

Responses of Chihuahuan Desert herbaceous annuals to rainfall augmentation

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Densities and biomass of annual herbaceous plants were compared on plots receiving supplemental water of 25 mm at 4-week intervals or 6.3 mm per week, and plots receiving only natural rainfall. During the first summer, there were no significant differences in total biomass between treatments, but the density and biomass of two species, *Astragalus tephrodes* and *Euphorbia micromera*, were greater on the watered plots. Several spring annuals responded to supplemental water and by late spring (April) there were decreases in biomass on the watered plots, with the greatest decreases on the 6.3 mm per week plots. Few species of summer annuals responded to supplemental water during the second year, possibly as a result of smaller rain events and/or limitation of available nitrogen. Root shoot biomass ratios were between 0.15 and 0.25 for winter–spring annuals and 0.04 and 0.03 for summer annuals.

Introduction

Precipitation is recognized as the main factor controlling germination, growth and productivity of annual herb species in desert ecosystems (Beatley, 1967, 1974, Went, 1948, 1949; Juhren, Went *et al.*, 1953; Tevis, 1958; Noy-Meir, 1973). These annuals or 'ephemeral' species are characterized by short life-cycles and the production of large quantities of seeds which remain dormant when microclimatic conditions do not meet germination and growth conditions. Seed reserves respond to rainfall events (pulses according to Noy-Meir, 1973) which surpass a certain threshold. Annual herb species have been classified into two groups: summer annuals, which germinate and grow after summer or early autumn rains when soil and ambient temperatures are high (over 20°C), and winter annuals, which respond to autumn or early winter rains when temperatures are below 20°C (Went, 1948; Beatley, 1966, 1974). In both groups, the minimum water quantity required to stimulate seed germination has been suggested to be about 25 mm (Went, 1949; Tevis, 1958; Beatley, 1974). Went (1948) observed that in the Mojave Desert, rains of slightly over 10 mm did not initiate germination, whereas rains of over 25 mm were completely effective. It has been suggested that the seeds respond to a minimum moisture threshold that has been selected to be sufficient for plants to complete their life-cycle since, in deserts, precipitation is largely unpredictable in its spatial and temporal distribution (Noy-Meir, 1973; Ludwig & Whitford, 1981). In addition, differences in temperature between summer and winter seasons affect the soil evaporation rates. Thus, low quantity of rainfall in winter can result in relatively high soil water availability. These differences

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affect the growth rates of species of winter and summer annuals. Summer annuals have a shorter life-cycle and a greater overlap of phenological phases than winter annuals. A large proportion of summer annuals are C_4 plants which have a high photosynthetic efficiency at high temperatures when water is available.

To date, with the exception of Tevis (1958) and Romney, Wallace *et al.* (1978), there are no field experimental studies on the effect of simulated rainfall on the biomass (standing crop) of the annual plants in desert systems, nor have there been studies to determine if the different species react similarly to a predetermined amount of water. It would be expected that species differ in their response to moisture depending on their origin, photosynthetic mechanisms and morphological and physiological adaptations. Based on the work cited above, we hypothesized that supplementary rainfall of 25 mm/month in a single event would result in a greater biomass and density of annual plants than 25 mm of water in four events of 6.25 mm each, spread evenly over that same time period, when this was added to the natural rainfall.

Methods

Studies were conducted on the New Mexico State University Experimental Ranch, 40 km north-east of Las Cruces, New Mexico (the Jornada Long Term Ecological Research Site). Nine plots of 7×15 m were set up on sandy alluvial fan (*bajada*) to the north and east of Mt Summerford, Doña Ana Mountains. This area is characterized by a shrub cover of creosotebush, *Larrea tridentata* (Ludwig & Whitford, 1981) and supports a variety of annual plants and the small perennial grass *Erioneuron pulchellum* (Whitford & Bryant, 1979). The 100-year annual rainfall average is 211 mm (Houghton, 1972), with most of that rainfall occurring during late summer from convectional storms. Summer maximum temperatures reach 40°C and freezing temperatures are recorded from October through mid-April (data from the Jornada Validation Site Weather Station).

