AN EXPERIMENTAL ANALYSIS OF STRUCTURE IN A DESERT PLANT COMMUNITY

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SUMMARY

(1) A field study was conducted in the Mojave Desert to determine the horizontal distribution of two co-dominating species and the degree of interference between individuals of the same species and of different species.

(2) Variance/mean analyses indicated that one of the co-dominating species (*Larrea tridentata*) is regularly distributed and the other (*Ambrosia dumosa*) is contagiously distributed.

(3) The results of a controlled removal experiment showed that water-related interference does occur at this site when water availability is low, and that at present, interference between species is usually more intense than that within a species. These results, together with nearest-neighbour analyses, revealed that regular distributions may not necessarily indicate present interference among individuals of the same species, but rather past interference.

(4) The importance of episodic seedling establishment and longevity in horizontal pattern development are also discussed.

INTRODUCTION

Quantitative investigations of desert vegetation indicate that biotic interactions play an important role in determining the structure of desert plant communities. In deserts, distributions suggestive of positive (one-sided, or mutually beneficial) interactions between species have generally been attributed to the amelioration of harsh environmental factors by one species, thereby benefiting the germination or survival of another (Went 1942; Muller 1953; Muller & Muller 1956; Turner *et al.* 1966; Steenbergh & Lowe 1969); whereas distributions suggestive of negative species interactions have been attributed to the intensification of environmental stress(es) by neighbouring plants (Shreve 1942; Woodell, Mooney & Hill 1969; Waisel 1971; Yeaton & Cody 1976; Yeaton, Travis & Gilinsky 1977). Characteristically, most investigations of biotic interactions in desert communities have not proceeded beyond the initial phase of detection and analysis of distribution patterns, and conclusions concerning cause have been based primarily on current quantitative theory, and not on the results of controlled field experiments.

We decided, therefore, to describe and analyse the plant associations in a desert community, and to evaluate, through field experiments, the relationships between community structure and within- and between-species interactions. Because of the inferred importance of competition (Beals 1968; Woodell, Mooney & Hill 1969; Waisel 1971; Yeaton & Cody 1976; Yeaton, Travis & Gilinsky 1977), and the occurrence of regular horizontal distributions in certain desert communities (Whittaker 1975), a simple

desert community was chosen, in which two species were co-dominant. One of them appeared to be regularly distributed. The specific questions asked were:—

(i) Do negative interactions occur between and within dominant species populations?

(ii) What is the significance of past and present-day interactions on community structure?

THE STUDY SITE

The study site was on a south-facing alluvial fan at an altitude of 925 m in the Mojave Desert at the base of the Ord Mountains, about 16 km north of the town of Lucerne Valley, San Bernardino County, California (latitude 34°33′N, longitude 116°53′W). This general area lies within the rainshadow of the San Bernardino Mountains and, therefore, receives only 10–15 cm of rain per year. Most of the precipitation falls between November and April, although thunderstorms occasionally occur in the summer. Additionally, large diel and annual temperature fluctuations are common. During the summer the difference between the maximum and minimum temperature in a 24-h period is as great as 20 °C, with maximum temperatures frequently reaching 40 °C, while in the winter, the temperatures may fall below 0 °C.

The terrain is level, ensuring even deposition of rainfall—a very important criterion in spacing and competition studies (Yeaton & Cody 1976). The vegetation is composed primarily of *Ambrosia dumosa** and *Larrea tridentata*, both of which are important components of many desert communities (Oosting 1956; Jaeger 1957; Wallace & Romney 1972; Beatley 1974) and are co-dominants over 70% of the Mojave Desert (Shreve 1942).

Ambrosia dumosa (Asteraceae) is a hemispherically-shaped, intricately-branched, drought-deciduous shrub, ranging in height from 2–6 dm. Its root system is derived from a segmented root crown and most of the roots are lateral. Generally, however, it lacks small, auxiliary rootlets (Wallace & Romney 1972). We excavated roots and found that the roots of *Ambrosia* growing in this area may extend to a depth of 70 cm.

Larrea tridentata (Zygophyllaceae), the exemplar of aspect dominance and drought tolerance in North American deserts (Benson & Darrow 1954; Barbour 1968), is a strong-scented, tall, multibranched, evergreen species with grey, brittle branches. Its range extends from Texas to California and from Nevada to north-central Mexico (Duisberg 1952). Its root system (again based on root excavations at this site) can be found down to 80 cm depth.

