Intraspecific competitive effects on water relations, growth and reproduction in *Encelia farinosa*

James R. Ehleringer
Department of Biology, University of Utah, Salt Lake City, UT 84112, USA

Summary. An experiment was conducted to assess the importance of intraspecific competition on water relations, growth and reproductive output in *Encelia farinosa*, a common deciduous-leaved shrub of the Sonoran Desert. Nearest neighbor analyses in monospecific stands indicated that plants exhibited a clumped distribution. Plant size and nearest neighbor distance were positively correlated, inferring intraspecific competition. Removal experiments monitored for two years indicated that plants now without neighbors had higher leaf water potentials, higher leaf conductances, and a greater leaf area than control plants. As a consequence, growth rates and reproductive output were significantly higher in plants without neighbors. These data strongly support the notion that warm desert plants with a contagious spatial distribution compete for water.

Introduction

The strong positive relationship commonly observed between plant primary productivity and precipitation in warm deserts clearly implies that water is a significant factor limiting the productivity of both annuals and perennial shrubs (Walter 1968, McMahon and Schimpf 1980, Ehleringer and Mooney 1983). In addition to the constraints on productivity imposed by abiotic factors, attention has also been focused on potential biotic limitations. Specifically, a number of studies have examined the spatial distribution patterns of perennial shrubs for indications of competitive interactions (Woodell, Mooney and Hill 1969, Barbour 1969, Anderson 1971). A regular distribution of plants (indirect evidence of competitive interactions) has been observed, especially under low precipitation situations. In addition, studies of intraspecific nearest neighbor relationships by Yeaton and Cody (1976), Yeaton, Travis and Gilinsky (1977) and Nobel (1981) on plants in these same deserts have shown positive correlations between plant size and nearest neighbor distance. Again this is indirect evidence of competitive interactions between plants.

Fonteyn and Mahall (1978, 1981) provided additional evidence that competition for water may be occurring between desert plants. In a series of plant removal experiments, they showed that when water availability was low plant water status (leaf water potential) was affected by the presence of neighbors. Their conclusion was that interspecific competition was usually more intense than intraspecific competition.

Although ample indirect evidence exists, none of the previous studies on desert plants have unequivocally demonstrated that interplant competition (either intra- or interspecific) is occurring, and that as a result of these interplant interactions growth, productivity and reproductive activity are reduced. The purpose of this paper is to 1) present data which inferentially demonstrate that intraspecific competition is occurring in a monospecific stand of *Encelia farinosa* Gray (Asteraceae), and 2) to describe an experiment conducted to measure the consequences of neighbor removal on physiological activity, growth and reproduction in *E. farinosa*.

E. farinosa is a drought-deciduous shrub, common to most of the Sonoran Desert of North America. Throughout most of its range, it is the dominant deciduous-leaved shrub, and in many areas it forms extensive monospecific stands. Productivity and physiological activity in this species are also positively correlated with water availability (Ehleringer, Björkman and Mooney 1976, Ehleringer and Mooney 1978, Ehleringer 1980, Ehleringer and Cook 1984). In response to reduced soil water availability, new leaves are produced with a reflective pubescence layer, which increases water use efficiency and allows the plant to maintain physiological activity later into the drought period (Smith and Nobel 1977, Ehleringer and Mooney 1978, Ehleringer 1982).

Methods and materials

This study was conducted in west central Arizona (lat. 34°57′N, long. 114°25′W, 540 m elevation) at a site approximately 9 km south of Oatman, Arizona. The vegetation for the area is typical for the Lower Colorado Valley portion of the Sonoran Desert (Shreve and Wiggins 1964). On south facing slopes and bajadas in this area, the vegetation is dominated by the subshrub *Encelia farinosa*. Throughout much of this area, this species forms monospecific stands. At other sites in this area, it is co-dominant with the evergreen leaved shrub *Larrea divaricata* and the cactus *Opuntia bigelovii*.

Soils and parent material at this site are volcanically derived. In general the area is rocky, with only thin soils (<20 cm) at best. Soil nutrient concentrations are low. The average soil nitrate and phosphorus concentrations were 2.2 ppm and 0.07%, respectively (soils analyzed by Utah State University Soil, Plant and Water Analysis Laboratory).

