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Soil moisture extraction by evergreen and drought-deciduous shrubs in the Mojave Desert during wet and dry years

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Annual and seasonal evapo-transpiration (ET) were compared among Mojave Desert shrubs with different leaf phenologies over a 3-year period during which annual precipitation varied from well below average to more than twice average. During the wet year, soil wetting fronts reached maximum depths of 0·75 m to > 1·95 m, depending on soil texture at the study sites. The evergreen shrubs *Larrea tridentata* and *Ephedra nevadensis*, and the drought-deciduous shrub *Ambrosia dumosa*, were able to extract soil water in a uniform manner to depths > 1 m. For stands of the deciduous shrub *Lycium pallidum*, a soil texture change at c. 0·75 m impeded percolation of water below that depth. There were no significant differences ($p < 0{\cdot}05$) in annual ET between the evergreen shrubs *Larrea* and *Ephedra* relative to the drought-deciduous shrubs *Ambrosia* and *Lycium* during the 3 years of the study. Early in the growing season, extraction of soil water from beneath plant canopies was slightly greater than from shrub interspaces for *Ambrosia*, *Ephedra*, and *Lycium*, but not for *Larrea*. For all species, annual soil water extraction from beneath plant canopies was not significantly different than that from shrub interspaces. The lower limit of soil water extraction (L_e) for the study sites varied from 4 to 10 volumetric per cent, depending on soil texture, and did not differ significantly among species. For all species, L_e was reached within 6 to 12 months following twice average precipitation during the period of November 1994 to March 1995. We conclude that ET in the Mojave Desert is dependent largely on winter precipitation and the amount of soil water available during the growing season rather than on species composition.

Keywords: Mojave Desert plants; soil moisture extraction; water balance; evapo-transpiration; deep drainage

Introduction

Long-term climatic records emphasize the high variability of annual precipitation in the Mojave Desert of southern Nevada, with records over a 60-year period that range from near 0 to more than double (~ 300 mm) long-term mean values (90–120 mm)

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at elevations below 1000 m (Rundel & Gibson, 1996). Because maximum precipitation and subsequent soil moisture recharge in the Mojave Desert generally occurs in the winter and early spring when minimum temperatures are below freezing, Mojave Desert perennial vegetation actively transpires for only 4 to 6 months during normal rainfall years (Smith *et al.*, 1995). During the remaining 6–8 months of the year, moisture is removed from the soil predominately through evaporation. Although a model simulation of plant water use for shrub-dominated communities of the Mojave Desert suggests that these communities generally extract all available soil moisture over a 1 to several year period (Lane *et al.*, 1984), this model was based on soil moisture measurements made at shallow depths (0·15–0·35 m) and estimated changes in soil moisture to a depth of only 1·5 m. Very wet year scenarios, when soil water would likely percolate to depths greater than 1·5 m, were not considered. Because Mojave Desert shrubs have sparse root densities below 0·5 m (Wallace *et al.*, 1980; Cody, 1986), water may remain stored in the soil profile, especially at deeper depths, during years with above average rainfall.

In this study, the quantity of water evapo-transpired from stands of Mojave Desert shrubs with different rooting depths and leaf phenologies was determined using a mass balance approach over a 3-year period. During these 3 years, annual precipitation varied from more than double the long-term average to less than one-half average precipitation. Changes in soil water content were measured in 0·2 m depth increments to maximum depths ranging between 1·35 m and 1·95 m at the base of plants and in the interspaces between shrubs. Seasonal and annual evapo-transpiration (ET) were compared to determine if water use varies among species or between shrubs with different leaf phenologies. We anticipated that the evergreen species *Ephedra nevadensis* and *Larrea tridentata*, which have the potential to exhibit growth at any time of the year given above freezing minimum temperatures and adequate soil moisture (Oechel *et al.*, 1972; Reynolds, 1986; Smith *et al.*, 1997), would extract more soil water throughout the year than the drought-deciduous shrubs *Ambrosia dumosa* and *Lycium pallidum*, which exhibit shorter periods of carbon fixation and growth (Smith *et al.*, 1997).

Methods

Study site

Research was conducted at the Nevada Test Site (NTS), located approximately 160 km north-west of Las Vegas. The NTS consists of 350,000 ha of arid and semi-arid land and includes the transition zone between the Mojave and Great Basin Deserts of western North America. The NTS was designated as a National Environmental Research Park in 1993 in order to study the impacts of energy development on the environment and to support ecological research. Excellent descriptions of climate gradients and variability as well as physical geography for the region are given by Rundel & Gibson (1996).

Eight sites within the Mojave Desert vegetation zone of the NTS were chosen for this study. Each site was selected such that a monoculture of one of four study species occurred within 3 m of neutron probe installation sites. Annual plants growing under or near target plant canopies were removed on a regular basis. Elevation of the sites ranged from 950 to 1150 m. Yearly rainfall at the NTS varies greatly but generally ranges from 85 to 160 mm and rarely exceeds 250 mm at elevations below 1000 m (Rundel & Gibson, 1996). Soil classification maps were not available for our study sites, but soils located at similar elevations on the NTS belong to the Thermic family, and would be classified as Entisols with an ochric epipedon (Rundel & Gibson, 1996). At each site, soil samples were collected in 0·2 m depth increments from the surface to 1 m or deeper and analysed for soil texture by the particle-size distribution method (Bouyoucos, 1962) and for bulk density by the core method (Blake, 1965).