In addition to natural rainfall, three of the nine plots received simulated rainfall once a month with 25 mm of water, hereafter called monthly watered plots, three plots with 6.25 mm every week, hereafter called weekly watered plots, and three plots did not receive supplemental watering (controls). The irrigation system sprinkler heads were 1.5 m above the ground and provided water drops above the shrub-canopy to mimic natural rainfall. Using an array of eight rain gauges on the plots, we recorded a 30 per cent variation in water input over the surface area of the plots. The irrigation of the plots was begun in June 1981 and continued through December 1982. On 27 October 1981 (autumn season), eight 0.16 m^2 quadrat frames were randomly placed under the canopy of *L. tridentata* and eight quadrat frames of the same dimensions were placed between shrubs (approximately two radii away from border of the *L. tridentata* canopy) in each plot. The average diameter and the height of all the herb species contained in the quadrat frames were measured. On 19 March (early spring), 22 April (late spring), 18 August (late summer), 11 September (early fall) and 5 October (late fall) 1982, we measured plants in five 0.16 m^2 quadrats per plot under *L. tridentata* canopies. Plants outside the plots were measured and then carefully harvested and oven-dried for 72 h at 60°C . The number of individuals of each species collected varied between 10 and 30 depending on their abundance. Regressions of dry mass on size were calculated for each species. The same procedure was used to calculate the relationship between size and dry weight of root systems for each species. However, because of small sample sizes, root data are not reported for all species. We calculated the biomass of the annual plants from height and diameter measurements using the regression equations in Table 1. These equations were derived from measurements of plants harvested from the edges of the plots using the procedures of Ludwig, Reynolds *et al.* (1975).

Table 1. Best fit regressions between biomass (Y) (g plant above-ground dry mass) and volume (V) or area (A) of annual plants occurring on the experimental plots

Species	Regression	r^2
<i>Astragalus tephrodes</i>	$Y = 0.0062 + 0.0028V\ddagger$	0.998
<i>Baileya multiradiata</i>	$Y = 0.0145 + 0.553V\ddagger$	0.918
<i>Bouteloua aristoides</i>	$Y = 0.0450 + 0.0157V^*$	0.966
<i>Crypthantha angustifolia</i>	$Y = 0.0078 + 0.616V\ddagger$	0.859
<i>Dithyrea wizlizenii</i>	$Y = 0.031 + 0.590V^*$	0.869
<i>Euphorbia micromera</i>	$Y = 0.0116 + 0.0033\ddagger A$	0.873
<i>Euphorbia serrula</i>	$Y = 0.0256 + 0.0055\ddagger A$	0.869
<i>Iva ambrosiaefolia</i>	$Y = 0.0589 + 0.0022V\ddagger$	0.905
<i>Mollugo cervina</i>	$Y = 0.0024 + 0.644V^*$	0.595
<i>Pectis angustifolia</i>	$Y = 0.0109 + 0.0033V^*$	0.812
<i>Phacelia coerulia</i>	$Y = 0.1246 + 0.0060V^*$	0.982

* Volume calculated as $4/3r^2h$.

† Area calculated as πr^2 .

‡ Volume calculated as r^2h where r = radius and h = height.

No data were collected between April 1982 and August 1982 because we found no ephemeral plants in the plots. From July 1981 through April 1982, data on moisture and soil temperature of the different plots at 5 and 10 cm depth were obtained 8–13 times per month from Wescor soil psychrometers. No data on soil temperature and moisture are available beyond that date, due to equipment problems. Unless otherwise indicated in the text, all data were analysed by ANOVA. Differences reported as significant in the text are at $p < 0.05$ or lower.

