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THE EFFECT OF NEIGHBORS ON ROOT DISTRIBUTION IN A CREOSOTEBUSH (*LARREA TRIDENTATA*) POPULATION[1]

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Abstract. We excavated and mapped the lateral extension of 32 creosotebush shrubs (*Larrea tridentata*) in the Chihuahuan desert of New Mexico to examine the effect of neighborhood interaction on root distribution. The smallest closed-angle polygon encompassing all roots of an individual was taken as a representation of its root system. Several geometrical characteristics of these polygons were measured and compared to interference vectors based on the location and size of the neighbors. We found that root systems were more developed away from the maximum competitive pressure of neighbors. Relation between root system shape and pressure from neighbors was stronger when the competitive vectors were integrating effect from all neighbors. Size of neighbors did not appear to contribute significantly to the relation. The resulting spatial pattern tended to reduce the overlap between neighboring root systems. Two conceptual models of root growth response to neighbors appear to explain our results. Both models assume that when the root system of neighbors meet, root growth is impaired or ceases at the zone of contact. In the non-overlapping, non-compensatory model, the decrease in root growth between two close neighbors is not compensated elsewhere, possibly affecting the overall plant performance. In the non-overlapping, compensatory model, a plant with a close neighbor responds by investing in root growth away from the competitive pressure or simply in zones free of neighbors. Under this model, two plants can be close to each other and not compete. Competition in the population is for space and only occurs when a plant root system is crowded on all sides.

Key words: competition; Jornada LTER; Larrea tridentata; neighborhood model; root competition.

INTRODUCTION

Creosotebush (*Larrea tridentata* [DC] Cov.) is one of the most widespread perennial plants in the southwestern deserts of North America (Barbour 1969). This evergreen xerophytic shrub is dominant over large areas and nearly pure stands are common. Field manipulations of soil resources showed that creosotebush is limited by both water and nitrogen availability (e.g., Ettershank et al. 1978, Cunningham et al. 1979, Sharifi et al. 1988, Lajtha and Whitford 1989). Thus, many researchers have suspected that intraspecific competition between neighboring shrubs for these scarce resources is intense.

Fonteyn and Mahall (1981) found that the water status of an individual creosotebush improves after removal of its neighbors. Shrubs in several creosotebush populations have been reported to be regularly distributed, apparently as a consequence of density-dependent mortality due to competition for water (Woodell et al. 1969, Fonteyn and Mahall 1981, Phil-

lips and MacMahon 1981, but see also Barbour 1973, Ebert and McMaster 1981). Others have attributed an inverse relation between the combined size of nearest neighbor shrubs and their distance apart to competition (Yeaton et al. 1977, Phillips and MacMahon 1981, Biehl 1984). These findings suggest that competition in creosotebush communities is a common phenomenon, intense enough to be detected.

The extent, size, and overlap of the root systems of neighboring individuals would appear to provide a good index of potential competitive interactions (Caldwell and Richards 1986). Creosotebush typically has a well-developed lateral root system, mostly superficial, extending far beyond the canopy (Chew and Chew 1965). Several root excavations of creosotebush individuals reported in the literature describe root distribution, branching, lateral extension, and biomass (Garcia-Moya and McKell 1970, Yeaton et al. 1977, Wallace et al. 1980, Biehl 1984). Other root excavations of creosotebush involve mapping of whole root systems, which provide a qualitative view of overlap between neighbors. For a single shrub growing on a desert bajada, Cannon (1911) found extensive overlap with the root systems of its neighbors; for one growing in a floodplain there was no overlap. Chew and Chew (1965) excavated and mapped 17 non-contiguous root systems and

FIG. 1. Monospecific stand of creosotebush on a bajada slope of Mount Summerford in the northern Chihuahuan desert.

describe "some overlap." For at least one individual, they found that roots seemed to be larger and grow farther in regions free of neighbors. Singh (1964) developed a rough map of the root system of 16 contiguous shrubs that shows very little overlap between neighbors; Ludwig (1977) excavated (but apparently did not map) 13 non-contiguous creosotebush shrubs near Singh's study site and observed similar qualitative patterns.