Study species

Four species were examined that differed in leaf longevity. *Larrea tridentata* (D.C.) Cov. (creosote bush) and *Ephedra nevadensis* S. Wats. (Mormon tea) were selected as evergreen shrubs. *Larrea* is microphyllous and *Ephedra* is aphyllous with evergreen stems. *Ambrosia dumosa* (A. Gray) Payne (white bursage) and *Lycium pallidum* Miers (desert-thorn) were selected as drought-deciduous shrubs. These species were also chosen because they are widespread throughout the Mojave Desert and because in some areas they exist as near monocultures, providing an ideal situation for examining differences in water use among species. Two representative areas for each species were selected within a 60 km × 60 km area of the NTS, and five plant-centered plots were established at each site.

Plot establishment

Plant-centered plots were established by installing neutron probe access tubes at the edge of the target plant canopy and in the interspace halfway between that plant and another plant of the same species. The minimum spacing allowed between the target plant and the nearest plant of the same species was 1 m and the maximum spacing allowed was 3 m. No other plants were allowed to grow within a 2 m radius of the neutron probe tube placed in the interspace. This configuration ensured that the soil volume sampled by the neutron probe was influenced most directly by the target species. Plots were established on level ground to reduce runoff and runon. Holes for the installation of neutron probe access tubes were made with a gasoline-powered impact hammer (Cobra, Atlas Copco Inc., PA, U.S.A.) equipped with a split-spoon soil sampler. Tubes were installed to a depth of 1·95 m whenever possible, but this depth could not always be attained due to gravel or rock layers and substantial soil cave in. Rain gauges, consisting of 0·5 m sections of 0·3 m diameter PVC pipe that was sealed at one end, were placed at each site. A small amount of oil was placed in each rain gauge to prevent evaporation of collected precipitation between measurements.

Neutron probe measurements

Changes in soil water content among the shrub stands were examined by measuring volumetric soil water content (θ_v) with a neutron probe (Model 503 Hydroprobe, Campbell Pacific Nuclear Corporation, CA, U.S.A.) at 0·2 m depth increments beginning at 0·15 m and continuing to the maximum depth of access tube installation (0·75 to 1·95 m). The neutron probe was calibrated at four representative sites by comparing soil water contents from soil cores collected adjacent to neutron probe access tubes. The gravimetric per cent soil water content of the soil cores was converted to θ_v by multiplying the gravimetric water content by the bulk density of the soil. For all sites, linear regression of neutron probe data *vs.* θ_v of the soil cores yielded p-values of $< 0{\cdot}001$ and r^2 values from 0·86 to 0·98. The equality of the regression lines was tested using a general linear testing approach (Neter & Wasserman, 1974). Because the slopes and intercepts of the regression lines did not differ significantly, the lines were pooled with a resulting r^2 of 0·91. Initial neutron probe measurements were taken in August 1994, and then monthly measurements were made during the first week of

January through August each year. Measurements were not made during September through December.

Water balance equation

Evapo-transpiration (ET) was estimated from the simplified water balance equation

$$ET = P + \Delta S \qquad \text{(Eqn 1)}$$

where precipitation (P) and change in soil moisture (ΔS) are expressed in mm. Because plots were level, runon and runoff were assumed to be negligible. Deep drainage was also assumed to be negligible. The total amount of water in the soil profile (S) in mm was estimated for each tube on each sampling date by:

$$S = 2\left(1{\cdot}25\ \theta_1 + \sum_{i=2}^{n} \theta_i\right) \qquad \text{(Eqn 2)}$$

where θ_1 is the volumetric water content (%) at a depth of 0·15 m, θ_i is the volumetric water content (%) at subsequent 0·2 m depth intervals to the bottom of the access tube, and *n* is the number of 0·2 m intervals. This equation approximates integration under a curve by assuming a series of rectangles, each centered on a neutron probe estimate of volumetric water content (θ_v) above and below a particular depth (Anderson *et al.*, 1993). Because water content at the surface is so variable and cannot be estimated accurately with a neutron probe, a uniform water content was assumed from the surface to 0·15 m (θ_1). Hence, θ_1 is multiplied by 1·25 because θ_1 is an estimate of soil water content in the top 0·25 m soil interval, whereas θ_i are estimates of soil water content in the subsequent 0·2 m intervals ($0{\cdot}25 \div 0{\cdot}20 = 1{\cdot}25$).

A repeated measures analysis was performed on the ET measurements using the ANOVA procedure of SAS (SAS Institute, 1988) with species as the classification variable and precipitation as a covariate. Two sites for each species were used as replicates.

Results

Annual precipitation

Annual precipitation (P) varied greatly over the 3 years of the study (Fig. 1). During 1995, P ranged from 199 mm to 290 mm at the study sites, which was 1·6 to 2·3 times greater than the 33-year mean (126 mm; 1963–1995) measured at a station located centrally among the study sites. In contrast, 1996 was a dry year (29–54 mm) with P well below average (23–43%). During 1997, P ranged from 79 mm–125 mm. During all 3 years, the majority of precipitation occurred during November through March with only small rainfall events in the summer.

