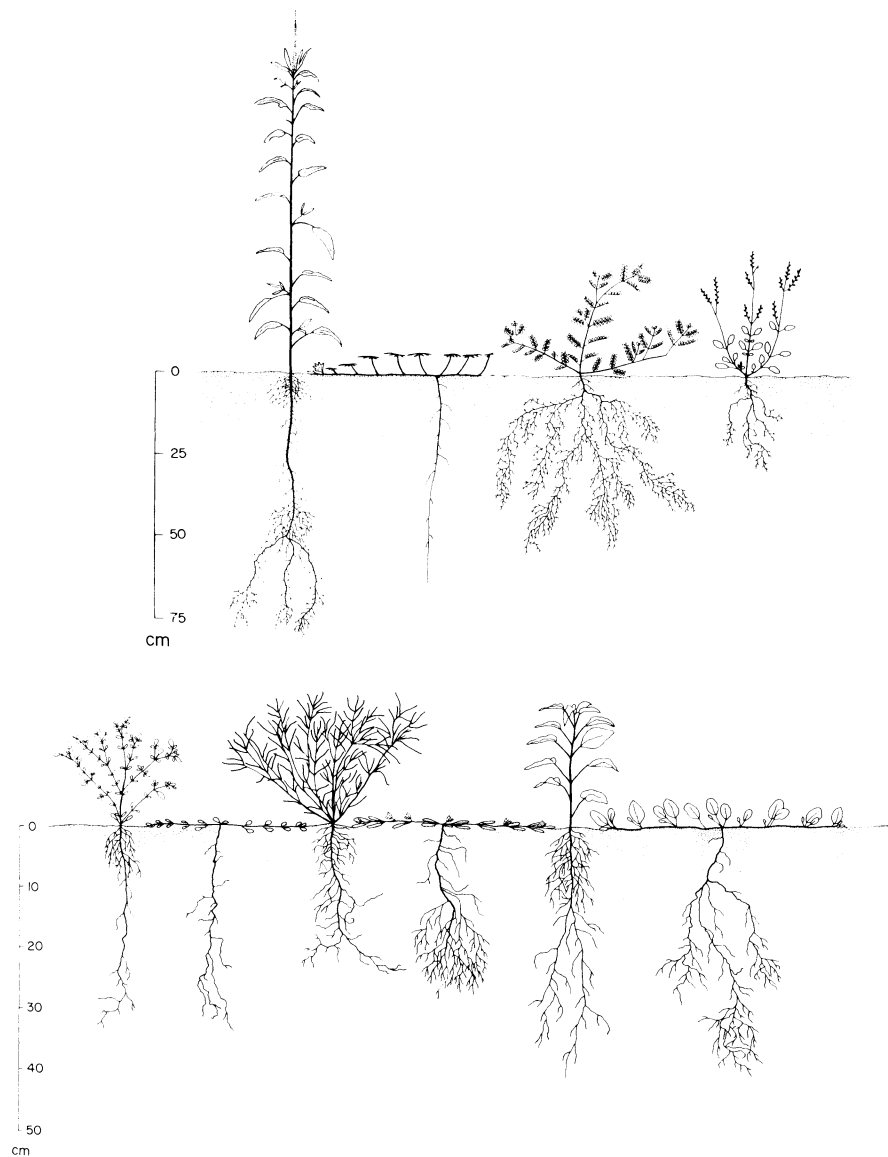


FIG. 2. Rooting distributions for Sonoran Desert summer annuals. Upper plate (left to right): *Amaranthus palmeri*, *Cucurbita digitata*, *Kallstroemia grandiflora*, and *Boerhaavia wrightii*. Lower plate (left to right): *Tidestromia lanuginosa*, *Boerhaavia spicata*, *Pectis papposa*, *Euphorbia abramsiana*, *Amaranthus palmeri*, and *Allionia incarnata*.

of leaf lamina perpendicular to direct beam); and therefore, their leaves would be expected to experience high irradiances throughout the day. *L. arizonicus* also showed paraheliotropic leaf movements (orientation of the leaf lamina parallel to the sun's direct beam), and thus received less irradiance than the other two species. *A. villosa* leaves occasionally exhibited solar tracking movements, but not on 20 March 1980. Net photosynthetic rates were high on all three leaf solar tracking species early in the morning, when leaf conductances were highest (Fig. 4). Peak photosynthetic rates of these three species were in the 30–40 $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$

range. Photosynthesis followed a pattern similar to leaf conductance, varying slightly in *L. arizonicus*, decreasing in the afternoon in *P. linearis*, and decreasing at midday and recovering in the afternoon in *M. rotundifolium*. Leaves of *A. villosa* did not exhibit the high early-morning photosynthesis rates observed in the other three species, but instead varied sinusoidally through the day with changes in the incident levels of solar radiation.