Does the spatial arrangement of the superficial roots of an individual creosotebush shrub reflect the long-term, integrated effects of competition with its neighbors? The aforementioned work provides some evidence to suggest this may be the case, but it is difficult to draw definite conclusions because of the qualitative nature of these data, which precludes the use of statistical inferences for hypothesis testing. The goal of this study is to quantitatively analyze the effect of neighbors on the spatial arrangement of root systems in creosotebush populations. We hypothesize that creosotebush roots are spatially arranged to reduce overlap with neighboring root systems. To test this hypothesis, we excavated shrubs and developed several indices of root system geometry that pertain to the relationship between the spatial arrangement of a shrub's root system and (1) the size and distance of its neighbors and (2) its interaction with the nearest neighbor alone vs. an integrated measure of interaction with all of its neighbors.

Study area

Our field work was conducted in the northern Chihuahuan desert on the Jornada Long Term Ecological Research (LTER) site, ≈ 40 km north-northeast of Las Cruces, New Mexico. Average annual precipitation, which is extremely variable, is 230 mm, with $\approx 52\%$ occurring during the summer months. Mean annual temperature is 15.6°C, and potential evaporation is 10 times greater than annual precipitation (Gile et al. 1981). During the summer of 1991 we established a 4 × 5 m

excavation plot on a bajada slope of Mount Summerford in a monospecific stand of creosotebush (Fig. 1). The soil is a loamy sand, classified as a Typic Haplargid of the Dona Ana series (Wierenga et al. 1987), with a hardpan calcium carbonate deposition layer (caliche) at 30–50 cm. We selected this site for the following reasons. (1) The shrubs were relatively small (≈ 1 m height, maximum) and since excavating and mapping are extremely labor intensive, this permitted a larger number of individuals to be excavated (32 shrubs total). (2) The shallow caliche hardpan limited the effective depth of soil available for root exploration, thus reducing the probability that the root systems of neighboring plants were at different depths. (3) Since the plot contained a single plant species, potential confounding effects of interspecific competition were eliminated. (4) This site is similar to one used by Singh (1964) in his excavation study of creosotebush ≈ 50 km south of the present site, thus permitting comparisons.

METHODS

Field measurements

The exact location of each plant in the plot, and those within 2 m outside the plot, was mapped and their height and cover measured. Over a two-mo period each of the 32 plants was excavated by hand, and all living roots larger than 2 mm were mapped as a projection onto an x–y coordinate system as illustrated in Fig. 2A. The roots mapped can be considered the more permanent part of the root system since smaller roots are generally temporary in nature, and their importance varies greatly in extent depending on the season and water availability (Eissenstat 1992). The aboveground portion of the excavated plants was collected, the dead branches were removed, and the remaining material was dried and weighed. A regression equation between cover and aboveground dry mass was determined using a zero-intercept, second-order polynomial model, as the one used by Ludwig et al. (1975). This equation allowed us to estimate the aboveground dry mass of individuals located just outside the plot, as needed in the neighborhood analysis.