Results

Natural rainfall July through October 1981 totalled 141.7 mm, all but 11 mm of which fell in August. Thus in August 1981, natural rainfall was five times greater than our supplemental watering. Winter rainfall November 1981 through March 1982 totalled 36 mm with no measurable precipitation in March. April to June 1982 was dry with a total precipitation of only 13.8 mm. In July, August and September 1982 there were 25 rain events that provided a total of 116.75 mm. The total water input by natural rain events was slightly higher in summer 1981 than in 1982, but the rainfall events were more evenly distributed in 1982.

Soil temperatures did not differ between treatments, but soil moisture was significantly higher on the supplemental rainfall plots over most of the study period (Fig. 1). The watered plots exhibited similar distributions of soil moisture, but the weekly watered plots had moister soils at the beginning of the autumn season (August–September 1981). In October 1981 there were no significant differences in total annual plant biomass between the control and monthly watered plots (Table 2). However, the total biomass on the weekly plots was greater than on the control. These biomass differences reflect the general differences in soil moisture over the summer growing season (Fig. 1). Between January and March 1982, the soil moisture at 5 cm depth in the watered plots was significantly higher than in the control plots ($p < 0.005$) (Fig. 1) and this is reflected in the plant biomass (Table 2). In March (early spring) the biomass in the monthly watered plots was greater than in the weekly watered plots and these plots had more biomass than the control plots. In late spring (April 1982) temperatures increased and soil moisture decreased, affecting plant growth in the watered plots. The most pronounced change occurred in the

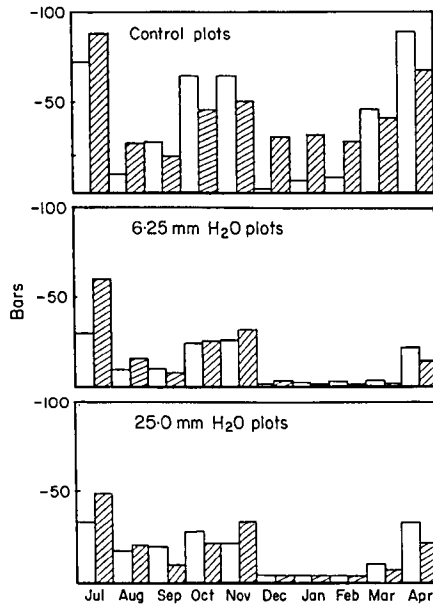


Figure 1. Average monthly soil water potentials (July 1981–April 1982) at 5 cm and 15 cm depths on plots receiving no supplemental rainfall (control), plots receiving 6.25 mm per week and plots receiving 25 mm every fourth week. □, 5 cm depth; ▨, 15 cm depth.

Table 2. Average biomass density of annual herbs (g dry weight/m²) growing under *Larrea tridentata* canopies on artificially watered plots. Numbers followed by the same letter are not statistically different ($p = 0.05$)

Treatments	Oct 1981	Mar 1982	Apr 1982	Aug 1982	Sept 1982	Oct 1982
0 mm	4.32a	1.88a	2.41a	0.00a	0.00a	0.17a
6 mm/week	9.74b	12.32b	1.58a	0.43a	0.63a	0.94a
25.0 mm/month	7.90ab	26.87c	19.09b	0.76a	0.24a	0.50a

weekly watered plots, where the plant biomass decreased almost six-fold. Although supplemental water had significant effects on several summer annuals during the second year of the study, most of the species did not respond to the experimental watering, e.g. *Bouteloua aristoides* and *I. ambrosiaefolia* (Tables 3 and 4). In 1982, several species exhibited sporadic occurrence with little or no relationship to the supplemental water.

During the late summer and autumn (August, September and October) 1982 we found no statistical differences between treatments attributable to the watering (Table 2). There were no herbaceous annuals in the control plots and numerous quadrats in the treatments had annuals, but with the zeros for some quadrats these were shown not to be different by ANOVA. There was, however, a real biological difference in biomass and density of herbaceous annuals in August and September 1982 (Tables 2 and 3).

