

REVIEW

Distribution of annual plants in North American deserts

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Early researchers concluded that the winter-annual flora was richest in the California deserts and became relatively poorer towards the east, whereas summer-annuals were richest in the deserts of western Texas and their richness progressively declined into eastern California. US/IBP Desert Biome and subsequent studies support these trends and add much relevant information. Winter-annuals have the C₃ photosynthetic pathway, whereas most summer-annuals have the C₄ pathway. While the Sonoran and Chihuahuan deserts have a few C₃ 'summer' annuals (actually 'winter' annuals which can persist into the summer), the Mojave Desert lacks C₃ summer-annuals. The Great Basin Desert has only a few prevalent winter or summer-annuals (mostly introduced species).

Studies of the micro-distribution of desert-annuals have shown their close association with perennial shrubs. Some shrubs produce substances that are reportedly toxic to some annuals; the role of such toxins in structuring annual plant communities is unclear. The importance of nutrients associated with shrub canopies on the micro-distribution of many desert-annuals is becoming evident through LTER and other studies.

Rationale

Many research efforts have sought to document the correlation between the distribution of annual plants and the soils and perennial vegetation within the four North American deserts (see reviews by Mulroy & Rundel, 1977, and MacMahon & Wagner, 1985). However, this documented information is quite disjunct and only allows for limited comparisons between these deserts. The United States International Biological Program, Desert Biome project (IBP/DB) was conducted at four desert sites in the Western U.S. (Fig. 1). The IBP/DB research sites were chosen to represent the major climates and vegetation types in four U.S. arid regions: (1) winter precipitation, short growing season, cold—Great Basin Desert (Curlw Valley, Utah); (2) winter precipitation, long growing season, hot—Mojave Desert (Rock Valley, Nevada); (3) bimodal (summer and winter) precipitation, year-long growing season, hot—Sonoran Desert (Tucson Basin, Arizona); and (4) summer precipitation, long growing season, hot—Chihuahuan Desert (Jornada Bajada, New Mexico). Thus, inter-site IBP/DB data on annual plant populations is available for the same years. However, much of this IBP/DB data is still only available as internal reports (Research Memoranda: see Szarek, 1979 for a listing). The current Long-Term Ecological Research (LTER) program includes one desert site (the Jornada site), which also involves research on annual plants.

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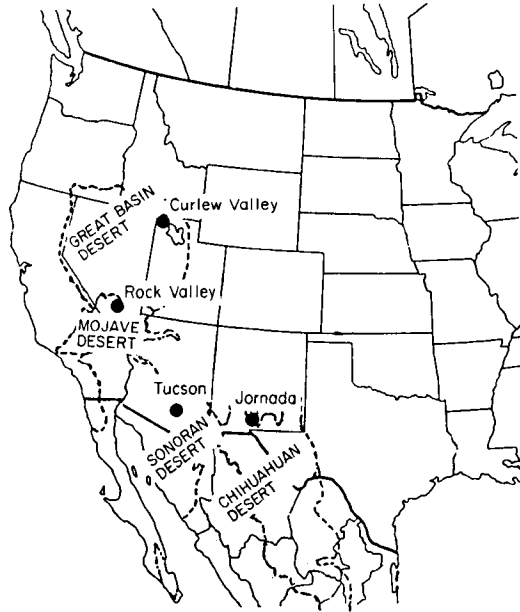


Figure 1. Locations for the Curlew Valley, Rock Valley, Tucson Basin, and Jornada Bajada U.S.A. International Biological Program, Desert Biome (IBP/DB) research sites in the Great Basin, Mojave, Sonoran and Chihuahuan deserts, respectively (after MacMahon & Wagner, 1985).

Our objective in this review is to examine the state of our knowledge on the distribution of desert-annual plants in North American deserts, including contributions from the IBP/DB and LTER projects.

Regional distribution

The ecological distribution of annuals within the Sonoran Desert is reported by MacDougal (1908), Marks (1950), Shreve (1951) and Tevis (1958*a,b*). Both Marks and Tevis provide information for the Lower Colorado Valley region of the Sonoran Desert. By applying water to simulate rain (Tevis 1958*a*), only three summer-annuals were induced to germinate during July, August and September, while 18 winter-annuals germinated from October, November and December waterings. Those annuals inhabiting upland Sonoran Desert around Tucson, Arizona are detailed by MacDougal, while Shreve presented general distributions over the entire Sonoran Desert (as then recognized, see MacMahon & Wagner, 1985).

