Precipitation and the relative abundances of desert winter annuals: a 6-year study in the northern Mohave Desert

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The relationship between winter annual plants and the amount and timing of precipitation was studied for 6 years in Rock Valley, Nevada, U.S.A. Sixty-two annual species, whose year-to-year densities commonly varied 100-fold, were encountered in sampling quadrats. While dominance–diversity curves varied markedly between years, the similarity in relative abundances of annuals between years was correlated with differences in September–October precipitation of the previous fall; thus, in a comparison of years, the more similar the amount of precipitation in the early fall months, the more similar the relative abundances of annuals.

Between-year differences in the total amount of fall and spring precipitation, or in precipitation in November–December or January–February, were not related to compositional similarity. Annual composition was not related to that of the previous year. The proportional abundance of species varied less than did their absolute abundances. These results suggest that compositional dynamics of annual plants in the Mohave Desert are keyed to processes that affect germination.

Introduction

Arid and semi-arid regions characteristically support an abundant flora of annual plants which complete their life-cycles in short time periods following substantial rainfall (Beatley, 1974; Mulroy & Rundel, 1977). They spend unfavourable dry periods, usually most of their lives, as seeds. They germinate, grow and reproduce in the weeks following the notoriously variable rains, when subsurface soil moisture is available (Went, 1948, 1949; Went & Westergaard, 1949; Tevis, 1958a; Beatley, 1967, 1974).

Certain life history features which characterize the annual plant habit have attracted much attention, particularly those factors which might affect local abundances. Allelopathic agents (McPherson & Muller, 1969), inhibitory effects of high annual densities on growth, fecundity and survivorship (Went, 1949; Klikoff, 1966; Inouye, Byers *et al.*, 1980) and the role of seed predators (Inouye, Byers *et al.*, 1980) have been suggested as important regulators of local annual abundance and composition. However, these factors are of minor importance compared to the roles of, and synergistic effects due to, water, soil and temperature (*cf.* Shreve, 1942; Went, 1949; Beatley, 1974; Mulroy & Rundel, 1977).

Winter annuals are the widely fluctuating plant constituents of the Mohave Desert and their densities, percentage cover and standing crop biomass typically vary by several orders of magnitude between years (Muller, 1953; Went, 1948, 1949; Beatley, 1969). This year-to-

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year variation is tied to differences in fall precipitation; typically, germination occurs following sufficient rainfall sometime during September to mid-December, after which seedlings grow vegetatively all winter; stems elongate in early spring and plants flower and set fruit in April–May. Mass germination of winter annuals occurs following fall precipitation events of at least 25 mm; 15–25 mm results in scattered germination (Tevis, 1958b; Beatley, 1966, 1967, 1974).

Although the above scheme is well accepted for Mohave Desert winter annuals as a whole, little is known about how variation in the timing and amount of precipitation affects the relative abundances of species in these associations. Species abundance relationships are, and have been for decades, of fundamental interest to ecologists. Between community differences in species abundance–diversity have been well documented and theoretically explored (for a review, see May, 1975). The general pattern for all communities is that there are some common species, some rare species and many species of varying intermediate degrees of abundance. Examining the species abundance relations of desert annual plants and how they vary over time (in the same location) should provide insight into community organization, while helping towards an understanding of their dynamics.

Unlike most previous studies focusing on community patterns of abundance–distribution, there appears to be but one main controlling factor of winter desert annual densities and net production in the Mohave Desert: the amount and timing of 'winter' precipitation (Turner, 1973). The number of mature plants in the spring depends on the number of seeds which germinate and the number of seedlings which survive the growth seasons. Germination is controlled by soil moisture and, to a lesser extent, by temperature (Went, 1948, 1949; Went & Westergaard, 1949; Juhren, Went et al., 1956; Tevis, 1958a, 1958b). Survival appears to be controlled by soil moisture (Beatley, 1967, 1974).

The present paper provides data and analyses from a 6-year study which addresses the following questions: how do the relative abundances of annuals vary, in relation to the marked year-to-year differences in overall densities and precipitation? If relative abundances of species show yearly variation, can the timing and/or differences in the amount of precipitation account for these dynamics? After precipitation is considered, how dependent is the relative abundance of annuals on the compositions of past years? A hierarchical approach is used here to answer these questions; first, the association-level patterns of relative abundances are examined without regard to individual species (viz. dominance–diversity curves); second, floral similarity between years is examined by ranking species by their relative abundances; finally, the year-to-year dynamics in the proportional and absolute abundances of individual species are studied.