Geometry of root system

Our analysis of the effect of interaction with neighbors on the spatial organization of root systems focuses on the symmetry of the root systems (Franco 1986). We assume that in the absence of neighbors, and in a relatively homogeneous area, the shape (i.e., horizontal extent) of the root system of an individual creosotebush should approximate a circle with the shrub in the center. We determined the actual shape of each excavated shrub's root system using the smallest closed-angle polygon that encompassed all roots (shaded area for shrub P_0, Fig. 2A). The center of this root system (C_0, Fig. 2A) is given as the centroid (center of gravity) of the polygon. To evaluate the discrepancy in the actual
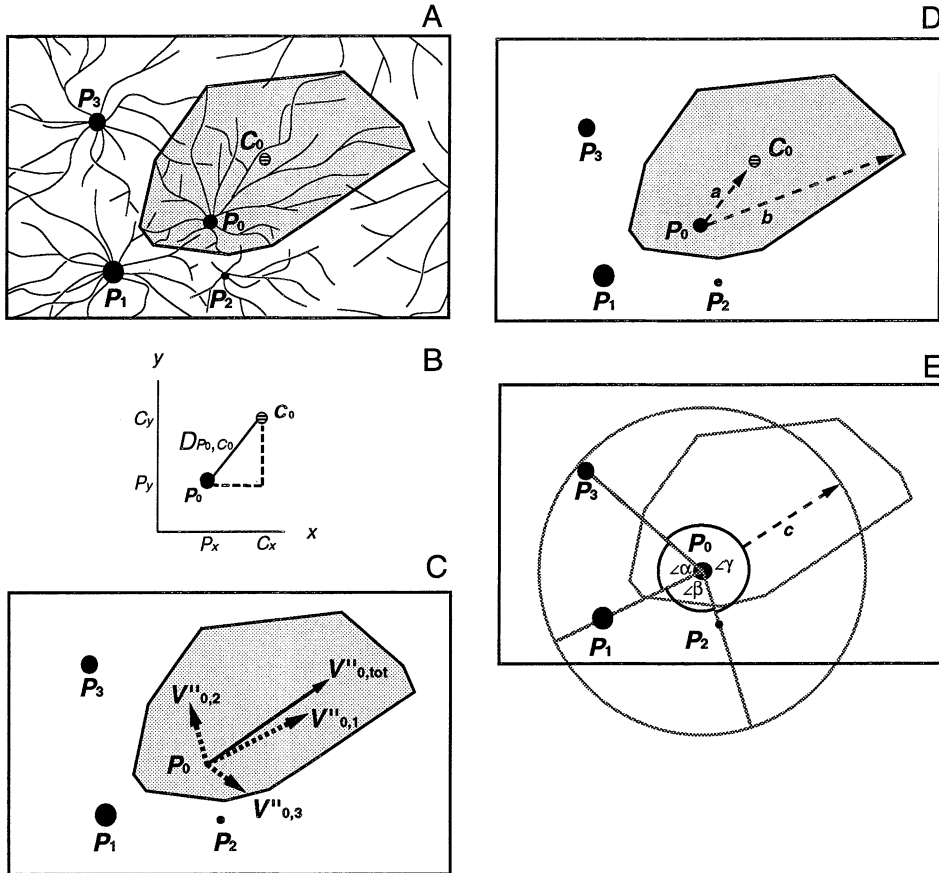
FIG. 2. (A) Determination of a root polygon from a map of root systems. The shaded area (root polygon of plant 0) is the smallest closed-angle polygon completely containing the root system of plant 0. C_0: centroid (center of gravity) of the root polygon of plant 0, taken as an estimate of the center of its root system; P_i: exact location of plant i, as defined by the location of its main stem. The root system illustrated has a displacement value of 0.668, and an eccentricity of 1.168. (B) Euclidean distance between points P_0 and C_0. (C) $V'_{0,i}$: competitive vector on plant 0 from neighbor i. $V'_{0,tot}$: total competitive vector on plant 0, as defined by the vectorial sum of the competitive vectors from each neighbor. (D) Main direction of root growth as estimated by (a) the direction from the main stem to the centroid of the root system and (b) the direction from the main stem to the most distant vertex of the root polygon. (E) c: central direction from the focal plant (P_0) to the greatest angle free of neighbors ($\angle\gamma$), in a circle of a given radius centered on P_0.

shape of the root system from a circular, centered one, we calculated displacement and eccentricity.

Displacement ("abcentricity" in Mead 1966) is a measure of how far the main stem of plant P is offset from the centroid of its root system, C (Fig. 2A), i.e.,

$$\text{displacement} = \frac{D_{P,C}}{S}, \quad (1a)$$

where $D_{P,C}$ is the Euclidean distance between points P and C (equal to $\sqrt{(P_x - C_x)^2 + (P_y - C_y)^2}$, Fig. 2B) and

$$S = \frac{\sum(\omega_i \cdot D_{C,\lambda_i})}{\sum(\omega_i)}, \quad (1b)$$

where λ_i is the location of the ith vertex of the polygon and ω_i is a weighting factor calculated as π minus the interior angle of the polygon at vertex i. Displacement

is 0 when the plant is at the centroid and, for a regular polygon, approaches 1 as the plant comes closer to a vertex of the polygon. Eccentricity ("eccircularity" in Mead 1966) is a measure of deviation of shape of the polygon from a circular outline, i.e.,

$$\text{eccentricity} = S\sqrt{\frac{\pi}{A}}, \quad (2)$$

where A is the area of the polygon. Eccentricity is always > 1, approaching one for a regular polygon as the number of sides increases (as the polygon becomes more like a circle), and increases (> 1) as the polygon becomes more elliptical.