The calculated intercellular CO_2 concentrations were somewhat lower than previously observed on these species under well-watered glasshouse conditions. Werk

TABLE 1. Root:shoot (mass:mass) ratios and photosynthetic pathways for Sonoran Desert winter and summer annuals. Data are means of pooled samples, except in those species where standard errors are presented. *n* indicates the number of individuals excavated.

| Species | <i>n</i> | Photo-synthetic pathway | Root:shoot ratio |
|---------------------------------|----------|-------------------------|------------------|
| Winter annuals | | | |
| <i>Abronia villosa</i> | 11 | C ₃ | 0.03 |
| <i>Atrichoseris platyphylla</i> | 5 | C ₃ | 0.38 |
| <i>Calandrinia ambigua</i> | 5 | C ₃ | 0.12 |
| <i>Camissonia claviformis</i> | 11 | C ₃ | 0.08 ± 0.01 |
| <i>Chorizanthe rigida</i> | 18 | C ₃ | 0.09 |
| <i>Cryptantha utahensis</i> | 11 | C ₃ | 0.09 |
| <i>Geraea canescens</i> | 10 | C ₃ | 0.11 ± 0.01 |
| <i>Malvastrum rotundifolium</i> | 10 | C ₃ | 0.15 ± 0.02 |
| <i>Mohavea breviflora</i> | 10 | C ₃ | 0.16 |
| <i>Palafoxia linearis</i> | 11 | C ₃ | 0.21 |
| <i>Phacelia crenulata</i> | 11 | C ₃ | 0.10 |
| <i>Plantago insularis</i> | 11 | C ₃ | 0.13 |
| <i>Polygonum aviculare</i> | 10 | C ₃ | 0.09 ± 0.01 |
| $\bar{x} \pm SE$ | | | 0.134 ± 0.023 |
| Summer annuals | | | |
| <i>Allionia incarnata</i> | 1 | C ₄ | 0.05 |
| <i>Amaranthus palmeri</i> | 8 | C ₄ | 0.16 ± 0.02 |
| <i>Boerhaavia wrightii</i> | 4 | C ₄ | 0.08 ± 0.01 |
| <i>Cucurbita digitata</i> | 3 | C ₃ | 0.22 ± 0.02 |
| <i>Euphorbia abramsiana</i> | 3 | C ₄ | 0.26 ± 0.03 |
| <i>Kallstroemia grandiflora</i> | 3 | C ₄ | 0.11 ± 0.03 |
| <i>Pectis papposa</i> | 4 | C ₄ | 0.08 ± 0.002 |
| <i>Tidestromia lanuginosa</i> | 3 | C ₄ | 0.09 ± 0.03 |
| $\bar{x} \pm SE$ | | | 0.131 ± 0.025 |

et al. (1983) showed that intercellular CO₂ concentrations averaged 261 μ L/L for winter desert annuals. The calculated midday intercellular CO₂ concentrations for *A. villosa*, *L. arizonicus*, *M. rotundifolium*, and *P. lin-*

earis were 142, 155, 164, and 182 μ L/L, respectively, implying that stomatal closure was proportionally greater in field-grown plants than in glasshouse-grown plants.

The diurnal courses of leaf water potential on 21 March 1982 were of similar magnitude to those measured on 20 March 1980, even though measurements were collected on different species (Fig. 3). Midday leaf water potentials were as low as -1.2 to -1.4 MPa in *Camissonia boothii*, *Eschscholtzia glyptosperma*, and *Salvia columbariae*, a decrease of ≈ 0.8 MPa from morning values. Leaf conductances to water vapor on 21 March 1982 were generally higher at midday and in the afternoon than those on 20 March 1980, perhaps reflecting the lower maximum VPD (2.2 kPa on 21 March 1982 vs. 4.2 kPa on 20 March 1980). There was no pronounced early-morning peak for leaf conductance, although maximum values all occurred before noon. This is probably because none of these species exhibited leaf solar tracking movements. All four species showed some recovery in leaf water potential values after 1400, but leaf conductance did not follow suit.