Study area and methods

Measurements on annual plant densities were made at the 46·1 ha US/IBP Desert Biome validation site in Rock Valley, Nye County, Nevada (36° 43′N, 116° 11′W; for further details of the study site, see Wallace & Romney, 1972; Turner, 1973). At 1046 m in elevation, the site is within the northern edge of the Mohave Desert scrub association (Shreve, 1942). Coverage of perennial shrubs was approximately 20%, of which eight species comprised 94–97% of the total: Ambrosia dumosa, Ephedra nevadensis, Eurotia lanata, Grayia spinosa, Krameria parvifolia, Larrea divaricata, Lycium andersonii and L. pallidum. Annual rainfall over a 14-year period (1963–76) averaged 138·1 (SD = 62·5) mm with an average of 60% (82·7 mm) falling between September and February.

Densities for all winter annuals were estimated from counts of individuals made in April–May in 20 × 50 cm quadrats (for 1971, 1973, 1974, 1975, 1976) or 50 × 50 cm quadrats (for 1972). There were 776 quadrats, arranged in sets of four around 194 points dispersed randomly throughout the study site. Rainfall was measured at weekly intervals with a clearview rain gauge for the fall and winter (September–February) prior to censuses.

Results

During the study period, substantial variation in precipitation (Table 1) and annual plant densities (Table 2) was recorded. The number of annual species varied from 42 in 1971 and 1972 to 56 in 1976. Year-to-year variation in estimated densities for many of the species was pronounced: e.g. the density of *Bromus rubens* varied almost 100-fold (from $0.073/m^2$ in 1973 to 6·780 in 1976); similar variation for *Vulpia octoflora* was recorded between 1971 and 1975.

Table 1. *Pre-census precipitation (mm) between 1970 and 1976 divided into four time periods*

Year*	Sept–Oct	Previous fall Nov–Dec	Jan–Feb	Total (Sept–Feb)
1971	0·0	37·4	8·1	45·5
1972	0·0	41·4	0·0	41·4
1973	40·4	29·7	70·9	141·0
1974	3·8	24·9	35·0	63·7
1975	25·9	35·3	5·1	66·3
1976	5·8	4·8	98·0	108·6

* Year of annual census.

Table 2. *Estimated mean densities* of winter annuals for each of the six years*

Species	1971	1972	1973	1974	1975	1976
Amsinckia tessellata	0·016	0.004	0·050	0·010	0·016	0.074
Antirrhinum filipes	0·000	0·000	0·000	0·000	0·001	0·000
Astragalus acutirostris	0·000	0·000	0·003	0·004	0·004	0·039
A. didymocarpus	0·000	0·000	0·081	0·016	0·008	0·190
A. lentiginosus	0·000	0·005	0·009	0·012	0·013	0·030
Bromus rubens	0·113	0·132	0·073	0·959	1·012	6·780
Calycoseris wrightii	0·001	0·001	0·004	0·000	0·004	0·029
Camissonia boothi	0·000	0·000	0·044	0·022	0·001	0·269
C. munzii	0·009	0·040	0·075	0·048	0·008	0·627
Caulanthus cooperi	0·009	0·035	0·107	0·003	0·098	0·545
C. lasiophyllus	0·005	0·004	0·301	0·027	0·237	4·915
Chaenactis carphoclinia	0·029	0·140	0·473	0·406	0·059	3·912
C. fremontii	0·109	0·244	0·204	0·852	0·112	1·606
C. macrantha	0·001	0·000	0·000	0·001	0·000	0·003
C. stevioides	0·012	0·022	0·045	0·097	0·016	0·548
Chorizanthe brevicornu	0·038	0·113	0·138	0·069	0·025	0·696
C. rigida	0·061	0·315	0·532	0·064	0·012	2·207
C. thurberi	0·000	0·000	0·000	0·000	0·000	0·001
Cryptantha circumscissa	0·026	0·056	0·080	0·278	0·092	0·907
C. dumetorum	0·000	0·000	0·000	0·358	0·062	1·163
C. micrantha	0·005	0·005	0·028	0·049	0·008	0·224
C. nevadensis	0·018	0·034	0·059	0·267	0·052	0·381
C. pterocarya	0·022	0.010	0·027	0·034	0·029	0·185
C. recurvata	0·022	0·064	0·162	0·484	0·073	0·933
Descurainia pinnata	0·018	0·025	0·269	0·147	0·212	0·461
Eriogonum maculatum	0·007	0·009	0·027	0·040	0·007	0·155
E. nidularium	0·003	0·004	0·003	0·008	0·009	0·042