Influence of neighbors on root geometry

We express competitive "pressure" from neighboring plants using vectors, where the length of a vector

represents the intensity of the pressure and its orientation represents the direction of the pressure. We use two formulas to compute a weighted vector length ($\text{len}[V]$) between an individual shrub and each of its neighbors. The competitive pressure on plant i by neighbor j is given by either

$$\text{len}[V_{i,j}] = \frac{1}{(D_{i,j})^2} \tag{3a}$$

or

$$\text{len}[V'_{i,j}] = \frac{W_j}{(D_{i,j})^2}, \tag{3b}$$

where $D_{i,j}$ is the distance between P_i and P_j. In vector V it is assumed that competitive pressure from neighbor P_j is inversely proportional to the square of its distance to P_i while in vector V' it is further assumed that competitive pressure is proportional to the neighbor's size. These assumptions are discussed in Weiner (1984). The total directional competitive "pressure" on plant P_i from its n neighbors is given respectively by $V_{i,\text{tot}}$ and $V'_{i,\text{tot}}$:

$$V_{i,\text{tot}} = \sum_{j=1}^{n} V_{i,j} \tag{4a}$$

$$V'_{i,\text{tot}} = \sum_{j=1}^{n} V'_{i,j}, \tag{4b}$$

which are vectorial additions (direction and length) of the competitive vectors of all neighbors of plant P_i (in Fig. 2C, for plant P_0, $V'_{0,\text{tot}} = V'_{0,1} + V'_{0,2} + V'_{0,3}$). Note that in Eq. 4a, the n neighbors are based on plants within 1.5 m of P_i, whereas in Eq. 4b, the n neighbors are based on $\text{len}[V'_{i,j}] > 200 \text{ g/m}^2$ but ≤ 2 m from P_i. Because the competitive pressure from a neighbor decreases with the square of its distance to the focal plant, the exclusion of more distant neighbors in the calculation of $V_{i,\text{tot}}$ and $V'_{i,\text{tot}}$ only slightly affects their value.

As a measure of total competitive pressure experienced by a plant, $V_{i,\text{tot}}$ and $V'_{i,\text{tot}}$ are conceptually different from commonly used interference indices. In neighborhood models, an interference index is used as a measure of competition in order to study the negative effects of neighbors on some measure of plant performance, such as growth or fertility (Weiner 1982, Pacala and Silander 1985, Leps and Kindlmann 1987, Bonan 1988). It can be as simple as being equated to the number of neighbors within a radius from a focal plant or calculated as an arithmetic sum of the competitive contribution from all neighbors regardless of the location of each neighbor relative to one another. An interference index with a large value means that a plant may experience strong competition, which may then be reflected in its performance. Since our goal is to study the influence of interaction with neighbors on the geometry of a plant root system, as opposed to plant performance, our competitive vectors are in-

tended to reflect the asymmetry in competitive pressure rather than an absolute pressure. A large value of $\text{len}[V_{i,\text{tot}}]$ or $\text{len}[V'_{i,\text{tot}}]$ suggests the presence of strong competition from a particular direction in space, and thus the geometry of the root system is likely to deviate from a centered, circular one. On the other hand, if neighbors of equal competitiveness are regularly distributed around a shrub, the individual vectors will cancel each other and the length of $\text{len}[V_{i,\text{tot}}]$ and $\text{len}[V'_{i,\text{tot}}]$ will be small, although the arithmetic sum of competitive pressure from neighbors may be large.