Annual ET

The simplified water balance equation was used to estimate ET for each species. The simplified water balance equation estimates ET based on P and changes in soil moisture (ΔS). Therefore, to estimate ET accurately, the entire volume of soil within which ΔS occurs must be sampled. In this study, the depth of soil within which ΔS was measured varied from 0·75 m to 1·95 m because gravel layers and soil cave-in limited the depth of neutron probe access tube insertion in some areas. At least one site for each species,

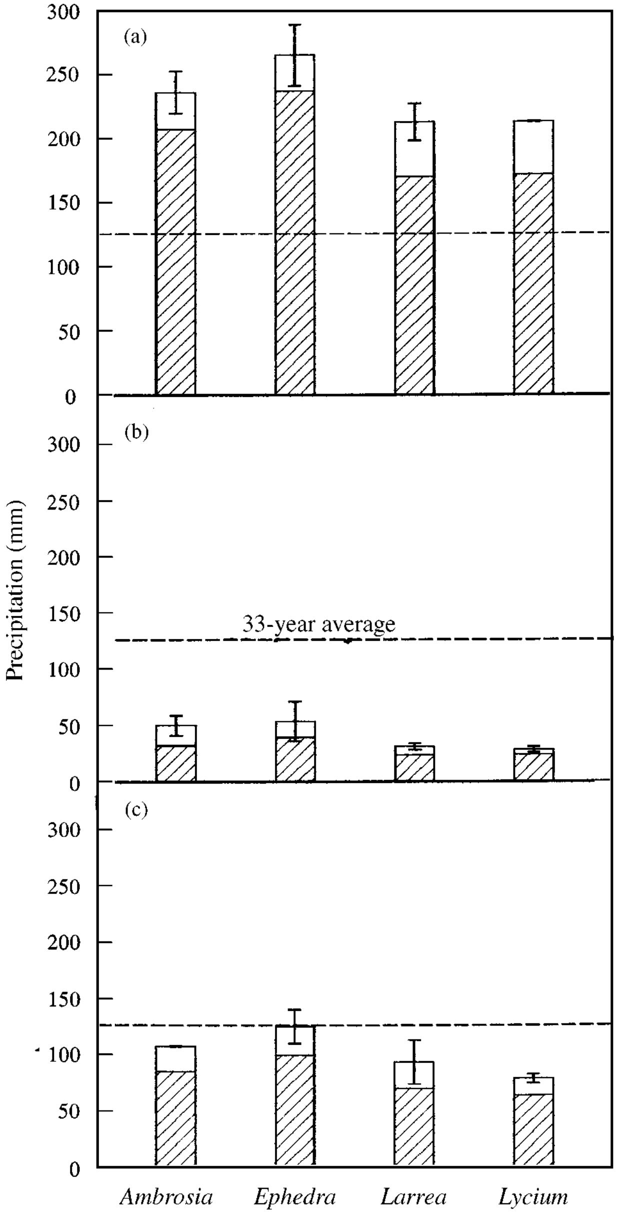

Figure 1. Mean ($N = 2$) annual precipitation for calendar years (a) 1995, (b) 1996, and (c) 1997, at Mojave Desert study sites dominated by *Ambrosia dumosa*, *Ephedra nevadensis*, *Larrea tridentata*, and *Lycium pallidum*. The open portion of bars represents precipitation received after March. Error bars represent standard error of the mean.

however, had a maximum access tube depth of 1·35 m or greater. During 1996 and 1997, which were below-average rainfall years, shallow access tubes were adequate for measuring ΔS and ET because no percolation of water was detected below the maximum depth of access tube insertion. During 1995, however, plots of θ_v distribution within the soil profile (data not shown) indicated that when annual precipitation was about twice the annual average, water percolated below access tubes with maximum depths $< 1{\cdot}35$ m (i.e., plots of θ_v distributions through time did not converge at or above the maximum tube depth). If water below the maximum tube depth was not depleted by plants, then ET would be overestimated at those sites because water that percolated to deeper soils would be erroneously attributed to ET.

The degree that ET is overestimated is expected to vary depending on the amount of water transported to deeper soils. In order to assess how greatly ET was overestimated during 1995 at sites with shallow tubes, we compared ET estimates made at sites with the deepest neutron probe access tubes to ET estimates for those same sites if only the upper portion of the soil profile was used (Table 1). The upper portion of the soil profile was set equal to the maximum tube depth at the replicate site (i.e. the site with more shallow tubes). Paired *t*-tests indicated that tube depth significantly effected ET estimates in some cases (Table 1). For *Ambrosia* and *Lycium*, tube depth had very little effect on ET estimates due to small ΔS below 1·35 m for these species. For *Ephedra* and *Larrea*, ET was overestimated to the greatest degree early in the growing season (January–March) when more water was stored at deeper depths. As the growing season progressed, ET was overestimated to lesser degrees and then underestimated late in the growing season because water that was extracted from deeper depths was not measured. Therefore, overestimation of ET early in the growing season was generally balanced by underestimation of ET late in the growing season. Because differences in annual ET between tube depths were small ($< 2\%$), we considered sites with different tube depths as replicates for the purpose of comparing annual ET among species.

Annual ET was strongly related to P ($r^2 = 0{\cdot}99$; $p < 0{\cdot}001$) (Fig. 2). Analysis of covariance indicated that neither species nor year significantly affected annual ET (Table 2). Therefore, all of the species responded to wet and dry years in a similar manner. In addition, *t*-tests to compare annual ET among plants with different leaf phenologies indicated that annual ET did not differ significantly between evergreen and drought-deciduous shrubs during the 3 years of this study (Fig. 3). Finally, paired

Table 1. *Mean (*N $=$ *5 plots per species) ET estimates (mm) made beneath four Mojave Desert shrub species at sites with deep neutron probe access tubes (i.e. maximum tube depth* $> 1{\cdot}35$ *m) when* ΔS *was measured to the maximum depth of tube insertion, and when* ΔS *was measured only for the upper portion of the soil profile; the upper portion of the profile corresponded with the same profile depth as the replicate site with shallow tubes.* *p $\leq 0{\cdot}05$ *between tube depths for a given time period and species*