The particular site chosen for study was a south facing slope, which consisted of a monospecific stand of *Encelia farinosa*. The population was analyzed using nearest neigh-

bor methods as described by Clark and Evans (1954) and Pielou (1962). In early December, 1981, twelve shrubs of approximately equivalent size were chosen from this population to be used in this study. Around six of the shrubs all other shrubs within a 2 m radius were removed. The remaining six shrubs served as controls. The size of these plants was initially determined, and then aboveground primary productivity, water relations and reproductive activity were monitored at periodic intervals thereafter.

The water relations parameters measured were leaf conductance to water vapor and leaf water potential. Leaf conductances were measured with a null balance porometer. Leaves from an entire twig were inserted into the porometer for each reading. The sample size was two twigs from each shrub for each reading. Leaf water potential was measured using a pressure chamber. Sample size at each reading was one twig per shrub. Additionally, solar photon flux levels (using a quantum sensor), air and leaf temperatures (using 36 gauge thermocouples), and vapor pressure deficit (vpd) (using a relative humidity sensor) were measured and then recorded on a data logger.

The relationship between leaf size (cm^2) and leaf width was initially determined by selecting leaves of various sizes from different plants and measuring their area with a leaf area meter. The relationship between leaf size (cm^2) and leaf width (mm) was size $= 0.293 \times$ width $- 2.00$, $r^2 = 0.89$. Thereafter, only leaf width was measured on ten randomly chosen leaves from each of the twelve shrubs.

Biomass and productivity were assessed from twig measurements and measurements of total plant size. Twigs are defined as that portion of the stem bearing leaves. Twigs were easily distinguished from the remainder of the stem by the presence of a thin layer of pubescence which persisted until the beginning of the next growing season. At each sampling period, the number of mature leaves per twig was counted for ten twigs on each of the shrubs. At approximately every second sampling period, the total number of active twigs was counted on each of the shrubs. At the end of the spring growing season in 1983 when plants were dormant, three non-flowering twigs and three flowering twigs from each of the shrubs were harvested and analysed for dry weight, Kjeldahl nitrogen and total nonstructural carbohydrate content. At the end of the experiment, all shrubs were harvested and total above ground dry weight was determined. Because of the rocky nature of the soils, reliable estimates of below ground biomass could not be obtained.

Reproductive success was estimated at the peak flowering period in the spring of 1983. The number of flowering heads per twig was estimated by counting flower heads on each of 25 twigs per shrub. The number of achenes produced per flower head was estimated by counts from dissected post-flowering flower heads. Both dead and developing achenes were included in the counts. Although, *Encelia farinosa* can flower both in the late spring and again in the fall, only spring flowering occurred during the study period as well as in the year before the study began.

Results

The shrub density at this site was 1.72 individuals per m^2. In a subsampling of 205 individual plants, only 5 were less than 2 years old (based on other seedling establishment studies also at this site). Since new plant establishments had
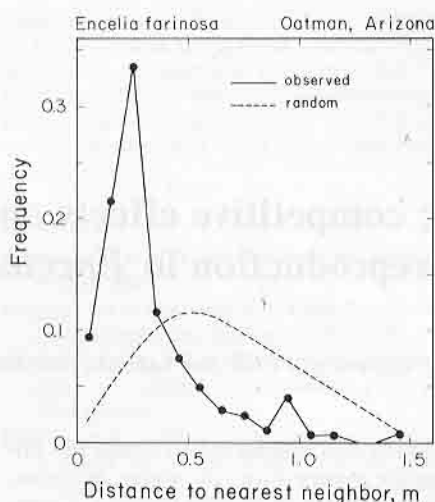

Fig. 1. The observed relationship between plant frequency and nearest neighbor distance for *Encelia farinosa* shrubs at Oatman, Arizona. Plotted also for comparison is the expected frequency distribution for randomly distributed shrubs

been observed in only the last two out of six years, all other shrubs were likely to have been at least 7–8 years old.

The nearest neighbor distance data clearly indicated that the distribution of individual plants was not random (Fig. 1). The vast majority of individuals were within 0.4 m of each other, and no individuals in the study area were more than 1.5 m apart. Using the Clark and Evans (1954) method for determining distribution patterns, the plants were clumped (R = 0.901, P < 0.01). A nearest neighbor analysis using the Pielou (1962) methodology also suggested that the distribution was clumped (chi-square = 429.7, P < 0.005). There were no obvious surface obstructions or topographic factors to explain the clumped distribution patterns. However, local variations in soil properties may exist that could make establishment more likey in one location than another.