MATERIALS AND METHODS

Area sampling design

During the autumn of 1976, a 2·5 ha site in the study area was marked out and subdivided into 5 × 5 m quadrats (Fig. 1). A random, stratified sampling technique was employed to obtain data representative of the entire area (Oosting 1956; Kershaw 1973).

Assessment of importance values of species

The relative importance of each species within the site was assessed by the importance value (IV) developed by Curtis & McIntosh (1951) and later modified by Skeen (1973). In 104 randomly-chosen 5 × 5 m quadrats the height and two diameters (one perpendicular to the other and one the longest possible) of each individual were recorded. The cover

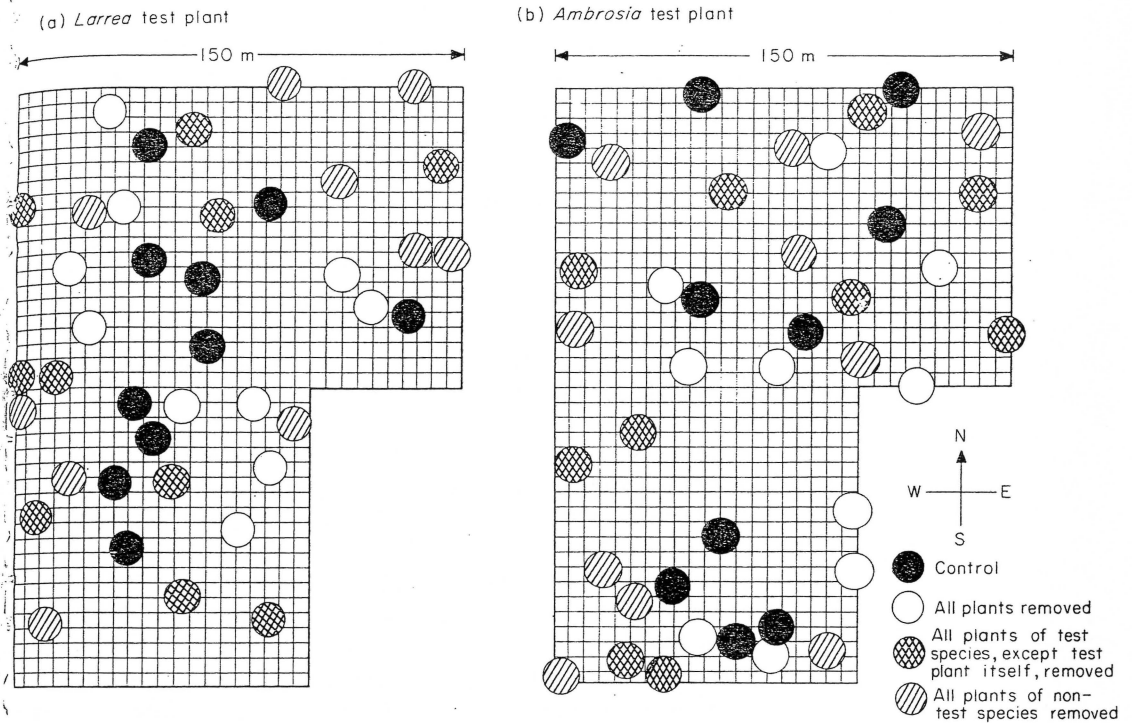* Nomenclature of plants follows that of Munz (1974).

(a) *Larrea* test plant   (b) *Ambrosia* test plant

FIG. 1. Sampling design and circular quadrat location on the experimental area in the Mojave desert. The radius of each experimental plot was 5·64 m. (a) *Larrea tridentata* as test plant; (b) *Ambrosia dumosa* as test plant. There is no overlap of quadrats in (a) and (b).

of each individual was determined by the crown-diameter method described by Mueller-Dombois & Ellenberg (1974). From these data, relative frequency, relative density, and relative crown cover were calculated.