Six of the species in the March 1979 midday survey (Table 2) were also measured in March 1980 or 1982. In five of the six, leaf-conductance values from the survey were in close agreement with midday values from the diurnal courses. In the sixth case, survey leaf-conductance values were higher in *M. rotundifolium*. However, leaf water potentials were also higher. Since maximum leaf conductance declines linearly with leaf water potential in *Malvastrum* (Forseth and Ehleringer 1982b), this is the likely explanation for that discrepancy.

By April 1979, leaf conductances and leaf water potentials were lower than in March (Table 2). The average leaf conductances in April were similar among

TABLE 2. Leaf water potentials and leaf conductances of water vapor for winter desert annuals at midday under natural conditions in Death Valley, California. Data are means $\pm 1 SE$.

| Species | March 1979 | | April 1979 | |
|-----------------------------------|-----------------------|--------------------|-----------------------|--------------------|
| | Water potential (MPa) | Conductance (mm/s) | Water potential (MPa) | Conductance (mm/s) |
| <i>Abronia villosa</i> | -1.10 \pm 0.06 | 6.7 | ... | 4.3 \pm 0.4 |
| <i>Astragalus lentiginosus</i> | -1.40 \pm 0.06 | 4.7 | ... | ... |
| <i>Atrichoseris platyphylla</i> | -1.07 \pm 0.14 | 18.7 | ... | 3.6 \pm 0.2 |
| <i>Camissonia claviformis</i> | -1.17 \pm 0.05 | 11.6 | -1.27 \pm 0.03 | 4.3 \pm 0.3 |
| <i>Chaenactis carphoclinia</i> | -1.70 \pm 0.00 | 11.2 | -3.33 \pm 0.29 | ... |
| <i>Chorizanthe rigida</i> | -1.64 \pm 0.12 | 7.9 | ... | ... |
| <i>Cryptantha utahensis</i> | -1.06 \pm 0.03 | 15.9 | -1.85 \pm 0.18 | ... |
| <i>Eschscholtzia glyptosperma</i> | -0.96 \pm 0.02 | 7.2 | ... | ... |
| <i>Geraea canescens</i> | -1.08 \pm 0.11 | 12.1 | ... | 3.2 \pm 0.0 |
| <i>Lupinus arizonicus</i> | -0.58 \pm 0.13 | 8.9 | -1.27 \pm 0.05 | ... |
| <i>Malvastrum rotundifolium</i> | -1.18 \pm 0.01 | 10.3 | -2.32 \pm 0.06 | 4.0 \pm 0.1 |
| <i>Mohavea breviflora</i> | -0.95 \pm 0.06 | 7.6 | -1.23 \pm 0.03 | ... |
| <i>Palafoxia linearis</i> | -1.04 \pm 0.02 | 7.5 | ... | ... |
| <i>Phacelia calthifolia</i> | -0.96 \pm 0.08 | 10.2 | -1.47 \pm 0.05 | 3.8 \pm 0.1 |
| <i>Phacelia crenulata</i> | -1.03 \pm 0.11 | 7.2 | -0.85 \pm 0.02 | 3.4 \pm 0.2 |
| <i>Plantago insularis</i> | -1.08 \pm 0.16 | 18.8 | ... | ... |
| <i>Polygonum aviculare</i> | -1.07 \pm 0.02 | ... | ... | ... |
| <i>Salvia columbariae</i> | -0.73 \pm 0.02 | 6.6 | -1.13 \pm 0.03 | ... |