Despite the lack of differences in total biomass production between control and monthly watered plots, the biomass and density of species such as *Astragalus tephrodes* and

Table 3. Biomass (g dry weight/m²) of selected herbaceous annual plants growing under *Larrea tridentata* canopies on artificially watered plots: 0 mm control, 6 mm/week, and 25 mm/month

Species	Treatment	Oct 1981	Mar 1982	Apr 1982	Aug 1982	Sept 1982	Oct 1982
<i>Astragalus</i> spp.	0	0.04	1.25	1.48		0	0
	6	0.08	1.68	0.97		0.16	0.32
	25.0	0.52*	15.51*	13.07*		0	0.16
<i>B. multiradiata</i>	0	1.67	0.64	0.93			
	6	0.99	7.21*	0.45			
	25.0	0.88	9.47*	1.01			
<i>E. micromera</i>	0	1.73			0	0	0
	6	5.70*			0.10	0.06	0.10
	25.0	5.47*			0.08	0.01	0.01
<i>E. serrula</i>	0	0.85			0	0	0
	6	2.56*			0.14	0.36	0.51
	25.0	0.66			0.01	0	0.04

* $P < 0.05$

Table 4. Mean densities (no. plants/m²) of annual plants growing under *Larrea tridentata* canopies on artificially watered plots: 0 mm control, 6 mm/week, and 25 mm/month

Species	Treatment	Oct 1981	Mar 1982	Apr 1982	Aug 1982	Sept 1982	Oct 1982
<i>A. leptroides</i>	0	5.08	6.25	8.33		0	0.25
	6	5.60	4.38	3.75		0.19	2.69
	25.0	10.42*	15.00*	11.67		0	0
<i>B. multiradiata</i>	0	4.43	2.08	3.33			
	6	3.39	7.92	0.83			
	25.0	3.26	6.67	2.50			
<i>B. aristoides</i>	0	3.39					
	6	2.60					
	25.0	0.52					

(continued overleaf)

Table 4. (continued)

Species	Treatment	Oct 1981	Mar 1982	Apr 1982	Aug 1982	Sept 1982	Oct 1982
<i>C. angustifolia</i>	0		0	0			
	6		0.83	0			
	25.0		0	0.42			
<i>D. wislizenii</i>	0		0	0			
	6		0.42	0.42			
	25.0		0.42	0.42			
<i>E. micromera</i>	0	4.69			0	0	0
	6	11.07*			5.63	0.81	1.69
	25.0	11.20*			3.13	0.19	0.19
<i>E. serrula</i>	0	1.04			0	0	0
	6	3.91			0.44	0.63	0.19
	25.0	0.78			0.19	0	0.23
<i>Euphorbia</i> sp.	0	4.43					
	6	0.78					
	25.0	1.04					
<i>I. ambrosiaefolia</i>	0	0					
	6	1.56					
	25.0	0.26					
<i>M. cervina</i>	0	1.30					
	6	0.26					
	25.0	5.21*					
<i>P. angustifolia</i>	0	0.52					
	6	0					
	25.0	0.26					
<i>P. coerulia</i>	0	0					
	6	0.83					
	25.0	0					

* $p < 0.05$

Euphorbia micromera were significantly greater in the monthly watered plots (Tables 3 and 4). Biomass per plant of those species did not differ (Table 5). Total biomass and density of *A. tephrodes* in monthly watered plots was higher than in the weekly watered plots (Tukey's test, $p < 0.05$). Similar responses were observed in March and April of 1982 (Tables 3 and 4). In contrast, total biomass and density of *E. micromera* in the monthly plots did not differ significantly from weekly plots.