When the canopy sizes of these plants were plotted as a function of distance to the nearest neighbor, it was clear that plants increased in size when they were farther apart (Fig. 2). The mean plant size increased linearly as mean distance between plants increased up to a distance of about 0.5 m. Thereafter, plant size appeared to remain constant as distance between plants increased. Since on the average plant canopies did not overlap and there was open space between the shrubs, it was concluded that if competition were occurring it was *not* likely to be for any aboveground resource. More likely, if competition was occurring, it was between shrubs for a belowground resource such as water and/or nutrients.

Given the inference that intraspecific competition may be occurring, an experiment was designed to measure the consequences of competition on individual plant performance. The treatment was to remove all neighbors within a 2 m radius of a shrub. From the nearest neighbor analysis, it appeared that plants were never this far apart naturally, and therefore, any potential neighbor effects would be greatly reduced.

As estimates of physiological activity, leaf conductance to water vapor and leaf water potential were measured. Previous investigations by Ehleringer and Cook (1984) have demonstrated that leaf conductance in *Encelia farinosa* is

positively and linearly related to the photosynthetic rate under moderate to high irradiances. Therefore, leaf conductance estimates should also be reliable estimates of the photosynthetic rate.

Early in the growing season (February 21) when soil water was abundant, there were no differences in the diurnal courses of leaf conductances or in the leaf water potentials between those plants with their neighbors removed and the control plants (Fig. 3). Leaf conductances to water vapor peaked at approximately 0.25 mol m^{-2} s^{-1} during midday in both sets of plants and decreased under lower irradiances in the late afternoon and early morning hours. Leaf water potentials decreased from -1.6 MPa in the morning to -1.9 MPa at midday in both sets of plants.

The rains ceased in late March and by April 23, clear differences existed between the plants without neighbors and the controls. In those plants without neighbors, leaf conductances reached the same midday values as previously measured in February (approximately 0.25 mol m^{-2} s^{-1}), before decreasing in the afternoon as vpd increased. Leaf conductances in the control plants peaked at 0.10 mol m^{-2} s^{-1} early in the morning, and were significantly lower than

in the plants without neighbors. Correspondingly, leaf water potentials differed by 0.5 MPa throughout the day between plants with and without neighbors. Leaf water potential in the control plants ranged from -3.24 to -3.46 MPa during the daylight hours, whereas in the plants without neighbors leaf water potential ranged from -2.26 to -2.60 MPa through the day.

By June 16, which was well into the drought period,

Fig. 4. The mean maximum leaf conductance to water vapor and midday leaf water potential for leaves of *Encelia farinosa* as a function of time at Oatman, Arizona. The lower plate represents the total precipitation received at Bullhead City, Arizona (30 km away), which is the closest precipitation station. Open circles represent plants with their nighbors removed and closed circles represent control plants. The vertical lines represent ± 1 SE
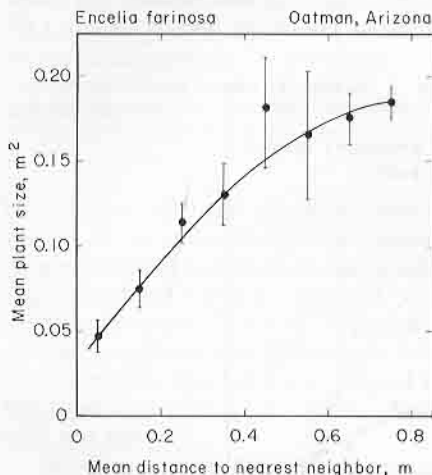