Table 2. (*continued*)

Species	1971	1972	1973	1974	1975	1976
E. thomasii	0·000	0·000	0·000	0·000	0·000	0·001
E. trichopes	0·017	0·035	0·015	0·013	0·005	0·101
Eriastrum eremicum	0·000	0·000	0·000	0·000	0·000	0·001
Eriophyllum pringlei	0·039	0·201	0·350	0·236	0·181	3·268
Eucrypta micrantha	0·000	0·000	0·001	0·000	0·000	0·000
Gilia cana	0·001	0·016	0·186	0·001	0·018	0·588
G. transmontana	0·014	0·016	0·063	0·003	0·021	0·556
Glyptopleura marginata	0·001	0·001	0·003	0·000	0·000	0·003
Ipomopsis polycladon	0·003	0·042	0·147	0·001	0·027	0·671
Langloisia schottii	0·001	0·003	0·009	0·000	0·000	0·139
L. setosissima	0·004	0·070	0·066	0·019	0·004	0·618
Lepidium lasiocarpum	0·000	0·005	0·014	0·000	0·193	0·149
Linanthus bigelovii	0.000	0·000	0·000	0·000	0·001	0·014
L. demissus	0·000	0·000	0·003	0·000	0·000	0·027
Lupinus flavoculatus	0·000	0·000	0·042	0·005	0·003	0·000
L. shockleyi	0·001	0·000	0·000	0·000	0·000	0·000
Lygodesmia exigua	0·001	0·010	0·031	0·029	0·007	0·196
Malacothrix glabrata	0·003	0·007	0·020	0·026	0·013	0·223
Mentzelia obscura	0·001	0·023	0·123	0·087	0·019	0·402
Monoptilon bellidiforme	0·000	0·000	0·000	0·001	0·000	0·001
Nama demissum	0·000	0·000	0·023	0·000	0·000	0·073
N. pusillum	0·000	0·000	0·001	0·000	0·000	0·001
Nemacladus glanduliferus	0·000	0·000	0·005	0·000	0·000	0·000
Oxytheca perfoliata	0·004	0·013	0·012	0·020	0·000	0·119
Pectocarya spp.†	0·025	0·241	0·572	0·162	0·522	2·601
Phacelia fremontii	0·004	0·023	0·071	0·022	0·003	0·264
P. vallis-mortae	0·042	0·126	0·057	0·062	0·007	0·346
Plagiobothrys jonesii	0·000	0·000	0·001	0·004	0·000	0·018
Rafinesquia neomexicana	0·004	0·036	0·021	0·003	0·000	0·029
Strephanthella longirostris	0·010	0·043	0·228	0·007	0·078	0·074
Stylocline micropoides	0·001	0·001	0·012	0·000	0·000	0·095
Vulpia octoflora	0·074	0·530	5·005	3·890	10·108	7.652
Number of species	42	42	52	46	44	56

.* Estimated densities per 0·25 m² for 1972; all other years for 0·1 m².

† *Pectocarya platycarpa, P. heterocarpa, P. recurvata* were present in all 6 years; *P. setosa* in 1974 only.

Marked variation in the profiles of relative species abundance was also evident (Fig. 1). Commonly referred to as dominance–diversity 'curves', these depict the relative abundances of species sequenced from the most to the least abundant. Plots for 1973–1975 show an inordinately abundant species (*Vulpia octoflora*) whose relative abundance reached a peak of 75·7% in 1975. For the other years, abundances were more equitably distributed among species. The role of precipitation in producing these differences is unclear. While the two driest years in terms of September–February rainfall (1971 and 1972) have similar dominance–diversity relationships, the two wet years (1973 and 1976) are very different. However, there were substantially more 'rare' species present in the wet years compared to the drier ones.