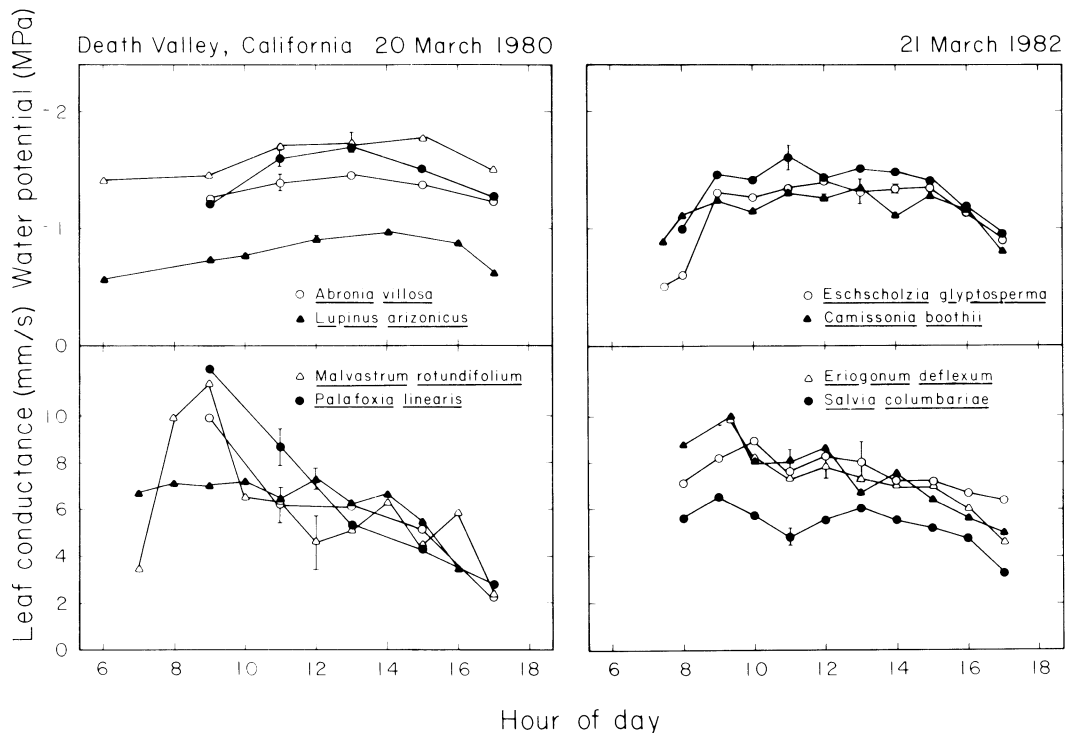


FIG. 3. Diurnal courses of leaf water potentials and leaf conductances of water vapor for desert winter annuals in Death Valley, California. Vertical bar indicates ± 1 SE.

the species (range, from 3 to 4 mm/s) despite the different leaf conductances on these same plants the month before. The data available on leaf water potentials were not complete enough to determine to what extent this component was responsible for the decline in leaf-conductance values, although the data for *C. claviformis* and *P. crenulata* did not suggest that leaf water potential was the primary factor responsible for the decline in leaf conductance.

Leaf water potentials and leaf conductances of summer annuals varied with microhabitat (Table 3). Mid-day leaf water potentials of plants outside the washes reached minima of -3.6 to -3.7 MPa; those on the edge of the washes, -2.0 to -2.8 MPa; and those in the washes, -1.1 to -1.4 MPa. Midday leaf conductances to water vapor ranged from 2.5 to 4.3 mm/s. The highest leaf conductances were measured on plants in the washes. As with the winter annuals, there was no significant correlation between average midday values of leaf conductance and leaf water potential among different species ($r^2 = 0.02$, $n = 7$, $P \gg .5$).

On a diurnal basis, summer annuals were exposed to higher air temperatures and VPDs than winter annuals. Leaf conductances of nonwash annuals (*Amaranthus palmeri* and *Kallstroemia grandiflora*) decreased throughout the day after an early morning maximum (Fig. 5). However, for plants in the washes (*Boerhaavia wrightii*, *Datura meteloides*, and *Proboscidea louisianica*), leaf conductances remained essen-

tially constant throughout the day. In neither set of plants did leaf conductances of water vapor exceed 6 mm/s; values were generally between 4 and 5 mm/s. Diurnal leaf water potentials remained fairly constant at ≈ -1.0 to -1.2 MPa in the plants in the washes and

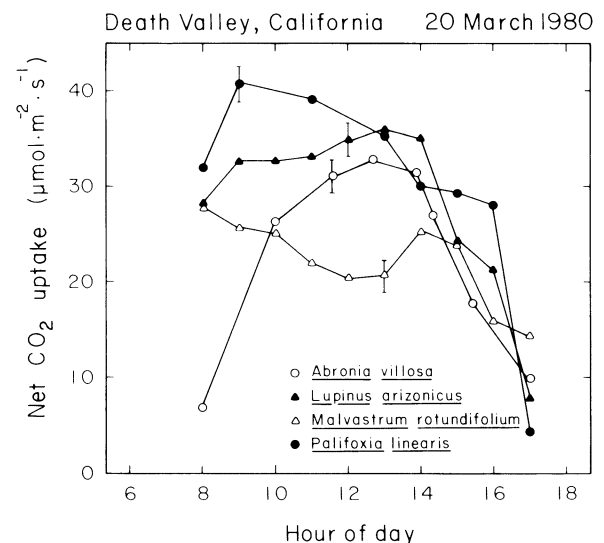


FIG. 4. Diurnal courses of net photosynthesis (as CO_2 uptake) in winter annuals in Death Valley, California. These data were collected on the same populations as for Fig. 3 (left). Vertical bars indicate ± 1 SE.