Horizontal pattern determination

The horizontal distributions of *Larrea* and *Ambrosia* in the study area were determined in a manner similar to that used by Woodell, Mooney & Hill (1969): 250 coordinates were selected at random, and each was used as either the corner of a 5 × 5 m quadrat or the centre of a 10 × 10 m quadrat. The actual distribution of numbers of individuals in the sampled quadrats was compared to that expected for the Poisson distribution which would be found if the plants were randomly distributed, and a Chi-square test made. Since this analysis demonstrated that the probability of getting the observed distribution if the plants really were randomly distributed was less than 0·01 for both species, the variance/mean method (significantly >1 = clumped, significantly <1 = regular) was employed to quantify the direction and degree of nonrandomness of each species. Whittaker (1975) discusses these methods.

Interference* field experiment

To test for the present-day degree of within- and between-species interference of *Larrea* and *Ambrosia*, a differential removal experiment was started during the winter of 1977.

* Interference, as described by Muller (1969), is a general term that refers to cases in which the presence of one plant proves deleterious to another.

Forty, non-overlapping, 100 m², circular plots (5·64 m radius) were circumscribed within the 2·5 ha site, using an average-size *Larrea* bush for the centre point and as the test plant (Fig. 1(a)). Before any removals each plot contained at least three *Larrea* and eleven *Ambrosia* bushes—a composition which approximates the average number of *Larrea* and *Ambrosia* per 10 m square quadrat and ensured the possibility that each monitored plant was subjected to some degree of interaction with neighbouring plants. From the forty plots, four categories (ten replicates each) were selected at random (see below and Fig. 2(a)):—

(1) Control—no plants removed.

(2) All *Larrea* and *Ambrosia* bushes except the centre *Larrea* one removed.

(3) All *Larrea* bushes except the centre one removed.

(4) All *Ambrosia* bushes removed.

To ensure that the only effect of the treatments would be the differential removal of potentially interfering shrubs, special care was taken to leave the surrounding soil undisturbed while cutting off the above-ground portion of the plants. Before any plant was removed, its height, diameter (two perpendicular measurements), and distance from the monitored plant were measured. In addition, any regrowth that occurred during the study by the stumps of these 'removed' individuals was immediately cut away. The removed plants were then brought back to the laboratory, dried at 100 °C in a forced-air oven for several days, and weighed for biomass determination. The height, diameter, and distance of the remaining plants from the monitored plants were also measured.

In addition to these plots with *Larrea* as the central test plant, the same number of plots with *Ambrosia* at the centre were treated in a reciprocal way (Figs 1(b), 2(b)).

After completing the various treatments, pre-dawn measurements of plant xylem pressure potentials were taken to evaluate the water status of the monitored plants, using
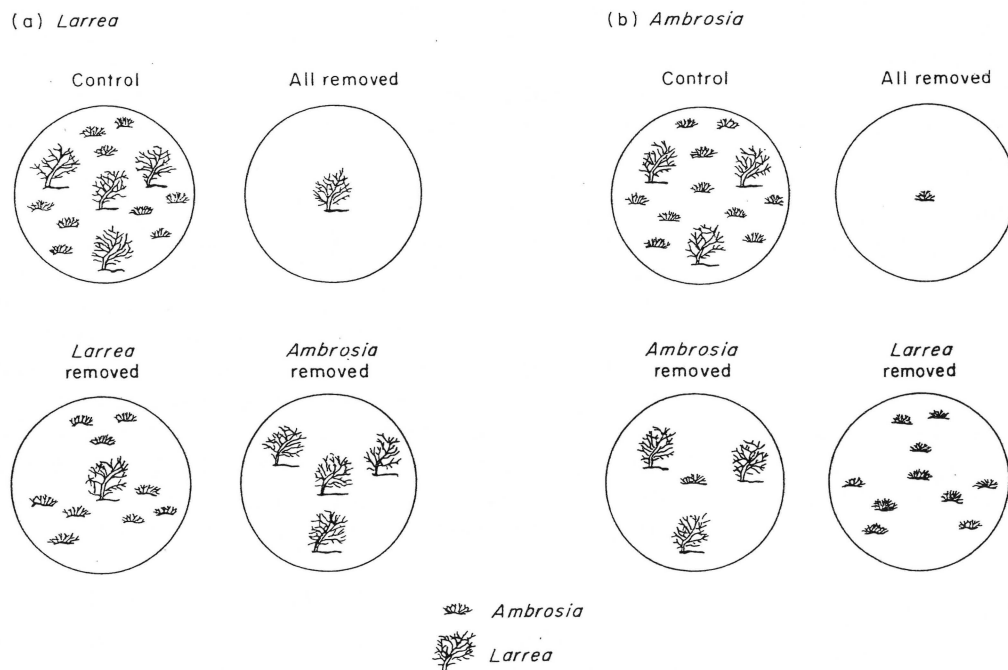