	Ambrosia dumosa		*Ephedra nevadensis*		*Larrea tridentata*		*Lycium pallidum*	
Profile depth	0–1·75 m	0–1·35 m	0–1·95 m	0–0·95 m	0–1·35 m	0–0·75 m	0–1·75 m	0–0·95 m
Aug–Jan	38*	39	53*	74	35*	33	49*	48
Feb	34	34	7*	21	22	22	33	20
Mar	29	31	57*	73	56*	65	44	57
Apr	27*	28	29*	20	37*	31	28	29
May	28	28	41*	26	28	28	36	36
Jun	32	33	29*	15	15	12	8	8
Jul	17*	15	17*	8	8	8	5	6
Annual ET	205*	208	233*	237	201*	199	203	204

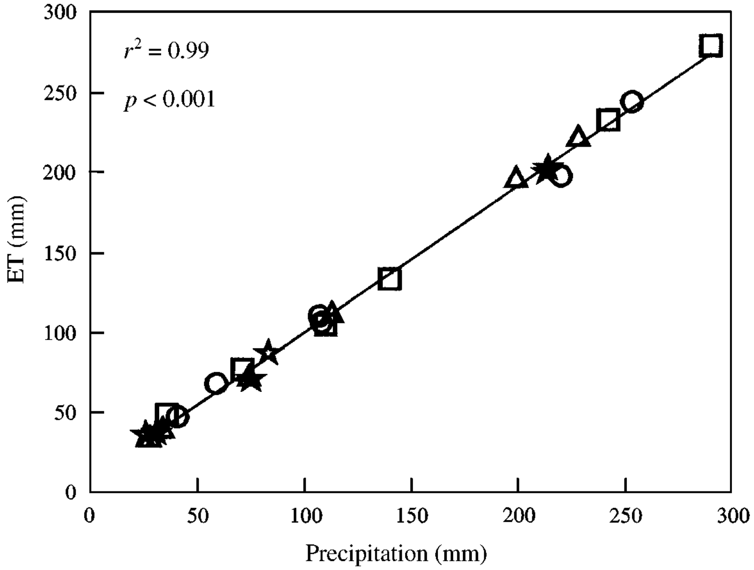

Figure 2. Linear regression of annual ET *vs.* annual precipitation at two Mojave Desert study sites each for *Ambrosia dumosa* (○), *Ephedra nevadensis* (□), *Larrea tridentata* (△), and *Lycium pallidum* (☆). Each data point represents mean values for five plants at a given study site.

Table 2. *Results of analysis of covariance showing effects of species and year on annual ET with precipitation at each study site as a covariate*

Source	df.	*F*-value	*p*-value
Species	3	0·07	0·98
Year	2	3·23	0·08
Species × year	6	1·8	0·19
Precipitation	1	258·4 ϕs	< 0·001

t-tests indicated that annual ET based on ΔS measured beneath plant canopies *vs.* ΔS measured in shrub interspaces did not differ significantly for any species (Table 3), indicating that soil water was depleted equally well beneath shrubs and in shrub interspaces over the course of the year.

Seasonal ET

Because drainage of water below the maximum access tube depth inflates ET estimates early in the growing season (see above), only sites with access tube depths ≥ 1·35 m were used for comparisons of seasonal ET among species during 1995, which was an exceptionally wet year with percolation of water below 1 m at most study sites. During 1996 and 1997, sites were treated as replicates for each species because drainage of water below shallow tubes did not occur, or was minor.

In order to examine seasonal patterns of ET, cumulative per cent annual ET measured beneath plant canopies was plotted through time for each species (Fig. 4).

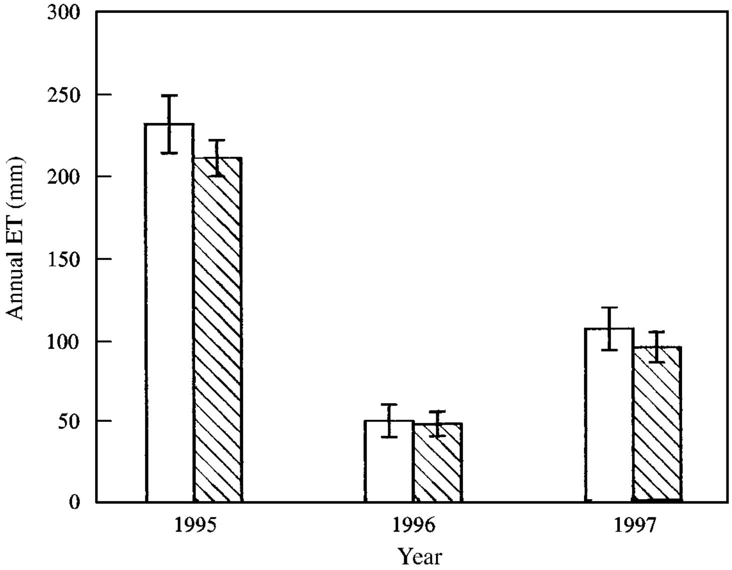

Figure 3. Annual ET among Mojave Desert shrubs with evergreen (□) and drought-deciduous (▨) phenologies. Error bars represent standard error of the mean ($N = 20$; 2 species × 2 sites × 5 plots at each site).

Table 3. *Mean (* N *= 10; 5 plots × 2 sites per species) annual ET (mm) ± standard error of the mean beneath shrub canopies and in shrub interspaces in the Mojave Desert of southern Nevada*

Year	*Ambrosia dumosa*		*Ephedra nevadensis*		*Larrea tridentata*		*Lycium pallidum*	
	canopy	interspace	canopy	interspace	canopy	interspace	canopy	interspace
1995	224 ± 7	221 ± 7	256 ± 8	256 ± 9	208 ± 4	211 ± 4	202 ± 1	205 ± 3
1996	56 ± 3	59 ± 3	60 ± 6	60 ± 5	35 ± 1	35 ± 1	37 ± 1	36 ± 1
1997	108 ± 1	107 ± 1	119 ± 5	119 ± 5	90 ± 6	88 ± 6	77 ± 2	77 ± 2

During 1995, ET was significantly lower ($p < 0{\cdot}05$) for *Ambrosia* relative to the other species from March through May. Lower ET values for *Ambrosia* beginning in March were a result of frost damage that killed the first set of *Ambrosia* leaves in mid February. The second flush of *Ambrosia* leaves was sparse during the remainder of the growing season. During 1996 and 1997, species was not significant ($p = 0{\cdot}61$ and 0·64, for 1996 and 1997, respectively), and neither was the species-by-date interaction term ($p = 0{\cdot}66$ and 0·13, for 1996 and 1997, respectively). These results indicate that seasonal differences in ET did not occur among species during those years.