A more quantitative way in which to examine association-level similarity of annuals between years is to compare their rankings of species abundances. Plant composition similarity between years was calculated using Kendall rank-order correlation coefficients (i.e. Kendall's *tau*; Siegel, 1956) using the estimated densities in Table 2. This technique
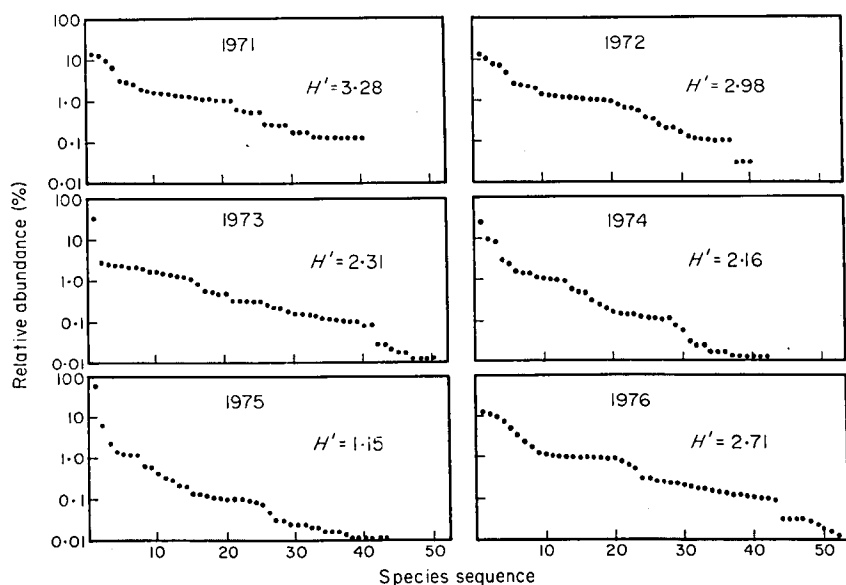
Figure 1. Relationship between the relative abundance or importance (expressed as a percentage on a logarithmic scale) and the rank of species for each of the 6 years studied. Evenness or diversity is given for each year and is defined as $H' = -\Sigma pi \log pi$ where pi is the proportion of all annuals (for that particular year) that were of species i.

uses ordinal ranking of species abundances in different years and tests directly for the degree of similarity in their composition. Absolute concordance in the relative abundances of species between years would result in a *tau* of 1·0. The relative abundance of annuals for each year was compared with that for every other year, resulting in 15 values of similarity (i.e. *tau*; Table 3).

Table 3. *Between year comparison of annual similarity in composition and precipitation. Annual similarity was computed using Kendall's tau. Absolute differences in precipitation (mm) for four time periods are given. All values for* tau *are significant* (p < 0·05)

Years compared	tau	Sept–Oct	Nov–Dec	Jan–Feb	Total (Sept–Feb)
1971 with 1972	0·78	00·0	4·0	8·1	4·1
1971 with 1973	0·59	40·4	7·7	62·8	95·5
1971 with 1974	0·64	3·8	12·5	26·9	18·2
1971 with 1975	0·55	25·9	2·1	3·0	20·8
1971 with 1976	0·64	5·8	32·6	89·9	63·1
1972 with 1973	0·69	40·4	11·7	70·9	99·6
1972 with 1974	0·69	3·8	16·5	35·0	22·3
1972 with 1975	0·58	25·9	6·1	5·1	24·9
1972 with 1976	0·69	5·8	36·6	98·0	67·2
1973 with 1974	0·57	36·6	4·8	35·9	77·3
1973 with 1975	0·61	14·5	5·6	65·8	74·3
1973 with 1976	0·67	34·6	24·9	27·1	32·4
1974 with 1975	0·58	22·1	10·4	29·9	2·6
1974 with 1976	0·65	2·0	20·1	63·0	44·9
1975 with 1976	0·63	20·1	30·5	92·9	42·3

All the species listed in Table 2 were included in the analysis, regardless of how many years they were actually present; if particular species were not present in a given year, they were treated as having zero density and the ranking of species with comparable abundances was calculated through the standard formula for handling ties (see Siegel, 1956, p. 218). Plant composition similarities between pairs of the 6 years (tau) are listed with the respective absolute differences in precipitation between years in Table 3. The latter variables represent the absolute year-to-year differences in the amount of pre-census rainfall during (1) September–October (= early fall), (2) November–December (= late fall), (3) January–February and (4) the total for September–February. Table 3 shows that all values for tau are highly significant. Hence, despite differences in the dominance–diversity curves between years, there are strong consistencies in the relative abundances of species. However, the values for tau are sufficiently variable (from 0·55 to 0·78) to require further examination.