Fig. 2. The relationship between mean plant size and the mean distance to the nearest neighbor for *Encelia farinosa* shrubs at Oatman, Arizona. Vertical lines indicate ± 1 SE. Data are from same subpopulation as presented in Fig. 1
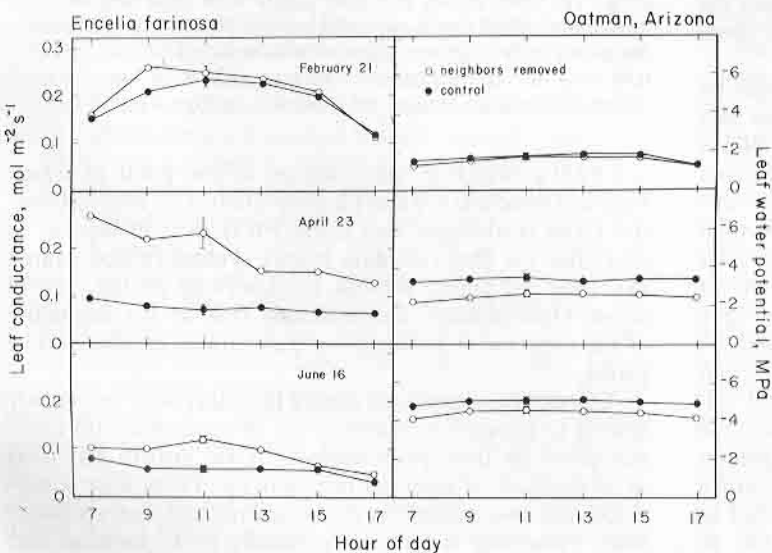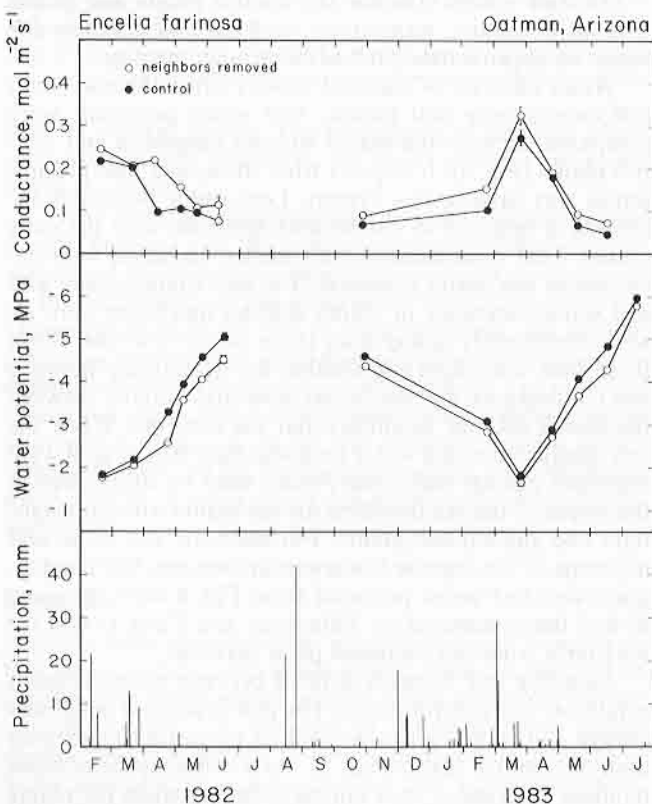

Fig. 3. The diurnal courses of leaf conductance to water vapor and leaf water potential for leaves of *Encelia farinosa* shrubs at different times during a growing season in Oatman, Arizona. Open circles represent plants with their neighbors removed and closed circles represent control plants. The vertical lines represent ± 1 SE

the differences in water relations parameters between the control plants and plants without neighbors still persisted. Leaf conductances reached midday values of 0.12 mol m^{-2} s^{-1} in plants without neighbors and 0.06 mol m^{-2} s^{-1} in the control plants. Throughout the day, leaf conductances were significantly higher in the plants without neighbors. Significant difference also existed in the leaf water potentials. Leaf water potentials reached midday minima of -5.06 and -4.56 MPa for the control plants and plants without neighbors, respectively, and were consistently different by approximately 0.5 MPa through the day.

As an estimate of seasonal activity rates, the maximum leaf conductance and midday leaf water potentials were compared between the plants without neighbors and control plants (Fig. 4). It appears from these data that precipitation was driving this system. Leaf water potentials increased in response to rainfall and decreased after the rains ceased. Leaf conductances consistently decreased with decreases in leaf water potential. The leaf conductances and leaf water potentials of plants without neighbors were always consistently higher than those of the controls. From these data, one might ask whether the relationship between leaf conductance and leaf water potential differed between the plants without neighbors and the controls. When the leaf conductance and water potential data from Fig. 4 were regressed against each other, there were no differences in the slopes of the relationships for the plants without neighbors and the control plants. Furthermore, the slope and intercept of the regressed relationship between leaf conductance and leaf water potential from Fig. 4 were the same as had been measured by Ehleringer and Cook (1984) for long-term laboratory-stressed plant material.