Many of the *A. tephrodes* measured in October overwintered, especially in the monthly watered plots. In early spring, *A. tephrodes* was the most abundant species and showed a significant increment in total biomass density and biomass per plant in the monthly watered plots. Spring annuals exhibiting significant responses to water supplementation were *Baileya multiradiata* and *Dithyrea wislizenii*.

Baileya multiradiata had higher total biomass and biomass per plant in the monthly watered plots compared to the controls, but did not differ significantly from the weekly watered plots. Despite the greater biomass observed in early spring in the monthly watered plots (26.44 g/m^2) compared to the biomass existing in October 1981 (8.55 g/m^2), the number of species was considerably less (Table 4) and *A. tephrodes* accounted for about 60% of the total biomass (Tables 2 and 3). During early spring, two species which were not present in the fall season, *D. wislizenii* and *Cryptantha angustifolia*, appeared in the samples. Both were present only on the watered plots.

Biomass comparisons of plants growing under *L. tridentata* canopies and in intershrub spaces showed no significant differences in the control plots, but in the weekly and monthly watered plots the biomass production was greater under shrubs than in open areas (Tukey's test, $p < 0.05$). In October 1981, the supplemental watering also produced a significant increase in *Iva ambrosiaefolia* (Tables 3 and 4). The diversity of species (H') was lower in the weekly and monthly watered plots compared to the control plot (Table 6). This may be related to increases in significance of *E. micromera* in the watered plots (Tables 3 and 4).

The root-shoot biomass ratios of the desert annuals for which we had sufficient data were 0.15 for *B. multiradiata*, 0.25 for *A. tephrodes*, 0.04 for *E. micromeris* and 0.03 for *E. serrula*. These ratios were used to compute the root biomass production in the experimental plots (Table 7).

Discussion

Our results partially support the hypothesis that the responses of herbaceous annuals are more pronounced with a single rain event of 25 mm than with 25 mm of water shared in 4 weekly applications of approximately 6 mm. This was particularly evident in responses of overwintering herbaceous annual and the spring annuals. Clearly, however, the responses of these desert annual plants to rainfall were not simple quantitative nor qualitative responses. Our data support the statement of Loria & Noy-Meir (1979) that it is difficult to make generalizations about desert annuals because species differ in their demographic responses to environmental conditions.

Growth responses of desert annuals are complex and may be tied to factors other than water or in addition to water. For example, several investigators have reported that North American desert annuals are more abundant under shrub canopies than in intershrub spaces (Muller, 1953; Patten, 1978; Parker, Fowler *et al.*, 1982). In this study, on the first sampling date, we found no differences in herbaceous annual plant biomass under shrubs and in intershrub spaces on the unwatered plots, but found significantly higher herbaceous annual plant biomass under shrubs than in intershrub spaces on water amended plots. It is possible that the natural rainfall was insufficient to stimulate enough production to allow a second-level limiting factor to be detected. The supplemental rainfall, by stimulating additional growth, could have forced plants in the intershrub spaces to encounter nitrogen depletion not encountered by plants under shrub canopies. Nitrogen content of soils under

Table 5. Average mass (g dry weight/plant) of annual plants growing under *Larrea tridentata* canopies on artificially watered plots: 0 mm control, 6 mm/week, and 25 mm/month

Species	Treatment	Oct 1981	Mar 1982	Apr 1982	Aug 1982	Sept 1982	Oct 1982
<i>A. tephrodes</i>	0	0.01	0.20	0.18		0	0
	6	0.01	0.37	0.26		0.84	0.12
	25.0	0.05	1.03*	1.12*			0.11
<i>B. multiradiata</i>	0	0.37	0.31	0.28			
	6	0.29	0.91	0.54			
	25.0	0.27	1.42*	0.40			
<i>Bouteloua</i> sp.	0						
	6						
25.0							
<i>Cryptantha</i> sp.	0		0	0			
	6		0.01				
	25.0		0	0.07			
<i>D. wislizenii</i>	0		0	0			
	6		5.93	0.40			
	25.0		4.48	6.50			
<i>E. micromera</i>	0	0.37			0	0	0
	6	0.51			0.02	0.07	0.06
	25.0	0.49			0.03	0.05	0.05
<i>E. serrula</i>	0	0.17			0	0	0
	6	0.45			0.32	0.57	2.68
	25.0	0.38			0.05	0	0.17
<i>Euphorbia</i> sp.	0	0.16					
	6	1.04					
	25.0	0.35					
<i>I. ambrosiaefolia</i>	0						
	6	0.19					
	25.0	0.08					