To examine whether there is a relationship between the intensity of competitive pressure and the shape of a plant root system, we tested for a positive correlation between length of various competitive vectors and the displacement or eccentricity of root polygons, using a one-sided t test. We also compared the direction of the competitive vectors with direction of root growth. The direction from the center of the plant to the centroid of its root system was taken as a measure of the main direction of root growth (direction a in Fig. 2D). Statistical inferences were determined using analysis of circular data (Batschelet 1981). Using direction from a focal plant to the center of its root system as the zenith, the angle to the orientation of competitive pressure was measured. For each plant, a vector of length equal to unity and of direction equal to this angle was determined and the mean vector (sum of the 32 vectors divided by 32) was calculated (the use of the "mean vector" in the statistical analysis of direction should not be confused with our use of vectors to express competitive pressure). The length of the mean vector, always between 0 and 1, gives an indication of a preferential direction of the 32 vectors. A small mean vector indicates that the 32 vectors point in any direction in relation with the direction of root growth, suggesting no relation between the two. The closer the mean vector is to unity, the larger the probability of a preferential direction. Statistical significance is determined by the Raleigh test (Batschelet 1981). If the mean vector is significant, its orientation expresses the central tendency in the relation between direction of root growth and competitive pressure. If we suppose that a plant should have its root system mostly developed away from the zone of maximum competitive pressure (i.e., in the same direction as the competitive vector), the expected difference between the two vectors (i.e., the orientation of the mean vector) should be 0°. Statistical difference from the expectation, which changes with mean vector length, is based on charts published in Batschelet (1972 and 1981).

Using the same approach of comparisons of directions, we tested whether the main orientation of root growth was directed toward zones free of neighbors (as defined by the location of their main stem), independent of the exact distance or size of its actual neighbors. We established a circle around each plant (Fig. 2E), determined the largest arc of circle free of neighbors

($\angle\gamma$ in Fig. 2E), and considered the center of the arc as the main direction free of neighbors (direction c in Fig. 2E). Since the radius of the circle may strongly affect the result, we performed the analysis using circles of three different radii: 1.0, 1.5, and 2.0 m. Lastly, as a surrogate to direction to centroid as a measure of the direction of root growth, we used direction from the plant to the most distant vertex of the root polygon, which is also the most distant root tip (direction b in Fig. 2D), and compared it with the various direction of competitive pressure.

Determination of root system overlap

To estimate the amount of overlap of root polygons within the boundary of the plot, we measured the proportion of surface of the plot unoccupied by root polygons, the proportion with no overlap (one root polygon only), and the proportion of surface having from two overlapping root polygons up to six. This measure is imperfect since, on the one hand, the way root polygons are determined tends to overestimate root overlap, and on the other hand, roots coming from plants located outside the plot are unknown, which decreases the estimate of the overlap. However, this measure is a useful relative index when compared with the amount of overlap that would result if each plant had a circular, centered root system with the same surface area (see Fig. 5).

RESULTS

Cover and dry mass

Cover of an individual shrub varied from 8.0×10^{-3} to 1.28 m², with an average of 0.33 ± 0.29 m² (mean $\pm$ 1 SD). Most shrubs had one to several dead branches. Aboveground dry mass (living branches only) of the 32 shrubs excavated ranged from 10.1 to 948.2 g, with an average of 256.9 ± 241.5 g. The relation between cover (C) and dry mass (DM) is given by:

$$DM = 722.7C + 122.08C^2 \quad (R^2 = 0.749).$$

Creosotebush reproduces vegetatively by axis-splitting as it matures (Vasek 1980). There was no evidence of axis-splitting in our excavated shrubs, probably because of their small size.