Simple nonparametric correlation analyses demonstrated that composition similarity between years (i.e. tau) was related to differences in the amount of precipitation for two time periods: September–October and November–December with, respectively, negative and positive correlations (Table 4). Since between year precipitation differences for these two time periods were also correlated ($r_s = -0·315$), partial correlation techniques were used to isolate which of the two represents the stronger relationship.

The correlation between tau and the differences in September–October rainfall, holding effects due to differences in November–December precipitation constant, was significant (partial tau = $-0·434$; $p < 0·05$; see Siegel, 1956, p. 223). However, that between tau and November–December rainfall differences became insignificant when the effects due to September–October rainfall were factored out (partial tau = 0·204; $p > 0·05$). These results suggest that the more similar the precipitation in early fall (September–October), the more similar the rankings of relative species abundances the following spring.

How dependent are annual plant associations on the patterns of relative species abundances of past years? To answer this question, compositional similarity between years (tau) was correlated with the respective number of years (YR) separating the two censuses: e.g. YR would equal 4 in a comparison of annual similarity between 1971 and 1975. Table 4 shows that the proximity of years had very little relationship with annual composition similarity ($r_s = 0·09$; $p \geqslant 0·10$).

There was a loose relationship between differences in the dominance–diversity curves (Fig. 1), rainfall and similarity in the ranking of relative species abundances. The years most similar in their species rankings and September–October rainfall (1971 and 1972; Table 3) have the most similar dominance–diversity relationships, whereas the years most

Table 4. *Spearman rank correlation coefficients (r_s) between annual composition similarity between years (tau) and the absolute differences in precipitation for the four periods and for the total period. Correlations between tau and the number of years separating censuses (YR) are also given. See Table 3 for data used to generate these correlations*

| tau	Sept–Oct	Nov–Dec	Jan–Feb	Total (Sept–Feb)	YR
tau	−0·453*	0·454*	0·296	0·025	−0·090
Sept–Oct		−0·315	−0·093	0·465*	−0·255
Nov–Dec			0·719**	0·128	0·401
Jan–Feb				0·653**	0·094
Total					−0·026

* $p < 0·05$.
† $p < 0·01$.

different in precipitation during this period (1971 and 1973; 1972 and 1973) have very different dominance–diversity and species rankings. The role of precipitation in promoting these differences is suggested by a negative correlation between September–October precipitation and diversity (as H'; $r_s = -0.701$; $p < 0.15$). This again suggests that variation in the amount and timing of precipitation is tied to composition dynamics of annual plants in Rock Valley. Figure 2 shows that the integrity of this composition varies substantially less than year-to-year densities *per se*; i.e. the relative variability (expressed here as a coefficient of variation) in the proportional abundance of species was much less compared to their fluctuations in density over the 6-year period. This implies that while annual densities may fluctuate radically from year to year, the proportion of each to the whole remains relatively constant.

Discussion

In this paper, I have identified precipitation in the early fall as a major factor determining winter annual composition in the Mohave Desert. Further, it is a combination of the amount and timing of rainfall, not the relative abundance of annuals in immediately preceding years or the total amount of fall–spring precipitation, that figures most significantly in the dynamics of relative annual abundances. If post-germination survival to maturity is a factor determining composition, differences in post-germination precipitation (i.e. precipitation during January–February or December–November) should also be correlated with annual similarity between years. The results presented here clearly show this not to be the case and suggest that lability in the relative abundances of desert winter annuals is largely attributable to processes controlling germination. Other workers who have measured survivorship in desert annuals report similar values, despite large differences in precipitation, floristic composition and study sites: 42% (for the Sonoran Desert; Inouye, Byers *et al.*, 1980) and 46, 50 and 38% (for the Mohave Desert; respectively, Juhren, Went *et al.*, 1956; Tevis, 1958*b*; Beatley, 1967). From these studies, and the present one, it is clear that the dynamics of germination may be more sensitive to environmental vagaries than the subsequent differential survival of individuals and species (*see also* Went, 1949).