Standing leaf biomass differed between plants without neighbors and control plants. The plants without neighbors always had larger leaves as well as more leaves per twig than did control plants (Fig. 5). As a consequence of these biomass differences, even during February when the plants had the same leaf conductance, the plants without neighbors were fixing carbon at a higher rate, because of their greater biomass. Total canopy leaf area indices for the plant in February, 1982 averaged 0.99 ± 0.13 and 1.70 ± 0.19 for the control plants and plant without neighbors, respectively. The largest differences in productivity between the plants without neighbors and the control plants would have occurred late in the growing seasons (April–June), when the leaf conductance and canopy leaf area differences were greatest.

Although both sets of shrubs responded to drought by decreasing their leaf areas, the relationship between leaf area and leaf water potential differed between the plants without neighbors and the controls (Fig. 6). At any given leaf water potential, the plants without neighbors were able to maintain approximately three times more leaf area than the control plants. At first this may suggest that the water relations characteristics differed between the two sets of plants. This was not the case. More likely the data in Fig. 6 indicate that when the leaf water potentials and perhaps soil water potentials were equivalent, the plants without neighbors were able to draw water from a greater soil volume than could the control plants. As a consequence, the plants without neighbors were able to support a greater leaf area at any water potential than could the control plants. Leaves from both sets of plants were predicted to have abscised completely by a leaf water potential of
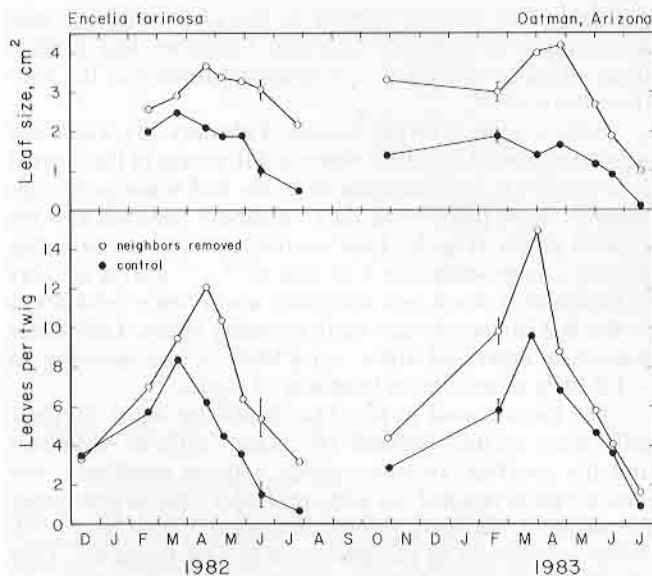

Fig. 5. Leaf size and the number of active leaves per twig as a function of time for *Encelia farinosa* at Oatman, Arizona. Open circles represent plants with their neighbors removed and closed circles represent control plants. The vertical lines represent ± 1 SE
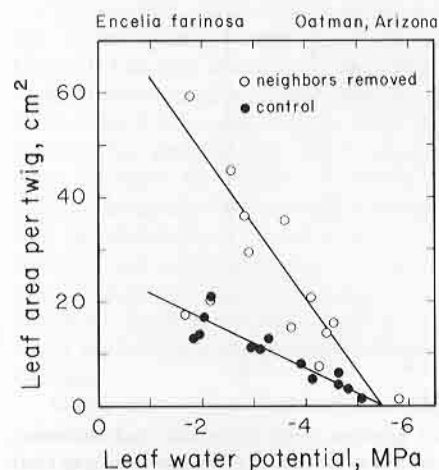

Fig. 6. The relationship between the leaf area per twig and midday leaf water potential for *Encelia farinosa* shrubs at Oatman, Arizona. The open circles represent plants with their neighbors removed and closed circles represent control plants. The relationship for plants with neighbors removed was area $= 77.4 + 14.1 \, \psi$, $r^2 = 0.86$, and for control plants was area $= 26.5 + 4.7 \, \psi$, $r^2 = 0.83$. These relationships are derived from data in Figs. 4 and 5

-5.5 MPa, which is quite similar to the point at which both leaf conductance and photosynthetic rate also intersect the x-axis (Ehleringer and Cook 1984). It is of interest to note that the first two data points (February and March 1982) for the plants without neighbors lie on the control curve. Undoubtedly, this indicates that at the beginning of the experiment productivity was similar in both sets of plants.