FIG. 2. Diagrammatic representation of the experimental treatments. (a) *Larrea tridentata* as test plant; (b) *Ambrosia dumosa* as test plant.

the Scholander pressure bomb method (Scholander *et al.* 1965). These measurements were taken just before dawn because xylem pressure potentials at that time are thought to reflect soil moisture availability (Ritchie & Hinckley 1975). To obtain accurate measurements of xylem pressure potential, the following procedure (which usually took no more than 15 min) was strictly adhered to: three twigs (each approximately 15 cm in length) were cut with pruning shears from various branches, quickly sealed in a plastic bag, and brought back to the bomb for immediate measurement. In order to minimize the effects of pruning damage to the monitored plants, the forty *Larrea* and forty *Ambrosia* plants were randomly divided into two permanent sampling groups (five plants/treatment), for a total of twenty plants per group. These groups were then sampled alternately at 2-weekly intervals.

RESULTS

Quantitative description of the community

Importance values (IV) for each species were calculated to assess the biological contribution of each species to this desert community (Table 1). It is obvious from the IVs that *Larrea* (40%) and *Ambrosia* (49%) are co-dominant in this area. Although both species have similar IVs, the values of the components making up each IV are dissimilar: *Ambrosia* not only has a higher relative frequency (47%) than *Larrea* (35%), but also a much higher relative density (78% *v.* 15%); whereas *Larrea* has a much greater relative cover (70% *v.* 24%).

The results of the variance/mean analyses that were derived from the 10×10 m quadrat data are shown in Table 2. In this area, *Larrea* has a variance/mean quotient $(\sigma^2/\bar{x})$ of 0·57, whereas *Ambrosia* has a $\sigma^2/\bar{x}$ quotient of 5·0. These results clearly indicate, as did those based on some 5×5 m quadrat data ($\sigma^2/\bar{x}$ quotients of 0·26 and 1·60 for *Larrea* and *Ambrosia* respectively), that the horizontal distribution of *Larrea* is regular and that of *Ambrosia* contagious.

TABLE 1. Importance value, and its components, for various species in 104 random 5×5 m quadrats in the experimental area in the Mojave desert.

| | Species | | | | |
Measure	Larrea tridentata	Ambrosia dumosa	Ephedra spp.	Others (combined)	Total
Frequency (/104)	75	102	31	8	216
Density (/104 quadrats)	112	591	51	9	763
Crown cover (m²/104 quadrats)	129	44	13·3	0·7	187
Relative frequency (%)	35	47	14·4	3·7	100
Relative density (%)	14·7	78	6·7	1·2	100
Relative crown cover (%)	70	23·5	7·1	0·4	100
Importance value (%)	40	49	9·3	1·8	100

TABLE 2. Horizontal distribution of two shrub species in the Mojave desert. The distribution of both species is significantly nonrandom at $P = 0·001$ using Student's *t*-test. All values are based on 250 random 10×10 m quadrats.

Species	Mean density ($\bar{x}$) (shrubs/100 m²)	Variance (σ^2)	$\sigma^2/\bar{x}$	Distribution
Larrea tridentata	3·62	2·06	0·57	Regular
Ambrosia dumosa	19·5	97	5·0	Contagious

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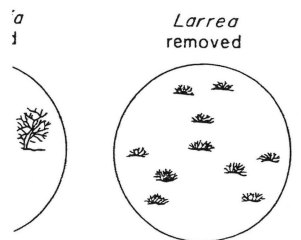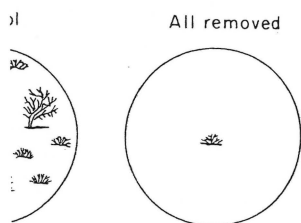ants. From the forty plots,
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It was primarily because of these results and the association of such patterns in deserts with plant–plant interactions—specifically, in the case of *Larrea*, competition for moisture (Woodell, Mooney & Hill 1969; Beals 1968; Yeaton & Cody 1976; Yeaton, Travis & Gilinsky 1977)—that the previously described removal experiment was implemented.