Table 5. (continued)

Species	Treatment	Oct 1981	Mar 1982	Apr 1982	Aug 1982	Sept 1982	Oct 1982
<i>M. cervina</i>	0	0					
	6	0					
	25.0	0.01					
<i>P. angustifolia</i>	0	0.02					
	6	0					
	25.0	0.08					
<i>P. coerulia</i>	0		0				
	6		1.10				
	25.0		0				

Table 6. Shannon-Weaver Diversity Indices of annual herbs on artificially watered plots, and unwatered control plots

Treatments	Oct 1981	Mar 1982	Apr 1982	Aug 1982	Sept 1982	Oct 1982
0 mm	0.85	0.24	0.25	0.00	0.00	0.16
6 mm/week	0.75	0.48	0.31	0.30	0.52	0.36
25.0 mm/month	0.65	0.30	0.30	0.24	0.26	0.29

Table 7. Mean root biomass of selected species of annual plants growing in plots receiving supplemental water at rates of 0 mm, 6.25 mm/week, and 25 mm/month. Biomass calculated on the basis of mean root:shoot ratios

Species	Rainfall	Oct 1981	Mar 1982	Apr 1982	Aug 1982	Sept 1982	Oct 1982
<i>A. tephrodes</i>	0	0.0057	0.033	0.038			
	6	0.0059	0.088	0.038			
	25.0	0.0190	1.186	0.95			
<i>B. multiradiata</i>	0	0.002	0.008	0.015			
	6	0.003	0.166	0.011			
	25.0	0.003	0.175	0.020			
<i>E. micromera</i>	6	0.033	—	—	0	0	0
	6	0.162	—	—	0.007	0.003	0.0003
	25.0	0.181	—	—	0.004	0	0.0006

shrub canopies is considerably greater than in intershrub spaces (West & Klemmedson, 1978; Parker, Fowler *et al.*, 1982).

The marked reduction in biomass of summer annuals during the second year of study is probably due to soil nitrogen deficiencies that developed as a result of two successive large herbaceous annual crops. The antecedent flushes of summer and winter annuals from the first year of study produced a large dead root biomass under the shrub canopies. Those roots had been decomposing for 90+ days by the time the second set of summer annuals germinated. Parker, Santos *et al.* (1984) found that fungi growing on dead annual roots immobilize considerable available nitrogen. If most of the mineralized nitrogen was immobilized by saprophagous fungi, growth of summer annuals could be suppressed in the second summer because of available soil nitrogen deficiency. Since the natural rainfall alone triggered growth of a low number of plants, water was apparently the only factor limiting herbaceous annual production. However, with supplementary rainfall, larger numbers of plants (higher densities) would produce a higher nutrient demand, thereby causing higher densities of annuals to occur where nutrient concentrations are higher. There is some indirect evidence that nutrient limitation, especially nitrogen, can limit productivity in arid ecosystems when there is sufficient moisture for plant growth (Ludwig & Flavill, 1979; Floret & Pontanier, 1982; Penning de Vries & Djiteye, 1982). Romney, Wallace *et al.* (1978) reported increases in biomass production in eight species of Mojave Desert annuals when fertilized with ammonium nitrate at 100 kg/ha. We suggest, therefore, that the reduced summer annual biomass was the result of nutrient limitation rather than a differential moisture response.