Growth measurements during the study were necessarily limited to parameters which could be measured with minimal effect on total plant biomass. Twig growth was used as an estimate of seasonal productivity. Twigs were subdivided into two categories (reproductive and nonreproductive). Flowering is located terminally in *E. farinosa* and

Table 1. Twig characteristics (leaf and reproductive structures not included) of *Encelia farinosa* shrubs with neighbors removed and control plants at Oatman, Arizona. Plants were sampled on July 15, 1983 and were in an inactive state. Data are $\bar{x} \pm 1$ SE

	Control	Neighbors removed
Biomass, g		
non-reproductive	0.12 ± 0.01	0.20 ± 0.02
reproductive	0.19 ± 0.02	0.62 ± 0.15
Kjeldahl nitrogen, mg g^{-1}		
non-reproductive	11.4 ± 0.8	11.3 ± 1.1
reproductive	7.6 ± 0.4	8.4 ± 1.1
Carbohydrate (TNC), %		
non-reproductive	25.9 ± 1.2	32.8 ± 2.5
reproductive	27.8 ± 1.3	30.6 ± 2.4

Table 2. Reproductive characteristics of *Encelia farinosa* shrubs with neighbors removed and control plants at Oatman, Arizona. Plants flowered each spring and plants were sampled during late flowering on April 23, 1983. Data are $\bar{x} \pm 1$ SE

	Control	Neighbors removed
Percentage twigs flowering	29.6 ± 5.5	79.8 ± 6.2
Flowers heads per twig	2.47 ± 0.11	3.77 ± 0.22
Achenes per flower head	39.7 ± 7.2	87.4 ± 8.5
Achenes per twig	98	329

typically not all twigs flower at once or during the same season. At the end of the growing season, the consequences of increased leaf biomass and increased gas exchange activity in the plants without neighbors were clearly evident in the twig biomass (Table 1). Reproductive twigs in plants without neighbors were three times larger than those from control plants. Similar trends existed for twigs which had remained vegetative, although the magnitude of the difference was less.

Substantial carbohydrate and nitrogen reserves are necessary for flowering and seed production. During flowering, these reserves are drawn from both stem and twig storage reserves (Ehleringer and Cook unpublished data). The data for the two sets of plants suggested that Kjeldahl nitrogen contents differed between twigs that flowered and those which remained vegetative. However, there were no differences in the nitrogen contents of flowering twigs between the two sets of plants or in the nitrogen contents of the nonreproductive twigs. There were no statistical differences in the carbohydrate contents of the four sets of twigs.

There were substantial differences in reproductive activity and these were related to the productivity differences between plants without neighbors and control plants (Table 2). A significantly greater proportion of the twigs in the plants without neighbors became reproductive (79.8% versus 29.6%). When these twigs went reproductive, the intensity of reproduction per twig was much higher in the plants without neighbors than in the control plants. Twigs in plants without neighbors produced 53% more flower heads per twig (3.77 versus 2.47), and 220% more achenes per flower head (87.4 versus 39.7) than did twigs in control plants. The consequence was that the reproductive activity per twig as measured by the total number of achenes produced was 3.4 times greater in plants without neighbors

Table 3. Biomass characteristics of *Encelia farinosa* shrubs used in the neighbor removal experiment at Oatman, Arizona. Samples for the initial and terminal measurements were collected in February, 1982 and November, 1983, respectively. Data are $\bar{x} \pm 1$ SE

	Control	Neighbors removed
Plant size (m^2)		
Beginning of experiment	0.215 ± 0.037	0.217 ± 0.010
End of experiment	0.228 ± 0.040	0.390 ± 0.037
Aboveground biomass (g)		
End of experiment	369.0 ± 67.9	690.6 ± 58.7

than in control plants. The percentage of achenes which matured was also greater in the plants without neighbors (83% versus 74%).

There were significant changes in plant size and aboveground biomass over the experimental period. Both control plants and plants without neighbors averaged the same size at the beginning of the experiment (Table 3). However, 16 months later at the end of the experiment, the control plants had increased an average 6% in area, while the plants without neighbors had increased 80% in area. The observed changes in plant area corresponded with the differences in aboveground biomass. At the end of the experiment, plants were harvested and the average dry weights were 369.0 and 690.6 g for the control plants and plants without neighbors, respectively.