Studies conducted in the Mojave Desert related annual plant distribution to seasonal temperature and precipitation, elevation, and regional vegetation: Went (1948) and Juhren *et al.* (1956) studied annuals in Joshua Tree National Monument (southern Mojave Desert) and Went & Westergaard (1949) studied them in Death Valley National Monument. The study in Joshua Tree provided densities for nine summer-annuals and more than 40 winter-annuals during 1948–1953 at 17 stations, while less detailed observations from 1939–1946 were given in the Death Valley study. Beatley (1965) related northern Mojave Desert (Nevada Test Site) annuals to regional geographic factors. In addition, Richard & Beatley (1965) related 140 species of winter-annuals and seven species of summer-annuals on the Test Site to the regional vegetation. Also on the Test Site, Beatley (1967) enumerated annuals within permanent plots from 1959–1966.

Only five annuals were cited as inhabiting four zones of shadscale vegetation of the Great Basin Desert, West & Ibrahim (1968). For the Chihuahuan Desert, the distribution of annuals in central New Mexico (Rio Grande River Valley) were enumerated by Gardner (1951) and for southern New Mexico volcanic and gypsum deposits (Tularosa Basin) by Shields (1956) and Shields & Crispin (1956).

These early studies examined the distribution of annuals 'within' the four North American deserts, but only Shreve (1951) has provided a detailed comparison 'between' these deserts. For the 109 winter-annual taxa listed as characteristic of upland Sonoran Desert, 73, 43, and 42 inhabit the Mojave, Great Basin and Chihuahuan deserts, respectively. Shreve's listings indicate that only 15 occur in all four deserts. Shreve also reported 496 winter-annual taxa for the Mojave Desert, mostly from California with numbers strongly diminishing towards the east. Shreve listed 84 summer-annuals as characteristic of the upland Sonoran Desert and also indicated that 56 of these are also present in the Chihuahuan Desert of west Texas, which has the greatest number of summer-annuals. Shreve concluded that winter-annuals are represented richly in the California deserts and diminish towards the east, whereas summer-annuals are more numerous in the deserts of western Texas and progressively decline towards the west.

Welkie & Caldwell (1970), Syvertsen *et al.* (1976) and Mulroy & Rundel (1977) have grouped desert-annual taxa by their C₃ and C₄ 'carbon reduction pathways'. Mulroy & Rundel found that summer-annuals in the California deserts had the C₄ photosynthetic pathway and that winter-annuals were C₃s. Although they found that a relatively large number of Sonoran Desert summer-annuals were C₃s, most of these also flowered in the winter (or were 'weedy' species). IBP/DB and LTER studies in the Chihuahuan Desert support the generality that all winter-annuals are C₃s and that most summer-annuals are C₄s, but some C₃s can persist and flower (or reflower) in the summer if moisture conditions are favorable (Kemp, 1983).

The IBP/DB studies corroborate the relative distinctiveness of the four North American desert-annual floras. Although some annual taxa are shared by one or more of these deserts, their prevalence (biomass) differs greatly; the same is true for the perennials that are shared by these four deserts (Hadley & Szarek, 1981; Ludwig, 1986, 1987; Szarek, 1979).

One major distinction between the four deserts is the paucity of prevalent annuals in the Great Basin Desert, as evidenced by the southern Curlew Valley IBP/DB site (Table 1). Only eight prevalent species were reported on this cold desert site during the 5-year IBP/DB study and four of these are European or Asian introductions. The three hot deserts

Table 1. Number of prevalent C₃ winter (W) and C₄ summer (S) annuals sampled on the four IBP/DB sites from 1971 to 1975. Prevalent annuals are defined as those with sufficient abundance as to be included in tables reporting density and biomass in IBP/DB Research Memoranda

North American Desert/ IBP/DB Site	1971		1972		1973		1974		1975	
	W	S	W	S	W	S	W	S	W	S
Great Basin South Curlew Valley	ND	ND	4	3	5	1	5	3	ND	ND
Mojave Rock Valley	41	NP	41	NP	55	NP	33	NP	43	NP
Sonoran Tucson Basin	ND	ND	ND	ND	46	NP	NP	10	NP	NP
Chihuahuan Jornada Bajada	NP	9	11	12	13	8	NP	7	12	NP

ND, no data reported; NP, absent or not present in sufficient abundance for sampling.