TABLE 3. Midday leaf water potentials and leaf conductances of water vapor for summer desert annuals under natural conditions in southwestern Arizona in August 1980. Data are means \pm 1 SE.

| | Leaf water potential (MPa) | Leaf conductance (mm/s) |
|---------------------------------|----------------------------|-------------------------|
| <i>Allionia incarnata</i> | -1.37 ± 0.17 | 2.8 ± 0.2 |
| <i>Amaranthus fimbriatus</i> | -2.00 ± 0.05 | 2.9 ± 0.3 |
| <i>Amaranthus palmeri</i> | -2.83 ± 0.11 | 4.3 ± 0.3 |
| <i>Boerhaavia wrightii</i> | -1.08 ± 0.10 | 3.8 ± 0.2 |
| <i>Cucurbita digitata</i> | ... | 3.9 ± 0.1 |
| <i>Datura meteloides</i> | -1.40 ± 0.00 | 4.3 ± 0.2 |
| <i>Kallstroemia grandiflora</i> | -1.53 ± 0.17 | 2.5 ± 0.2 |
| <i>Pectis papposa</i> | -3.63 ± 0.14 | ... |
| <i>Proboscidea louisianica</i> | -1.10 | 4.0 ± 0.1 |
| <i>Tidestromia lanuginosa</i> | -2.70 ± 0.17 | ... |

declined to minima of -2.7 to -2.8 MPa in the non-wash plants (Fig. 5).

DISCUSSION

Root : shoot ratios for both winter and summer desert annuals were quite low. These data support previous quantitative data for winter annuals by Bell et al. (1979) and qualitative observations by Cannon

(1911). The root : shoot ratios of desert annuals approach the low end of root : shoot ratios previously measured for herbaceous species (Bray 1963), and are certainly much lower than the ratios of 0.33 to 0.84 observed in the perennial Sonoran Desert vegetation (Ehleringer and Mooney 1983). There was no clear dichotomy between root : shoot ratios and photosynthetic pathway.

These annuals tapped only the upper 0.5 m of soil water. Mortality is not associated with the onset of reproduction, since plants begin to flower early in the growing season, but presumably occurs when the soil moisture reserves at these depths are depleted. Given heavy rains, vegetative and reproductive growth may continue simultaneously for extended periods. In some years, there is sufficient soil moisture from late-season storms for some of these annuals to "perennate" and live for 2 yr. This phenomenon has been documented in *Astragalus lentiginosus* (Beatley 1970) and has also been observed in *Eriogonum inflatum*, *Amaranthus watsonii*, and *Palafoxia linearis* (J. R. Ehleringer, *personal observation*).

Leaf water potentials for desert annuals may differ because of physiological differences (osmotic-adjustment vs. nonosmotic-adjustment species) and differences in microhabitat. The microhabitat differences are best illustrated in the comparison between wash and nonwash summer annuals: midday differences in leaf water potential may be as great as -1.5 MPa. The low leaf water potentials of active annuals imply that leaf osmotic adjustment to lower soil water potentials has occurred. Previous studies on the winter annuals *Gerardia canescens* and *Malvastrum rotundifolium* and the summer annual *Amaranthus palmeri* showed that these species were capable of actively lowering leaf osmotic potentials (Seemann et al. 1979, Forseth and Ehleringer 1982b, Ehleringer 1983). This alteration of internal water-relations parameters enables these species to maintain stomatal opening and, thus, gas-exchange activities down to lower leaf water potentials than would have been possible without this adjustment. On the other hand, leaves of the winter annuals *Lupinus arizonicus*, *Erodium cicutarium*, and *Amsinkia intermedia* do not possess the ability to adjust osmotically to lower soil water availability (Forseth and Ehleringer 1982b, Monson and Smith 1982).

In comparison with other life forms, winter and summer desert annuals have midday leaf water potentials that are much higher than values measured for evergreen desert perennials during the growing season (Strain 1970, 1975, Odensing et al. 1974, Bennert and Mooney 1979, MacMahon and Schimpf 1981), and are at the high end of the range measured for herbaceous and drought-deciduous desert perennials (Halvorson and Patten 1974, Smith and Nobel 1977, Nobel 1978, Pavlik 1980, Roy and Mooney 1982). Our midday leaf water potentials are consistent with values reported in other studies (Ehleringer et al. 1979, Seemann et al.