Seasonal comparisons of ET measured beneath plant canopies relative to ET measured in shrub interspaces are shown in Fig. 5. We limit presentation of these data to 1995 because no significant differences between ET in shrub interspaces *vs.* beneath plant canopies occurred during 1996 due to lack of precipitation. Patterns of ET measured between shrub interspaces *vs.* beneath plant canopies were similar during 1995 and 1997. For *Ambrosia*, *Ephedra*, and *Lycium*, ET was slightly greater beneath

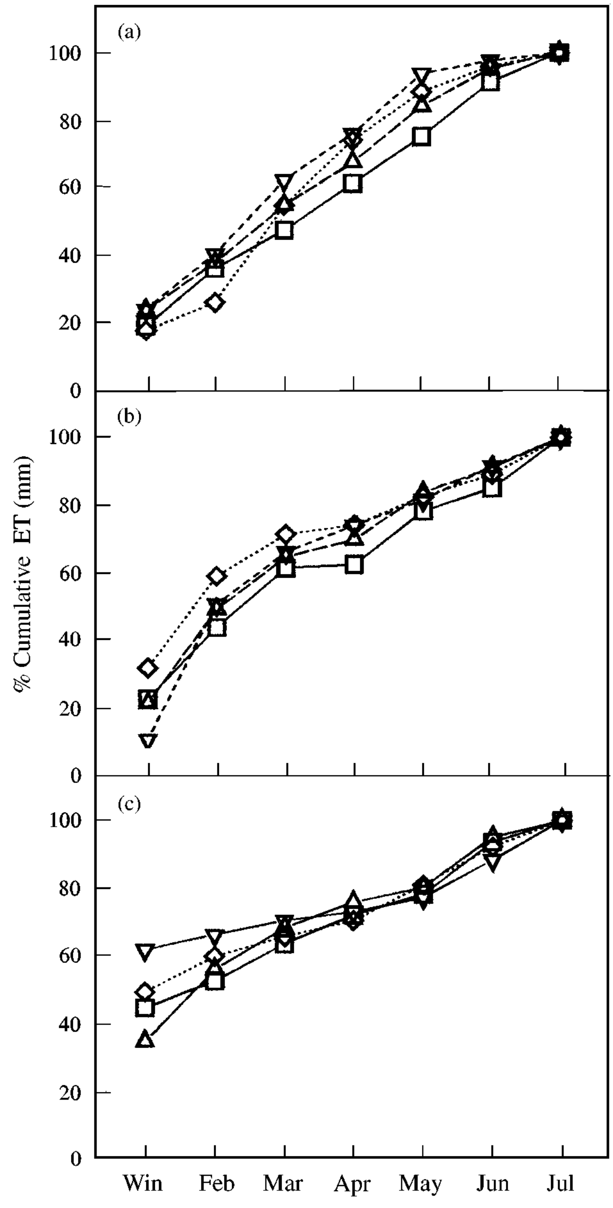

Figure 4. Per cent cumulative annual ET by month for *Ambrosia dumosa* (□), *Ephedra nevadensis* (△), *Lycium pallidum* (▽), and *Larrea tridentata* (◇) in the Mojave Desert of southern Nevada. For (a) 1995, (b) 1996, and (c) 1997. For 1995, ET values for each species are means of five plants at one site with deep neutron probe access tubes. For 1996 and 1997, ET values for each species are means for two sites × five plants at each site. 'Win' on the *x*-axis refers the period of September through January.

plant canopies relative to shrub interspaces early in the growing season (Fig. 5), indicating greater extraction of soil water from beneath plant canopies when soil water contents were high. By April, there were no differences in ET measured beneath plant canopies relative to shrub interspaces for *Ambrosia*, *Ephedra* or *Lycium*, indicating equal rates of soil water depletion from beneath plant canopies and in shrub interspaces.