Interference field experiment

To assess interference among neighbouring plants in this community, the xylem pressure potentials of the monitored plants were measured at 2-weekly intervals
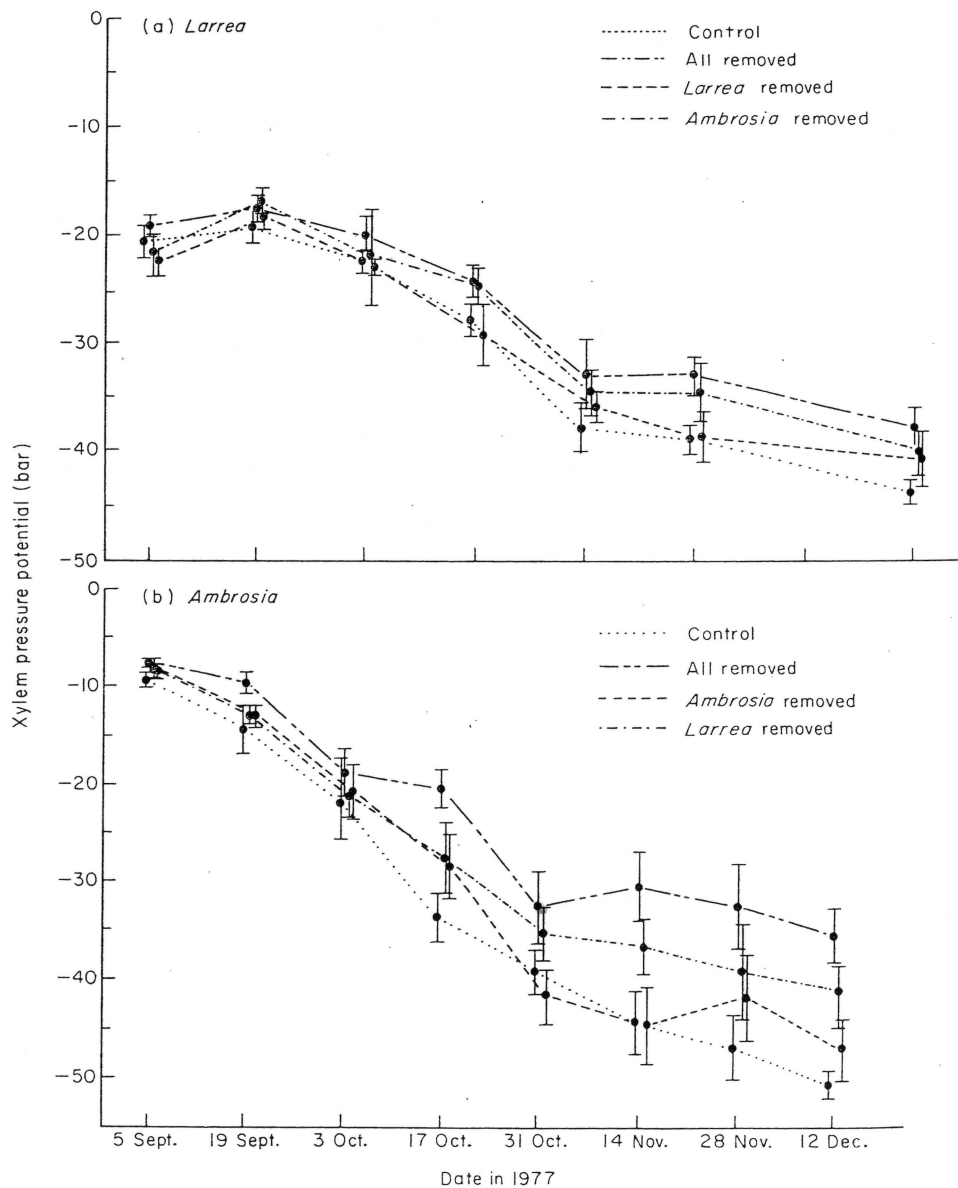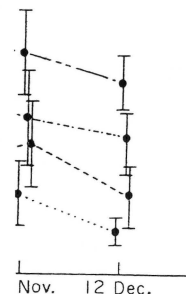