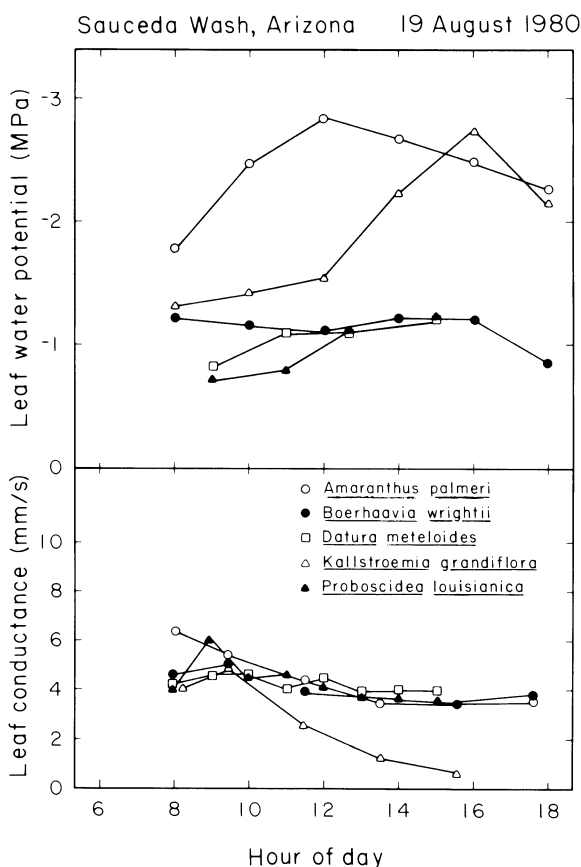


FIG. 5. Diurnal courses of leaf water potentials and leaf conductances of water vapor for desert summer annuals in Saucedo Wash, Arizona. Vertical bar indicates \pm 1 SE.

1979, Wallace and Szarek 1981). However, leaf water potentials of several annuals (e.g., *Chaenactis carphoclinia*, *M. rotundifolium*, *Pectis papposa*, and *Amaranthus palmeri*) are quite low; therefore, desert annuals cannot all be classified as drought evading in the traditional sense.

Our estimates of leaf conductances of water vapor imply that photosynthesis and transpiration rates in desert annuals are higher than in desert evergreen and drought-deciduous perennials, but not exceptionally higher than have been reported for some agricultural species. There are notable exceptions to this trend. Several winter annuals (*Atrichoseris*, *Cryptantha*, *Geraea*, *Malvastrum*, *Palafoxia*, *Plantago*) had unusually high leaf conductances in March, and this has also been reported for other desert annuals in the field (Mooney et al. 1976, Ehleringer et al. 1979, Seemann et al. 1980b, Forseth and Ehleringer 1982b).

The available data suggest that high leaf conductances and photosynthetic capacities are not characteristic of all desert annuals, but are certainly characteristic of a large fraction of them. The unusually high values reported thus far for glasshouse and field-grown desert annuals (Mooney et al. 1976, Forseth and Ehleringer 1982a, Toft and Percy 1982, Ehleringer 1983, Werk et al. 1983) are from plants grown and measured under conditions of high moisture and nutrient availability. Since a number of environmental and plant factors interact to influence gas-exchange activity, the occurrence of such favorable circumstances is probably quite limited under natural conditions and could severely limit the time periods in which such high photosynthetic rates are achieved in the field.

The gas-exchange data for the leaf solar tracking species (Fig. 4) show that these species utilize the enhanced solar radiation levels incident on the leaves early in the morning. This is also the time that leaf conductances are highest and VPDs are lowest. Since the stomata of leaves of both solar trackers and non-solar trackers close in response to a VPD increase, and because VPDs are not as low in the late afternoon as in the early morning, it would appear that the major carbon-gain advantage of solar tracking is limited to the early morning hours (Forseth and Ehleringer 1983a, b).

In summary, leaf conductances and leaf water potentials are high in desert annuals, and in some circumstances and species, may be unusually high. This is consistent with the idea that these annuals are ephemeral and drought-evading. However, it is clear that some winter and summer desert annuals are capable of tolerating low leaf water potentials and therefore are not drought-evading in the traditional sense. Root/shoot ratios of both winter and summer desert annuals are quite low, suggesting that only a small fraction of the carbon gained is used for water acquisition; carbon is instead used for vegetative and reproductive growth.

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