Root geometry

In the majority of shrubs, a few major roots (plus several smaller roots) extend to a depth of 0.15–0.30 m and then sharply diverge horizontally in all directions. Usually this change in direction occurs before the roots reach the underlying caliche hardpan. On average, roots extend 0.5–1 m horizontally from the main stem, with a maximum of 2.1 m, before dividing into rootlets smaller than 2 mm diameter. Roots have few ramifications, and the diameter appears to remain constant between two nodes. When projected on a two-
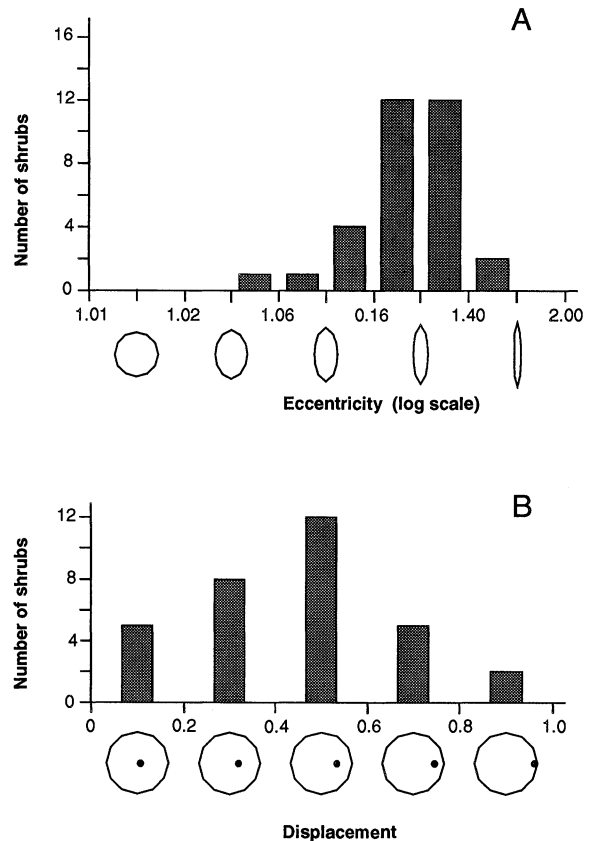

FIG. 3. (A) Eccentricity values of the root polygons. Note that the eccentricity axis is in a log scale to better represent a gradual elongation in shape. (B) Displacement values of the root polygons.

dimensional map, root systems of neighboring shrubs occasionally overlap, contrary to Singh's map (1964).

The shapes of the root system of the shrubs in this plot are diverse. Values of eccentricity varied from 1.06 to 1.43 (Fig. 3A). The root systems are often displaced relative to the location of the main stems, with displacement values varying from 0.09 to 0.98 (Fig. 3B). We found no correlation between competitive pressure from individual neighbors and the displacement of a root system (Table 1). However, displacement is correlated with magnitude of the total competitive vectors V'_{tot} ($P < 0.05$), and the correlation with V_{tot} is just above the limit of significance level. In fact, inclusion of the size of the neighbor in the calculation of the competitive vector barely improves the correlation with displacement, compared to the vector taking into account only distance to neighbor ($t = 1.80$, $P = 0.041$ for V'_{tot} compared with $t = 1.61$, $P = 0.059$ for V_{tot}). There is no correlation between competitive pressure and eccentricity, except for a positive correlation with the third competitor ($t = 2.14$, $P = 0.021$); we have no ecological interpretation for this correlation.

There are significant correlations between the direction of root growth and all measures of competitive

TABLE 1. Correlation between displacement and eccentricity of root polygon, and length (len) of competitive vectors.

Competitive vector†	Displacement	Eccentricity
$len[V_{i,1}]$	0.115	0.093
$len[V_{i,2}]$	0.047	0.086
$len[V_{i,3}]$	−0.047	0.163
$len[V_{i,tot}]$	0.283	−0.010
$len[V'_{i,1}]$	0.283	0.107
$len[V'_{i,2}]$	0.030	−0.090
$len[V'_{i,3}]$	−0.018	0.364*
$len[V'_{i,tot}]$	0.312*	0.095

* $P < 0.05$ (t test, one-sided).

† Ordered according to decreasing length: for plant i, $V_{i,1}$ is the competitive vector from the neighbor j resulting in the largest $1/(D_{i,j})^2$ (i.e., the nearest neighbor of plant i), while $V'_{i,1}$ is the competitive vector from the neighbor resulting in the largest $w_j/(D_{i,j})^2$.