Table 2. Number of winter-annual forbs observed on a Chihuahuan Desert LTER study transect in the spring of 1982 and 1983, along with the previous seasons precipitation

	1982	1983
Number of annual forbs observed	15	26
Number of forb species 'not' observed in the other year	7	18
Number of prevalent forbs (cover > 0.1%)	2	15
Previous Autumn (September–November) precipitation (mm)	17	76
Previous Winter (December–March) precipitation (mm)	19	103

(Mojave, Sonoran, Chihuahuan) had more summer and winter annuals, with prevalent species numbering up to 55.

A large difference between the three hot desert IBP/DB sites is the absence of prevalent C_4 summer annuals at the northern Mojave Desert Rock Valley site (Table 1). This absence, however, is not applicable to more southern portions of the Mojave Desert where C_4 s were reported by Johnson (1976); all these were summer-annuals. There also appears to be a complete lack of C_3 summer-annuals in the Mojave Desert (Mulroy & Rundel, 1977). On average, the proportion of C_3 to C_4 taxa on the IBP/DB Sonoran and Chihuahuan desert sites was about 2:1, but this ratio varied greatly from year to year.

An example from the Chihuahuan Desert LTER project (Jornada site) illustrates how different even two 'desert spring-blooms' can be. Contrasting the spring of 1982 with that of 1983, both years had mexican poppy (*Eschscholzia mexicana*) blooms (about 3% cover both years), but in the spring of 1982, 15 winter-annuals were observed on the site while 26 were observed in the spring of 1983 (Table 2). A more striking difference, however, was that seven of the 15 species present in 1982 were not observed in the spring of 1983, even though the previous autumn and winter moisture conditions were much more favorable for a 'bloom' in the spring of 1983. Further, only two species were prevalent (cover > 0.1%) in the spring of 1982, compared to 15 prevalent species in 1983.

Micro-distributions

Went (1942) observed the micro-distribution of annual plants within the shrub communities of the Sonoran and Mojave Deserts and concluded that while certain taxa were associated strongly with specific shrubs, others were not. Where annuals were associated with shrubs, it appeared to be related to the organic debris accumulated around the bases of the shrubs, suggesting a more favorable nutrient micro-habitat. Since Went's early observations, the greater productivity of some annuals under the canopy of *Cercidium microphyllum* compared to open spaces has been documented for the Sonoran Desert (Patten, 1978), and in the Chihuahuan Desert, Parker *et al.* (1982) have measured a significantly greater density and biomass for many annuals (and higher levels of nitrogen) under the canopies of *Larrea tridentata*. Results have not been consistent; Halvorson & Patten (1975) found no significant differences in density of annuals under and outside several Sonoran Desert shrubs along a gradient. However, as noted above, Patten (1978) measured increased production by many annuals under the canopy of *Cercidium*.

Went (1942) also observed the phenomenon that whereas few annuals occurred under

living *Encelia farinosa* shrubs, many occurred under dead *Encelia*. A toxic, water-soluble principle from *Encelia farinosa* leaves was later established by Muller (1953) and Muller & Muller (1956). The toxin effectively inhibited the growth of several shrub-dependent and shrub-independent winter-annual taxa in water culture. Although the above studies strongly indicate chemicals (nutrients and/or toxins) as major agents in the micro-distribution of annuals, soil physical properties and fire are also important factors (Adams *et al.*, 1970). The significance of allelopathy in the micro-distribution of annuals is unclear, but the importance of nutrients has been well documented (Gutierrez *et al.*, 1988).