Discussion

If plants were competing for limited amounts of water in this desert habitat, we would expect that the removal of surrounding plants would enhance water availability to the remaining plant. The removal of neighbors from monospecific stands of *Encelia farinosa* indeed results in a greater water availability as measured by leaf water potentials. These higher leaf water potentials are also associated with higher leaf conductances to water vapor at all times of the year, except during the wettest part of the growing season. Ehleringer and Cook (1984) have shown that the leaf conductance to water vapor is very tightly correlated with photosynthetic rate in *Encelia farinosa*. Thus, although photosynthetic rates were not measured in this study, it seems quite likely that photosynthetic rates were also higher in plants with their neighbors removed.

Since leaf area per twig was higher on plants with their neighbors removed, the total rate of carbon gain by individual twigs on these plants was also higher. This is the case even early in the growing season when leaf conductances to water vapor were similar on both control plants and those with their neighbors removed. From the data it appears that twigs from plants with their neighbors removed gained approximately three times as much carbon as those of control plants. It is not surprising that this also translated into a roughly three fold difference in reproductive output per twig as well. From these results, I conclude that intraspecific competition is occurring in monospecific stands of *E. farinosa*, and that as a consequence, the rates of carbon gain and reproduction per plant are reduced.

Previous investigations on the adaptive significance of leaf pubescence in *E. farinosa* have shown that both leaf photosynthetic rate and water use efficiency were enhanced by the presence of a dense pubescence layer, especially

under late spring and summer conditions (high air temperatures and reduced water availability) (Smith and Nobel 1977, Ehleringer and Mooney 1978, Ehleringer 1980). Whereas an increased photosynthetic rate has an immediate benefit to the carbon balance of the plant, an increased water use efficiency under soil-water limited conditions is only of benefit if other adjacent plants don't utilize this resource first. The results of the present study suggest that under most conditions, *E. farinosa* shrubs compete for limited soil water. Thus, it is likely that increased water efficiency *per se* is not selected for, but arises secondarily as a result of increased leaf reflectance (to reduce leaf temperatures). However, since individual sunlit leaves under water stress are light-saturated at moderate irradiances (Ehleringer and Cook 1984), individual plants may benefit from an enhanced leaf water use efficiency by being able to retain a larger fraction of the total leaf area.

Earlier studies of desert plants had inferred that intraspecific competition was occurring, presumably for water (Woodell et al. 1969, Yeaton and Cody 1976, Yeaton et al. 1977). More recently, Fonteyn and Mahall (1981) again inferred from observed regular plant distribution patterns that intraspecific competition was structuring *Larrea divaricata* (a long-lived evergreen shrub) populations. However, removal of surrounding *Larrea* shrubs had no effect on the leaf water potential of the remaining central shrub. They concluded that interspecific competition was occurring since removal of *Ambrosia dumosa* (a shorter-lived deciduous-leaved shrub) significantly improved water availability to *Larrea*.

The distribution of *Ambrosia dumosa* shrubs is clumped (contagious) as it is for *Encelia farinosa* in this study. However, based on leaf water potentials measured on plants in a removal experiment, Fonteyn and Mahall (1978, 1981) concluded that intraspecific competition for water was not occurring in this clumped-distribution species. Moreover, in contrast to the observations in this study, they observed that there was no correlation between plant size and distance. This is interesting in that *E. farinosa* and *A. dumosa* are both dominant shrubs in their respective desert habitats and share similar physiognomies and spatial distribution patterns. Yet in one species there is a clear indication that intraspecific competition is occurring, and in the other species there are no detectable intraspecific interactions.

Nobel (1981) investigated the distribution of *Hilaria rigida*, a common Sonoran Desert grass, and found a positive relationship between distance and size of the clump. However, his water relations studies did not show that competition for water was occurring between plants of *H. rigida*. Instead Nobel (1981) reported that transpiration was limited by the ground area occupied by roots such that clumps of various sizes transpired the same amount of water per unit ground area per day. More recently, Robberecht et al. (1983) have shown that if neighboring *H. rigida* clumps are removed, the water relations and productivity of the remaining clump are both improved.

Growth and productivity of *E. farinosa* are limited by low precipitation in their native habitat (Ehleringer et al. 1976, Ehleringer and Mooney 1983, Ehleringer 1984). The results of this study demonstrate that the presence of intraspecific neighbors further decreases water availability, and therefore productivity. As a consequence, reproductive activity, which is dependent on the rate of carbon gain, is further reduced.

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