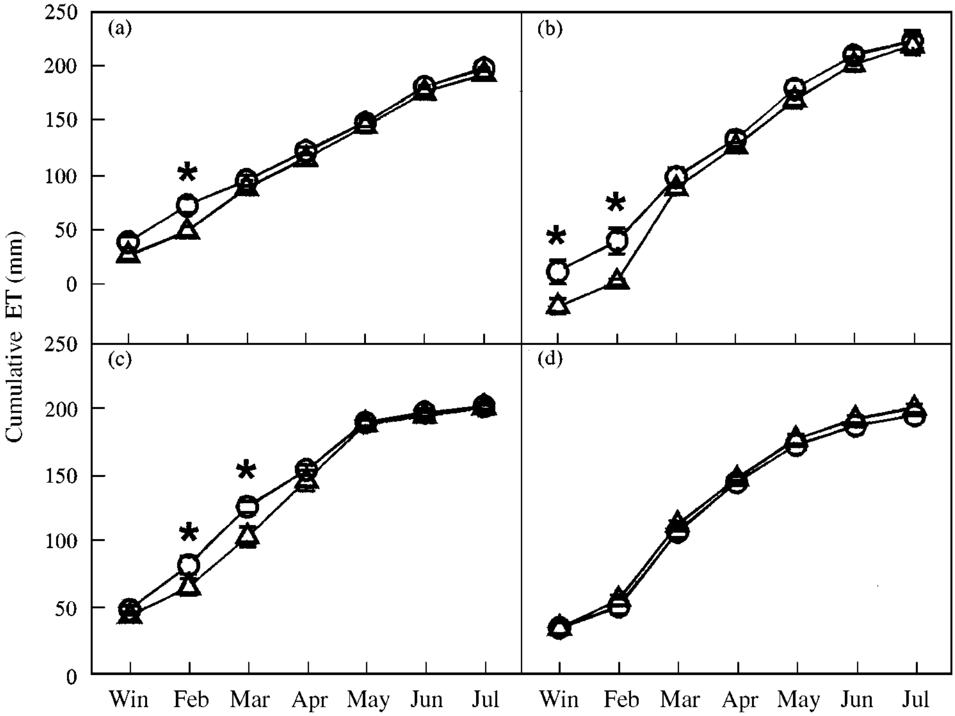

Figure 5. Cumulative ET by month beneath plant canopies (○) and in shrub interspaces (△) for (a) *Ambrosia dumosa*, (b) *Ephedra nevadensis*, (c) *Lycium pallidum*, and (d) *Larrea tridentata* during 1995. 'Win' on the x-axis refers the period of September through January. $*p \leq 0{\cdot}05$.

For *Larrea*, ET measured beneath plant canopies was nearly identical to that in shrub interspaces throughout the year (Fig. 5).

Patterns of soil water storage and depletion

To examine patterns of soil water storage and depletion, the distribution of θ_v throughout the soil profile was plotted for each species and sample date at all study sites (Fig. 6). We limit presentation of these data to 1995 because soil water storage and patterns of depletion were most pronounced during this wet year. We further limit presentation of the data to sites with deep neutron probe access tubes (i.e. maximum tube depths $> 1{\cdot}35$ m) because patterns of water depletion from shallow soils did not vary among sites. Examination of soil water distribution at sites with deep access tubes allowed us to determine (1) to what depth water percolated and (2) to what depth soil water was extracted.

Maximum depths of soil wetting fronts varied depending on soil texture. At the *Ambrosia* and *Ephedra* sites, which had fairly uniform sandy soil textures throughout the zone of θ_v measurement (Table 4), water percolated to 1·75 m and to $> 1{\cdot}95$ m, respectively (Fig. 6). At the *Larrea* and *Lycium* sites, drainage of water below 1·15 m and 0·75 m, respectively, was impeded because of changes in soil texture at those depths (Table 4).

Patterns of soil water depletion indicate that *Ambrosia*, *Ephedra*, and *Larrea* were able to extract water uniformly to soil depths below 1 m (Fig. 6). Because a soil texture