Mulroy & Rundel (1977) have reviewed some of the physiological, morphological and phenological characteristics of desert-annuals related to their distribution, but some additional points seem appropriate. Based on a detailed study of root morphology, Cannon (1911) concluded that while winter-annuals develop tap root-systems and summer-annuals develop diffuse root-systems, both groups penetrate and occupy similar soil depths. However, the depth and volume of soil occupied by roots of annuals is related directly to the amount and depth of penetration of soil moisture (Gutierrez & Whitford, 1987*a,b*). Typically, winter-annuals only establish and mature when autumn and winter precipitation is adequate for their tap-roots to penetrate relatively deeply in the soil (> 20 cm), whereas summer-annuals can germinate and successfully establish their diffuse-roots with relatively small summer rain showers.

Germination, emergence and establishment responses of desert-annuals to environmental factors have been studied by unmanipulated field observations (e.g. Went, 1949; Juhren *et al.*, 1956; Beatley, 1967; Kemp, 1983), by manipulated field experiments (e.g. Tevis, 1958*a*; Gutierrez & Whitford, 1987*a,b*), and by controlled laboratory or greenhouse experiments (e.g. Went, 1949). In general, precipitation amounts must exceed about 25 mm and air temperature minimums must be above 18–22°C to trigger germination and emergence of summer-annuals (see Beatley, 1974). Ambient air temperature maxima must be below 18–22°C (with adequate soil moisture) to stimulate germination-emergence in winter-annuals. High temperature 'pre-treatment' is known to enhance the germination of several Mojave and Sonoran Desert winter-annuals (Capon & Van Asdall, 1967).

Survival of desert-annuals to mature fruit set following germination-emergence is generally below 75%. Tevis (1958*b*) reported survivorship between 6% and 73% for 14 fall-germinated winter-annuals of the Sonoran Desert. Survival of the most abundant winter-annual, *Plantago insularis*, was 55%. Juhren *et al.* (1956) studied 12 sites in Joshua Tree National Monument (southern Mojave Desert) and reported winter-annual survival for 15 taxa of 9–71%. In the northern Mojave Desert, Beatley (1967) found an average of 38% survival (range 10–63%) for 53 taxa of autumn-germinated winter-annuals on 13 sites and a 60% average survival rate (range 44–83%) for 58 spring-germinated winter-annuals on 62 plots. These studies and preliminary results from our LTER project in the Chihuahuan Desert suggest that, as a generalization, about 50% of the individuals of populations of winter-annuals will survive to fruit set, on average, and that survivorship of summer-annuals is probably higher, but further population studies are needed.

Although details from our IBP and LTER studies are not presented here, the rate of development and duration of phenological stages (phenophases) for winter-annuals and summer-annuals are different. In the Chihuahuan Desert the phenophases of summer (C₄) annuals are sequenced rapidly over a 3–20-week period during the warm season of the year (hence the reference to summer or warm-season annuals). The majority of winter (C₃) annuals have an extended (20–45 week) development period (autumn germination, overwintering as vegetative rosettes, spring flowering-fruiting). A few 'winter' annuals germinate in the spring and rapidly progress to flowering and fruiting.

Another difference between winter-annuals and summer-annuals from our IBP and LTER studies was that the winter-annuals (e.g., *Lepidium* and *Cryptantha*) tend to produce flowers and fruits from a terminal inflorescence. Individuals of these species survive the winter as prostrate rosettes and then bolt to form inflorescences at the ends of

shoot apices. In contrast, individuals of summer-annuals (e.g., *Euphorbia* and *Pectis*) have shoot apices which produce numerous axil or lateral flowers or inflorescences. These summer-annuals will commence an early production of axil flowers, yielding mature seed long before the vegetative shoot ceases to produce new leaves and flowers.

Although a complete review is beyond the scope of this paper, a mention of a few studies will illustrate the importance of ants, rodents, termites and birds on the micro-distribution of desert-annuals. Tevis (1958c) studied the rate of collection of desert-annual seeds by harvester ant, *Veromessor pergandei*, in the Coachella Valley (lower Colorado region of the Sonoran Desert). He observed selective foraging and postulated that both the composition and distribution of desert-annuals is influenced by harvester ants. Beatley (1969) concluded that the availability of desert-annual seeds greatly influenced the success of reproduction in rodent population in the Mojave Desert. The effect of termites on desert-annual communities has also been shown to be considerable (Gutierrez & Whitford, 1987b). For further references to the role of animals on the distribution of desert annuals, see the review by Graetz (1981) and reviews in Whitford (1986).

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