Germination thresholds are keyed to several factors. Both temperature (Barton, 1936; Koller, 1956) and light (Evenari, 1949; Koller, 1956; Schultz, Sister *et al.*, 1963) have been
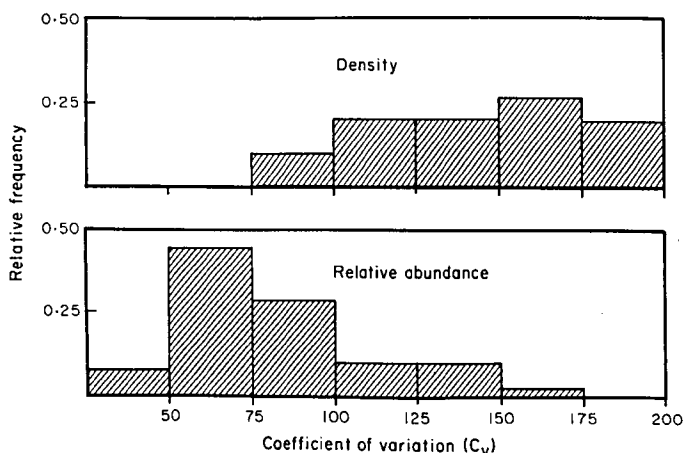
Figure 2. Measures of the year-to-year variability in density (top) and proportional abundance (bottom) using the coefficient of variation ($C_v = sd_i/\bar{x}_i \times 100$) calculated for each species *i*. Histograms are based on a C_v for each species calculated over the 6-year study period.

isolated as important factors in determining the germination of desert annual plants. However, for winter annuals in the Mohave Desert, the interaction between temperature and soil moisture may be of overriding importance in determining cues for germination (Went 1949; Went & Westergaard, 1949). That individual species differ in germination requirements is supported by the work of Soriano (*see* Koller, 1959). He subjected four Mohave Desert annuals (i.e. *Filago*, *Eriophyllum*, *Annastatica* and *Pectocarya*) to artificial rainfall and found moisture thresholds for germination to vary two- to three-fold between the species. Other interspecific differences in germination requirements are temperature-(McDonough, 1964) and light-dependent (Evenari, 1949).

Even though their germination thresholds may vary, winter annual plants in the Mohave Desert appear to be a set of species that share many requisites for growth and reproduction; they also show remarkable similarity in their phenological schedules, which are tied to seasonally available and ephemeral soil moisture. However, each species responds individually to the environmental conditions that influence germination during that year; the end result is composition dynamics which are correlated with the variable of overriding importance to germination, early fall precipitation. It could be argued that if, through evolutionary time, the biology of individual annual species in Rock Valley had converged to an optimum mode of behaviour, composition make-up should be more static than shown here. Another possibility is that the patterns of relative abundance might be the result of random fluctuations of species independent of environment (and evolution) and there would be no correlates of composition similarity. The results presented here oppose both views and support an individualistic view of winter desert annuals in the Mohave Desert.

It is surprising that annual composition was not correlated with that of the previous year, even after accounting for differences in precipitation. This suggests that seed reservoirs are little affected by year-to-year variation in annual fecundity and that there are enough seeds of each species to maintain integrity of composition, despite variation in precipitation. It is well known that the seeds of desert annuals may lie dormant in the soil for 10 years or more before germinating (*cf.* Cohen, 1966; MacArthur, 1972). Moreover, low germination percentages are common in the field or even under laboratory conditions that appear ideal (e.g. Koller, 1959; McCleary, 1968). Together, these features indicate a life history that ensures success over several years and is adapted to the extremely unpredictable rainfall patterns of desert habitats.

The research presented here is unusual because of its duration. Very few studies on desert annuals extend more than 2 or 3 years. However, if we are to understand the dynamics of desert annuals, we need long-term studies that are commensurate with the time that seeds remain viable in the soil. Only when more data of the sort presented here is made available can we understand even the most basic relationships between environmental variability, biological processes and the abundance and distribution of this important group of species.

References

Barton, L. (1936). Germination of some desert seeds. *Contributions of the Boyce Thompson Institute*, 8: 7–11.