FIG. 3. Differential effects of removal treatments on stem xylem pressure potentials of (a) *Larrea tridentata* and (b) *Ambrosia dumosa* during autumn 1977. Bars are ±2 S.E.; n = 15.
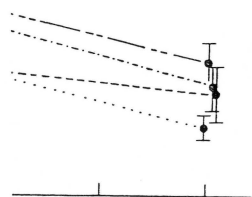
throughout three consecutive seasonal wetting and drying cycles. Theoretically, if the plants were undergoing water-related interference, then the xylem pressure potential in the test plants in the control plots would drop more quickly than would that of test plants in plots from which all or selected neighbours had been removed; i.e. the water status of the monitored plants growing in the treatment plots would remain higher for a longer period of time than it would in those growing in the control plots. Furthermore, because of the diagnostic design of the experiment, the relative intensity of both within- and between-species interference could be determined.

The results collected in autumn 1977, illustrated in Fig. 3, exemplify the results of the first two wetting and drying cycles (spring 1977, autumn 1977) after the various treatments had been carried out. Shortly after 60 mm of rain fell on 17 August 1977, the mean xylem pressure potential of *Larrea*- and *Ambrosia*-monitored plants reached very high values for the respective species, with no consistent differences among treatments. As the soil moisture became depleted and the xylem pressure potentials decreased, differences among the experimental categories developed and remained consistent throughout the driest periods. On 14 November, for example, in the *Larrea*-centred plots the mean xylem pressure potential of the monitored *Larrea* plants in the control plots (−39·0 bar) was significantly lower than that of the *Larrea* plants in the plots from which all neighbouring plants had been removed (−33·7 bar) and in the plots from which *Ambrosia* had been removed (−34·6 bar), but not significantly different from the mean xylem pressure potential of the monitored *Larrea* plants in the plots from which all other *Larrea* plants had been removed (−39·3 bar). Similar results were obtained in the *Ambrosia*-centred plots. On the same day, the mean xylem pressure potential of the monitored *Ambrosia* plants in the control plots (−44·2 bar) was significantly lower than that in the plots from which all other plants had been removed (−30·5 bar) and in the plots from which *Larrea* had been removed (−36·5 bar), but not significantly different from the mean xylem pressure potential of the monitored plants in the plots from which *Ambrosia* had been removed (−44·6 bar). These results are representative of those obtained throughout the driest periods of both the spring 1977 and autumn 1977 wetting and drying cycles. They appear to indicate that water-related interference does occur at this site when water availability is low, and that, with the present horizontal arrangement of individuals, interference among individuals of different species is commonly more intense than that among individuals of the same species.

Measurements taken during the third successive wetting and drying cycle (spring 1978) showed responses similar to the preceding ones, except for the *Larrea* plants in plots from which other *Larrea* plants had been removed (Table 3). At the end of this cycle, when

TABLE 3. Differential effects of removal treatments on plant xylem pressure potentials measured on 31 July, 1978. Values are mean ($n = 15$) $\pm$ S.E. Within a column, treatments with a superscript letter in common differ significantly at $P = 0.05$ using Student's *t*-test.

Treatment	*Larrea* Xylem pressure potential (bar)	Treatment	*Ambrosia* Xylem pressure potential (bar)
(i) Control	−54·7 ± 1·1[b,c,d]	(v) Control	−50·2 ± 3·3[b,d]
(ii) All except the test *Larrea* plant removed	−47·2 ± 2·7[a,d]	(vi) All except the test *Ambrosia* plant removed	−39·9 ± 3·4[a,c]
(iii) All *Larrea* except the test plant removed	−50·1 ± 2·1[a]	(vii) All *Ambrosia* except the test plant removed	−49·8 ± 2·6[b,d]
(iv) All *Ambrosia* removed	−51·3 ± 1·7[a,b]	(viii) All *Larrea* removed	−42·4 ± 3·1[a,c]

the soil-water availability was very low, the mean xylem pressure potential of the monitored *Larrea* in these plots (−50·1 bar) was significantly higher than that of the monitored *Larrea* in the control plots (−54·7 bar). This indicates that at least during this cycle, interference among neighbouring *Larrea* bushes did occur.