FIG. 4. Root system overlap expressed as the proportion of surface covered by a certain number of root systems.

pressure from neighbors (Table 2). In every case, the directions are the same, i.e., the angle of the mean vector is never significantly different from 0°. Correlations based on competitive pressure from all neighbors are always stronger than competition from any individual neighbor. Including neighbor size in the calculation of the competitive index only slightly improves the correlation with total competitive vector. The correlation with the main direction free of neighbors was greatest with a neighborhood of 1.5 m of radius.

There are also correlations between direction to the most distant root tip and most directions of competitive pressure (Table 2), although these correlations are always smaller than between direction to polygon centroid and competitive pressure. In all but one case these correlations are also related to a direction not significantly different from 0°.

These interactions of root growth with neighbors affect the amount of overlap in root systems (Fig. 4). The proportion of the surface area of the plot occupied by a single root system (no overlap) is almost twice as much as if the same root systems were circular, centered on the plant. Most overlap in root polygons involves no more than three plants. More extensive overlap (four plants or more) would be 5 times more important if the root systems were circular (Fig. 5). Also, the excavated root systems seem to better utilize the available area, leaving 4 times less surface area unoccupied by any plant than if they were circular (Fig. 4).

DISCUSSION

Our results demonstrate that competitive interactions with neighbors affect the spatial arrangement of root systems in creosotebush. The reduction in root system overlap suggests that competition for resource in creosotebush is primarily through competition for available belowground space. In contrast, interspecific
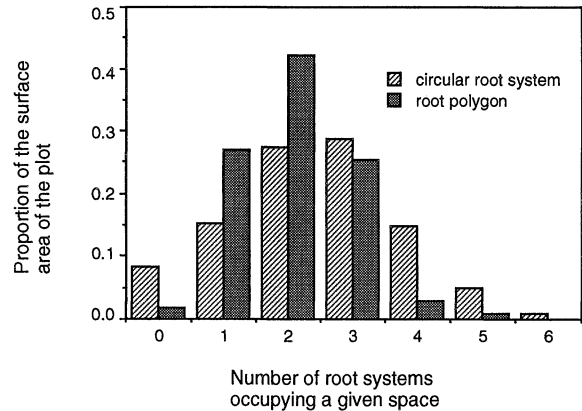
interaction has been frequently shown to involve extensive intermingling of root systems (Caldwell and Richards 1986). The spatial arrangement of the root system is the complex result of the interactions with several neighbors rather than with the nearest neighbor alone. Initially, we expected a larger neighbor to have a greater effect than a smaller one, but inclusion of size of neighbors along with distance in the computation

TABLE 2. (A) Relation between main direction of root growth (from location of main stem to root system centroid) and various directions related to neighbors. (B) Relation between direction to most distant root tip and various directions related to neighbors.

	A) Main direction to root growth		B) Direction to most distant root tip	
	Mean vector length†	Mean vector angle‡ (°)	Mean vector length†	Mean vector angle‡ (°)
$V_{i,1}$	0.372*	12	0.243	24
$V_{i,2}$	0.404**	17	0.279	8
$V_{i,3}$	0.323*	22	0.236	61
$V_{i,tot}$	0.618***	18	0.381**	23
$V'_{i,1}$	0.345*	21	0.235	10
$V'_{i,2}$	0.375**	12	0.312*	31
$V'_{i,3}$	0.324*	43	0.317*	70*
$V'_{i,tot}$	0.647***	12	0.448**	15
Free angle (1.0 m)§	0.491***	24	0.391**	26
Free angle (1.5 m)	0.658***	28	0.452***	21
Free angle (2.0 m)	0.543***	16	0.406**	10

* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

† Raleigh test. The size of the mean vector is indicative of the relation between the two directions. The Raleigh test provides the probability that the length of a vector is greater than 0.

‡ Probabilities is that the mean angle is different from 0° (i.e., that the two directions are the same) according to charts from Batschelet (1972, 1981). This probability was calculated only when the mean vector length was significantly greater than 0. Mean vector angles that were not tested are in italics.

§ Central direction of the largest arc free of neighbors. Length in parentheses corresponds to the radius of the circle used in the analysis.