Beatley, J. C. (1966). Winter annual vegetation following a nuclear detonation in the northern Mojave Desert (Nevada Test Site). *Radiation Botany*, 6: 69–82.

Beatley, J. C. (1967). Survival of winter annuals in the northern Mohave Desert. *Ecology*, 48: 745–750.

Beatley, J. C. (1969). Biomass of desert winter annual plant population in southern Nevada. *Oikos*, 20: 261–273.

Beatley, J. C. (1974). Phenological events and their environmental triggers in Mojave Desert ecosystems. *Ecology*, 55: 856–863.

Cohen, D. (1966). Optimising reproduction in randomly varying environments. *Journal of Theoretical Biology*, 12: 119–129.

Evenari, M. (1949). Germination inhibitors. *Botanical Review*, 15: 153–194.

Inouye, R. S., Byers, G. S. & Brown, J. H. (1980). Effects of predation and competition on survivorship, fecundity and community structure of desert annuals. *Ecology*, 61: 1344–1351.

Juhren, M., Went, F. W. & Phillips, E. (1956). Ecology of desert plants. IV. Combined field and laboratory work on germination of annuals in the Joshua Tree National Monument, California. *Ecology*, 37: 318–330.

Klikoff, L. G. (1966). Competitive responses to moisture stress of a winter annual of the Sonoran Desert. *American Midland Naturalist*, 75: 383–391.

Koller, D. (1956). Germination mechanisms in some desert seeds. III. *Calligonum comosum* L'Her. *Ecology*, 37: 430–433.

Koller, D. (1959). Germination. *Scientific American*, 200: 75–84.

MacArthur, R. H. (1972). *Geographical Ecology*. New York: Harper and Row. 269 pp.

May, R. M. (1975). Patterns of species abundance and diversity. In: M. L. Cody & J. M. Diamond (Eds), *Ecology and Evolution of Communities*, pp. 81–120. Harvard: Belknap Press; Cambridge: Cambridge University Press. 545 pp.

McCleary, J. A. (1968). The biology of desert plants. In: G. W. Brown (Ed.), *Desert Biology, Vol. 1*, pp. 141–194. New York: Academic Press. 452 pp.

McDonough, W. T. (1964). Germination responses of *Carnegia gigantea* and *Lemaireocereus thurberi*. *Ecology*, 45: 155–159.

McPherson, J. K. & Muller, C. H. (1969). Allelopathic effects of *Adenostoma fasiciculatum* 'chamise' in the California chaparral. *Ecological Monographs*, 39: 177–179.

Muller, C. H. (1953). The association of desert annuals with shrubs. *American Journal of Botany*, 40: 53–60.

Mulroy, T. W. & Rundel, P. W. (1977). Annual plants: adaptations to desert environments. *Bioscience*, 27: 109–114.

Schultz, Sister M. & Klein, R. (1963). Effects of visible and ultraviolet radiation on the germination of *Phacelia tanacetifolia*. *American Journal of Botany*, 50: 430–434.

Shreve, F. (1942). The desert vegetation of North America. *Botanical Review*, 8: 195–246.

Siegel, S. (1956). *Nonparametric Statistics for the Behavioral Sciences*. New York: McGraw-Hill. 312 pp.

Tevis, L., Jr. (1958a). Germination and growth of ephemerals induced by sprinkling a sandy desert. *Ecology*, 39: 681–687.

Tevis, L., Jr. (1958b). A population of desert ephemerals germinated by less than one inch of rain. *Ecology*, 39: 688–694.

Turner, F. B. (1973). Rock Valley Validation Site report. *US/IBP Desert Biome Research Memorandum*, 73–2. Logan: Utah State University. 211 pp.

Wallace, A. & Romney, E. M. (1972). *Radioecology and Ecophysiology of Desert Plants at the Nevada Test Site*. UCLA TID-25954. Los Angeles: University of California. 439 pp.

Went, F. W. (1948). Ecology of desert plants. I. Observations on germination in the Joshua Tree National Monument, California. *Ecology*, 39: 695–704.

Went, F. W. (1949). Ecology of desert plants. II. The effect of rain and temperature on germination and growth. *Ecology*, 30: 1–13.

Went, F. W. & Westergaard, M. (1949). Ecology of desert plants. III. Development of plants in the Death Valley National Monument, California. *Ecology*, 30: 26–28.