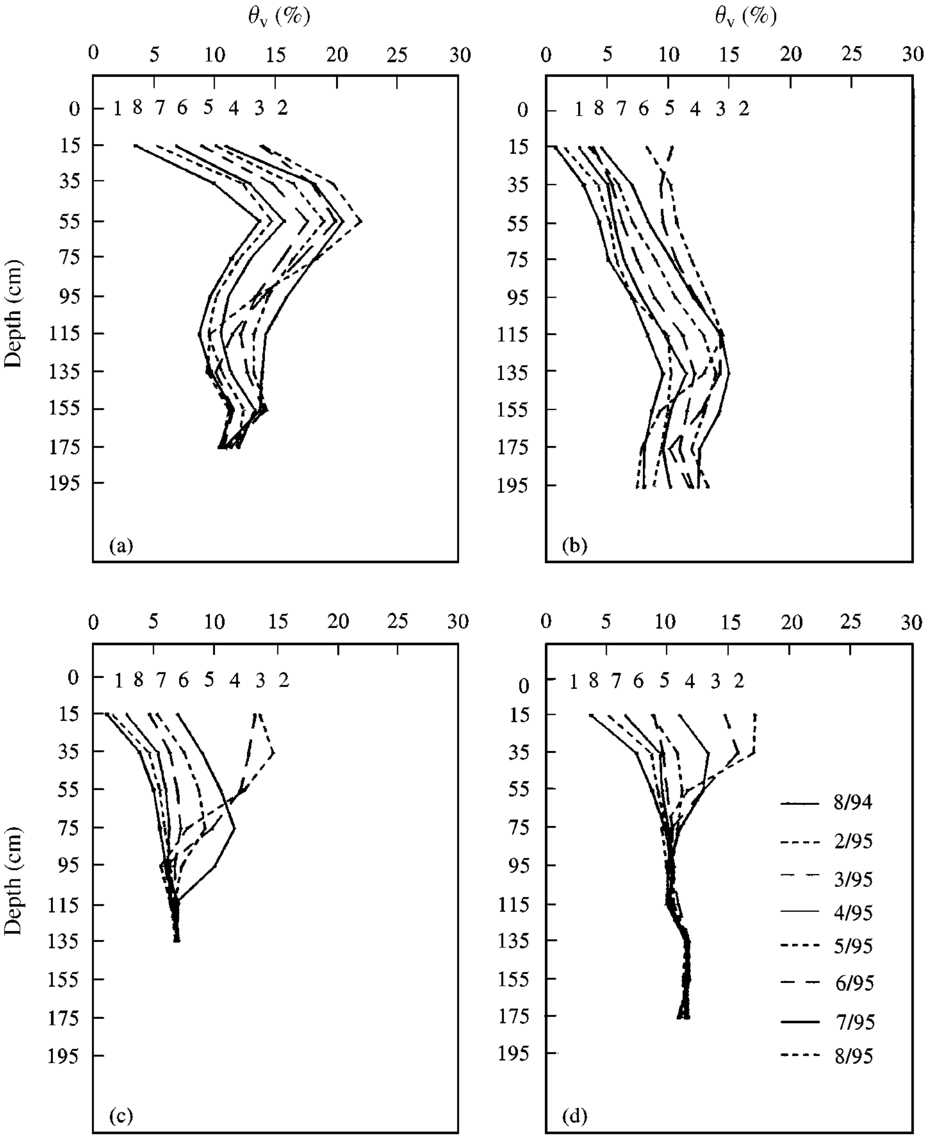

Figure 6. Distribution of volumetric soil water content θ_v (%) for (a) *Ambrosia dumosa*, (b) *Ephedra nevadensis*, (c) *Larrea tridentata*, and (d) *Lycium pallidum* at Mojave Desert sites with deep neutron probe access tubes from August 1994 to August 1995. The numbers at the top of the profile curves represent the sequence of sampling dates.

change impeded percolation of water at the *Lycium* site, we do not know if *Lycium* can deplete soil water below 0·75 m.

Lower limits of soil water extraction

The lowest θ_v were measured during August 1994 and August 1996 (Table 5). The θ_v on these dates were used to estimate the lower limit of soil water extraction (L_e) for the

Table 4. *Per cent sand, silt, clay and bulk densities (B.D.) (g cm* $^{-3}$*) for soils at the eight study sites. Deep sites had maximum neutron probe access tube depths greater than 1·35 m and shallow sites had maximum neutron probe access tube depths less than 1·35 m. * indicates depth interval at which a soil texture change occurs*

		Deep sites				Shallow sites			
Species	Depth (cm)	% Sand	% Silt	% Clay	B.D.	% Sand	% Silt	% Clay	B.D.
Ambrosia dumosa	5–25	78	20	3	1·7	89	5	6	1·5
	25–45	79	16	5	1·7	88	5	7	1·5
	45–65	75	20	5	1·7	90	4	6	1·5
	65–85	74	23	3	1·7	89	6	5	1·6
	85–105	76	18	5	1·4	88	4	8	1·6
Ephedra nevadensis	5–25	92	4	4	1·5	78	19	3	1·6
	25–45	93	5	2	1·7	80	11	9	1·6
	45–65	93	5	3	1·7	89	5	6	1·6
	65–85	87	12	1	1·7	91	3	6	1·7
	85–105	85	13	2	1·7	90	3	7	1·7
Larrea tridentata	5–25	76	10	14	1·7	75	15	10	1·6
	25–45	72	18	10	1·7	78	13	9	1·7
	45–65	78	14	8	1·7	80	12	8	1·7
	65–85	78	14	8	1·6	83	8	9	1·7
	85–105*	88	5	7	1·4	84	8	8	1·5
	105–125	90	4	6	1·3	82	10	8	1·5
Lycium pallidum	5–25	91	4	5	1·3	76	12	12	1·5
	25–45	93	2	5	1·6	78	7	15	1·3
	45–65	90	6	4	1·6	80	12	8	1·4
	65–85*	72	22	6	1·5	75	15	10	1·5
	85–105	73	22	5	1·5	86	6	8	1·6
	105–125	73	24	3	1·5				
	125–145	79	23	4	1·5				

study sites. Although L_e differed among sites due to differences in soil texture (Table 4), L_e did not differ significantly among species ($p = 0{\cdot}76$). The sites with the highest L_e (10%) corresponded to a higher silt content throughout the soil profile (the *Ambrosia* site) or below 0·65 m (the *Lycium* site) relative to the other study sites (Table 4). During 1995, L_e was reached at only three sites by the end of the sample period; the site with shallow access tubes for *Ambrosia* and the sites with deep access tubes for *Larrea* and *Lycium* (Table 5). During 1997, L_e was reached at both *Ambrosia* sites, the *Larrea* site with deep tubes, and the *Ephedra* site with shallow tubes (Table 5). The remaining sites had small amounts of extractable water left in the soil profile due to small rainfall events during the summer of 1997.

Discussion

We anticipated that the evergreen shrubs *Larrea tridentata* and *Ephedra nevadensis* would exhibit greater annual ET relative to the drought-deciduous shrubs *Ambrosia dumosa*

Table 5. *Mean volumetric soil water content (θ_v) throughout the soil profile and extractable water remaining within the soil profile (E_w) during August 1994, 1995, 1996, and 1997 for* Ambrosia dumosa, Ephedra nevadensis, Larrea tridentata, *and* Lycium pallidum *in the Mojave Desert of southern Nevada. Deep sites (d) had maximum neutron probe access tube depths greater than 1·35 m and shallow sites (s) had maximum neutron probe access tube depths less than 1·35 m*

Species	Site	Aug 94		Aug 95		Aug 96		Aug 97	
		θ_v (%)	E_w (mm)	θ_v (%)	E_w (mm)	θ_v (%)	E_w (mm)	θ_v (%)	E_w (mm)
Ambrosia	d	10	0	11	22	10	0	10	0
dumosa	s	4	0	4	0	4	0	4	0
Ephedra	d	6	0	7	15	6	0	7	15
nevadensis	s	7	0	8	11	7	0	7	0
Larrea	d	5	0	4	0	5	0	5	0
tridentata	s	6	0	7	8	6	0	7	8
Lycium	d	10	0	10	0	10	0	9	0
pallidum	s	7	0	8	14	7	0	8	14

and *Lycium pallidum* due to lower minimum xylem potentials and longer periods of carbon fixation for evergreen shrubs (Oechel *et al.*, 1972; Bamberg *et al.*, 1975; Smith *et al.*, 1997). Contrary to our expectations, annual ET did not differ significantly among species or between evergreen and drought-deciduous phenologies. Instead, annual ET reflected differences in precipitation, which varied greatly among years and study sites during the three years of this study.