DISCUSSION

The determination of the functional significance of negative species interactions in the formation and maintenance of desert plant communities has been the objective of numerous ecological studies. These studies, in general, may be placed into one of three categories, based on the method of analysis employed:

(a) Vegetational disparity studies. In this type of study, the vegetation growing in disturbed sites is compared and contrasted with the vegetation growing in undisturbed sites (Johnson, Vasek & Yonkers 1975; Vasek, Johnson & Brum 1975).

(b) Nearest-neighbour analyses. The nearest-neighbour method used by most workers is the one described by Pielou (1960). In this method, the distance between randomly chosen individuals and their nearest neighbour is recorded, as are the sums of the sizes of each nearest-neighbour pair. Linear regressions of size on distance are then calculated from these measurements. It is postulated that if these two variables are positively correlated, then there is interference between neighbouring plants (Yeaton & Cody 1976; Yeaton, Travis & Gilinsky 1977).

(c) Horizontal pattern studies. The underlying supposition of these studies is that certain horizontal patterns of distribution may be the result of interference (or lack of it) among individuals of the same species.

Of the three distributions most commonly recognized (contagious, random, and regular), regular distributions are of special interest, not only because they are known to develop primarily in deserts (Beals 1968; Barbour 1969; Woodell, Mooney & Hill 1969; Waisel 1971), but also because such distributions signify the importance of interference in the structural organization of desert communities. The earliest quantitative descriptions of regular distributions in North American deserts appeared in 1969 (Barbour 1969; Woodell, Mooney & Hill 1969). The latter workers correlated both the density and pattern of twelve *Larrea* populations with the annual rainfall received by each population. They found that the density of *Larrea* was greater in higher rainfall areas than in lower rainfall areas, and that, in general, the horizontal pattern of the shrubs in the former was clumped and that in the latter was regular. Based on these data and two theories: one developed by Walter (1962) and the other by Pielou (1959), they concluded (a conclusion that has become widely accepted) that:

(i) in the arid regions of the desert, plant cover decreases with a concomitant increase in lateral root growth, until almost all of the available space is fully occupied, and

(ii) regular spacing in areas of low rainfall is caused and maintained by root competition for available water.

In general, after reviewing the work of Woodell, Mooney & Hill (1969) and other studies of regular distributions, disturbed *v.* undisturbed site studies, and studies utilizing nearest-neighbour analyses, it becomes quite evident that biotic interactions are potentially of major functional importance in the structuring of desert communities. However, it also becomes evident that none of the studies conducted thus far are definitive, because the conclusions drawn in them have been based primarily on ecological theory. After the initial descriptions of the vegetation under study have been made, there has characteristically

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been a total reliance on statistical inference both in the formation of hypotheses and in the 'measurement' of the biological interactions responsible for the structure of the observed vegetation. While such descriptions and inferences are valuable they do not test for controlling mechanisms or directly 'measure' the extent of present or past biological interactions. What is needed to obtain such information is carefully designed, controlled field experiments (Connell 1975).

The significance of interference today and in the past

The results of the field experiment conducted in this study clearly indicate that interference does occur among the dominating plants in this area, and that, at present, between-species interference is usually more intense than that within species. The mechanism(s) responsible for the observed between-species effects on plant xylem pressure potentials, however, have not been determined. While it seems probable that the causal mechanism may be simple competition for water among individuals of the co-dominant species, it is possible that allelopathic root interactions may also occur. Further, it must be pointed out that even though the results obtained from the field experiment do indicate that interference between species is more intense than that within species, the importance of these interactions in the formation and maintenance of the patterns exhibited by *Larrea* and *Ambrosia* has not been directly assessed.

Between-species interference

If the mutual interference between *Larrea* and *Ambrosia* were of sufficient intensity to be deleterious to one or both populations, then one would expect these populations to become disassociated. To assess the degree of association between the two species we correlated the biomass of *Larrea* per quadrat with the biomass of *Ambrosia* in the same quadrat.

To measure these biomasses without cutting down any of the individuals growing in the sampled quadrats, log-log regressions of weight on volume were calculated for *Larrea* and *Ambrosia*, utilizing the plants previously removed when setting up the field experiment. Through use of these regressions, both of which had r^2 values of 0·88, the total biomass of *Larrea* and *Ambrosia* in each quadrat was determined. These data were then subjected to a Pearson product-moment correlation test, which revealed that there was no significant correlation between the biomass of these two species ($r = 0·09$), indicating that interference between the individuals of these species in the recent past has had little effect on their respective distributions. We suspect this may be largely due to frequent recruitment of *Ambrosia* seedlings as will be discussed later.