Growth and survival of annual plants may also be affected by rain events of less than 25 mm depending upon storm frequency. When soil temperatures were high and the soil water evaporation was high, small simulated rain events had little effect on plant growth. The opposite was true in early spring and fall. The response of desert annuals to small rainfall events requires additional investigation. As Sala & Lauenroth (1982) point out, plant species with short specific response times to increases or decreases in water status of the soil, will be able to utilize small quantity precipitation events. The ability of annual species to utilize small amounts of precipitation may be dependent upon rooting patterns and/or soil nutrient status. It is possible that small rainfall events might lessen many nutrient limitations because soil microbes mineralize nitrogen and phosphorous at lower water potentials than are required for plant growth. Rainfall events may also affect denitrification; thus, if nutrient limitations are important, plant responses to rainfall will change through time, as was seen in this study. However, responses to a series of small rainfall events, such as we studied, are not representative of those following a single small event.

Euphorbia micromera appeared to have a lower response threshold to water than other species since it had the same total biomass and density on the weekly and monthly watered plots. These results contradict the earlier finding of McKinney (1975) who pointed out that *E. micromera* only slightly increases its total above-ground biomass with additional soil moisture. Went (1948) found that *Mollugo cerviana* was locally very abundant after summer rain only; in our study this species was found only in October 1981, having greater representation in the monthly watered plots. In addition, many summer annuals appeared to require more than 25 mm of rainfall for germination and establishment, e.g. *B. aristoides*, *B. multiradiata*, *M. cervina* and *Pectis angustifolia*, because these species did not appear in the second summer of the experiment.

In a related study near our plots on the Jornada, Whitson (1975) used subsurface irrigation to maintain soil at field capacity. He found that summer annuals emerged and established themselves at low densities on the irrigated plots in June and early July and there were no summer annuals on the non-irrigated areas. Heavy rains in late July (cumulative = 88 mm) changed the soil moisture on the non-irrigated plots from -10 MPa to < -0.3 MPa, which resulted in high densities of summer annuals on all plots by

July 30. Whitson (1975) reported no significant differences in densities in some species: *P. angustifolia*, *M. cervina*, *B. intermedia* and *E. micromera* on the irrigated and non-irrigated plots from July 30–mid-September. Other species maintained higher densities on the irrigated plots. Whitson's data suggest that most species of summer annuals will germinate if soils are at field capacity. The lower densities he observed in the early summer probably reflect the proportion of the seed bank at depths in the soil where his subsurface irrigation was effective. In contrast to Whitson's data, we found that *E. micromera* and *M. cervina* responded to simulated rainfall, but soil moisture was not as high in our control plots as in Whitson's non-irrigated plots in late July and August.

There are few data on below-ground production in annual plants (Bell, Hiatt *et al.*, 1979). It is interesting that there was such a wide disparity between root:shoot ratios in the winter annuals, which had ratios in the range reported by Bell, Hiatt *et al.* (1979), and the summer annuals. The extremely low root:shoot ratios of the summer annuals are a function of the shallow depth of these root systems. Shallow roots may allow summer annuals to respond to small rainfall events that wet only the surface 1–5 cm.

Diversity was higher in the weekly watered plots than in the monthly watered plots (except in August 1981). These results suggest that when extra water is available, some species respond by increasing size or density and may, therefore, outcompete other species.

In summary, Chihuahuan Desert herbaceous annuals have different growth responses at the same soil moisture tensions. The responses of herbaceous annuals to water may be confounded by changes in available soil nutrients. Simple models that state that rain events of at least 25 mm are sufficient to elicit growth of desert herbaceous annuals, are of limited value. We suggest that species of annuals respond to combinations of rainfall events in a continuum of quantity, individual storm size and frequency of events. The responses of species of annuals to rainfall events may be linked to the availability of nutrients like nitrogen or phosphorus. An experimental approach using rainfall supplementation of varying designs may be used to elucidate the patterns of annual plant responses.

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