Annual precipitation was greatest during 1995, ranging from 1·6 to 2·3 times the average at the study sites. During this wet year, percolation of soil water to depths > 1 m was measured at sites dominated by *Larrea*, *Ephedra*, and *Ambrosia*. However, one site, dominated by the deciduous shrub *Lycium*, exhibited a wetting front to only 0·75 m. Percolation of soil water below 0·75 m at the *Lycium* site was impeded by a soil texture change from sand to loamy sand at that depth. Storage of soil water at deeper depths for *Larrea*, *Ephedra*, and *Ambrosia* provided an ideal situation for the investigation of patterns of soil water depletion from the soil surface to depths greater than 1 m.

Wallace *et al*. (1980) stated that virtually all of the root systems of *Ambrosia*, *Ephedra*, *Larrea* and *Lycium* were distributed in the top 0·5 m of soil in a sandy wash area of Rock Valley in the northern Mojave Desert. Although we did not quantify root length densities in this study, we observed sparse rooting for these species at depths of 0·5 m and below when trenches were dug at the edge of plant canopies during a concurrent study (Yoder, 1998). We therefore anticipated that during above-average precipitation years, water that percolated to depths $> 0·5$ m might remain stored in the soil profile due to sparse rooting of plants at those depths. Contrary to our expectations, the evergreen shrub *Larrea* and the drought-deciduous shrub *Ambrosia* extracted soil water uniformly to the maximum depth of soil water recharge (1·75 m and 1·15 m for *Ambrosia* and *Larrea*, respectively). The evergreen shrub *Ephedra* also extracted soil water in a fairly uniform manner to a depth of at least 1.95 m. These patterns of soil water depletion suggest that although rooting densities are low at greater depths, deep roots are important for soil water extraction. Greater water uptake from deeper soil depths, despite lower root densities at those depths, has been documented for a variety of species (Proffitt *et al.*, 1985; Sharp & Davies, 1985; Wan *et al*., 1993; Yoder *et al*., 1998), and may be partially attributed to less suberization of deep roots relative to shallow laterals (Wan *et al*., 1994).

Another factor that may increase the efficiency of deep roots for the species in this current study is hydraulic lift. Hydraulic lift occurs when stomata are closed and the plant is not transpiring. During hydraulic lift, water is absorbed by plant roots in moist soil layers and transferred to shallow roots in drier topsoil where the water then exits the roots and enters the drier soil due to a water potential gradient. The water remains in the shallow soil until stomata open and the transpirational stream for water movement from the soil through the plant and into the atmosphere is reinstated (Caldwell *et al*., 1998; Horton & Hart, 1998). Hydraulic lift has been documented for each of the species in this study (Yoder, 1998), and is thought to increase the efficiency of deep roots by allowing these roots to take up water 24 h a day rather than only during periods of transpiration (Caldwell *et al*., 1998).

Although the extraction of deep soil water may allow longer-term survival of desert plants, shallow and intermediate-depth lateral roots allow for the exploitation of more frequent, small to moderate precipitation events that recharge shallow and intermediate soil horizons. Gile *et al*. (1998) documented many horizontally spreading *Larrea* roots, some of which extended 4·5 m beyond the base of the plant. High horizontal root densities for *Larrea* may explain why we saw no differences in ET estimates based on θ_v beneath plant canopies relative to ET estimates based on θ_v in shrub interspaces for this species, even early in the growing season when θ_v was high and plants were most active. For *Ambrosia*, *Ephedra*, and *Lycium*, ET measured at the base of shrubs was greater than ET measured in shrub interspaces early in the growing season, indicating greater contributions of transpiration to ET beneath plant canopies when θ_v was highest. Despite these seasonal differences in ET at the base of shrubs relative to ET measured in shrub interspaces for *Ambrosia*, *Ephedra*, and *Lycium*, by the end of the growing season, θ_v had been depleted equally well beneath plant canopies and in shrub interspaces for each species.

The results of this study verify a general water balance model for the northern Mojave Desert which suggests that all available soil moisture will be extracted by Mojave Desert plant communities over a 1 to several year period (Lane *et al*., 1984), at least for depths above 1·95 m. Because some water percolated below the maximum depth of θ_v measurement (1·95 m) at one *Ephedra* site, we could not determine if *Ephedra* depleted water that percolated below that depth. For depths above 1·95 m, a small amount of extractable water remained in the soil profile at the end of August 1995, but by the following August, the lower limit of soil water extraction (L_e) was reached at all of the study sites. Values of L_e ranged from 4% to 10%, depending on soil texture and were not significantly different among species. These L_e are generally lower than those found on trench sites and in native plant communities in the Great Basin (11–12%) (Anderson *et al*., 1987).

In conclusion, this study has shown that during wet years precipitation can penetrate deep soil layers (*i.e.*, $>$ 1·5 m) in the Mojave Desert and that perennial species are able to utilize this mositure source. These results are consistent with other studies which indicate that the soil water balance is controlled by transpiration (Anderson *et al*., 1987; Schlesinger *et al*., 1987; Swank *et al*., 1988; Gee *et al*., 1994). Further, this study indicates that evergreen, perennial species such as *Larrea* do not extract more water throughout the year than drought-deciduous perennials. These results suggest that ET in the Mojave Desert is dependent largely on precipitation and the amount of soil water available during the growing season rather than on species composition.

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