Within-species interference

Larrea-Larrea. Of the results obtained from the field experiment, the most surprising were those derived from the *Larrea*-monitored plants growing in the plots from which all other *Larrea* plants had been removed. Because of previous speculations that water-related interference occurs among regularly distributed individuals (Woodell, Mooney & Hill 1969), we expected that the monitored *Larrea* plants in these plots would maintain significantly higher xylem pressure potentials than those growing in the control plots, where, presumably, interference for moisture among neighbouring *Larrea* plants was intense. This did not occur until the third wetting and drying cycle (Fig. 3(a) and Table 3), indicating that water-related interference is, at present, of minimal intensity.
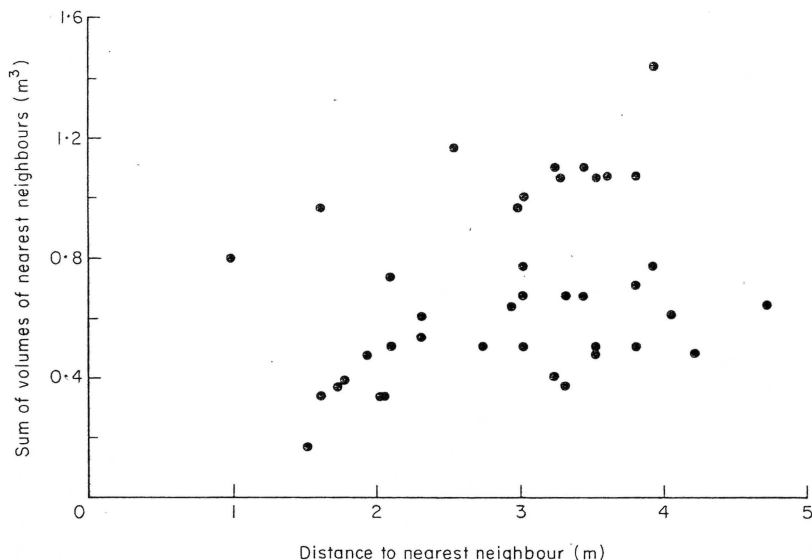
FIG. 4. Relationship, for *Larrea tridentata* in the Mojave desert, of separation to sum of volumes for 80 pairs of a plant and its nearest neighbour. The correlation, *r*, is 0·33; $P < 0.05$.

However, forms of interference other than those affecting plant water status could be operative.

To test further for the effects of plant interference (past or present) in this community, we also employed the nearest-neighbour analysis of Pielou (1960), which is based on the premise that positive correlations of plant size with distance between neighbouring plants are indicative of interference. This analysis (Fig. 4) showed these two variables to be positively ($P < 0.05$), but weakly correlated ($r = 0.33$), signifying the occurrence (albeit very small at present) of some type of plant interference.

Even though we cannot conclude from our study which type(s) of interference was or is of importance in determining the present horizontal distribution of *Larrea*, it is our opinion (based on the xylem pressure potential data and the belief that desert ecosystems are—as stated by Noy-Meir (1973)—'water controlled ecosystems . . .') that water-related interference was the underlying mechanism causing the *Larrea* population to become regularly distributed. We suggest that this population initially consisted of contagiously distributed individuals (as do many newly-established populations (Greig-Smith & Chadwick 1965; Laessle 1965; Mohler, Marks & Sprugel 1978; Schlesinger & Gill 1978)), that experienced intense within-species water-related interference due to the close proximity of constituent individuals, and that with time, this population became increasingly regular as more and more individuals died from the effects of the within-species interference. We further suggest that this process continued until the population became regularly distributed and the intensity of the interference (due to the increase in distance between neighbouring *Larrea*) was, concomitantly, reduced.

Ambrosia-Ambrosia. Given the results of the interference experiment concerning the regularly distributed *Larrea*, it is reasonable to expect that interference among the contagiously distributed *Ambrosia* shrubs would be intense. However, the xylem pressure potentials of the monitored *Ambrosia* growing in the plots from which all other *Ambrosia* plants had been removed were not significantly different from those growing in the control