A

B

C

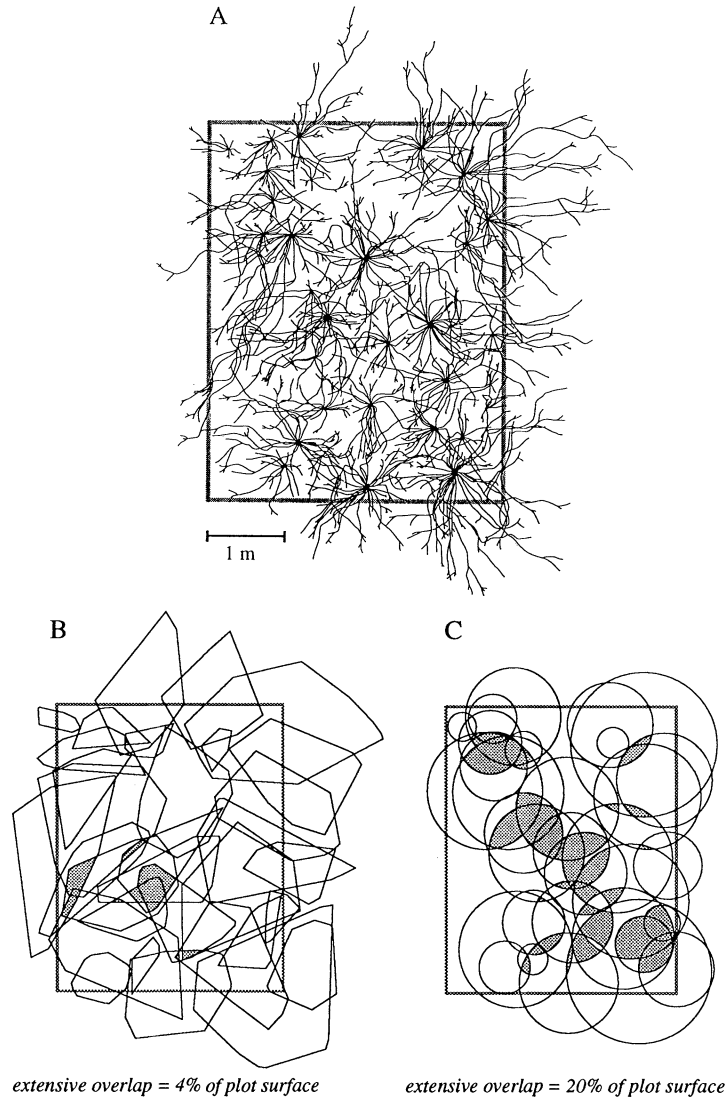*extensive overlap = 4% of plot surface*   *extensive overlap = 20% of plot surface*

FIG. 5. (A) Map of excavated root systems. The large rectangle represents the plot border. (B) Map of root polygons. The shaded area represents the surface where there is extensive overlap (at least four root polygons). (C) Map of hypothetical root systems: circular in shape, centered on the plant location and of surface area equal to their corresponding root polygon. The shaded area represents the surface where there is extensive overlap (at least four root systems).

of competitive pressure did not significantly improve correlations with plant responses. When branch dieback and herbivory are important, as it seems to be the case in our population, aboveground size may be a poor measure of the long-term competitive effects of neighboring plants.

Because excavation and detailed root mapping of a large number of shrubs are labor intensive and very time consuming, we purposely chose a population of relatively small individuals, similar to the one excavated by Singh (1964). We assume that the patterns we found apply to the more general case of larger individuals.

We present two conceptual models to explain the spatial arrangement of root systems found in our study.

We assume that the ability of a plant to obtain resources is related to the surface area explored by its root system so that a plant of a certain size, in absence of neighbors, has a root system of a specific area in order to reach optimum growth. We also assume that for an individual growing in isolation in a homogeneous site, roots will grow radially in all directions, so that the root system will be circular with the plant in the center (Fig. 6A). With non-compensatory plants (Fig. 6C), root growth in all directions is fixed except that when the root system of neighbors meet, growth is impaired or ceases at the zone of contact. The root system shows displacement away from the competitive pressure. As a result of the interaction, the total area of the root system is reduced, possibly slowing the

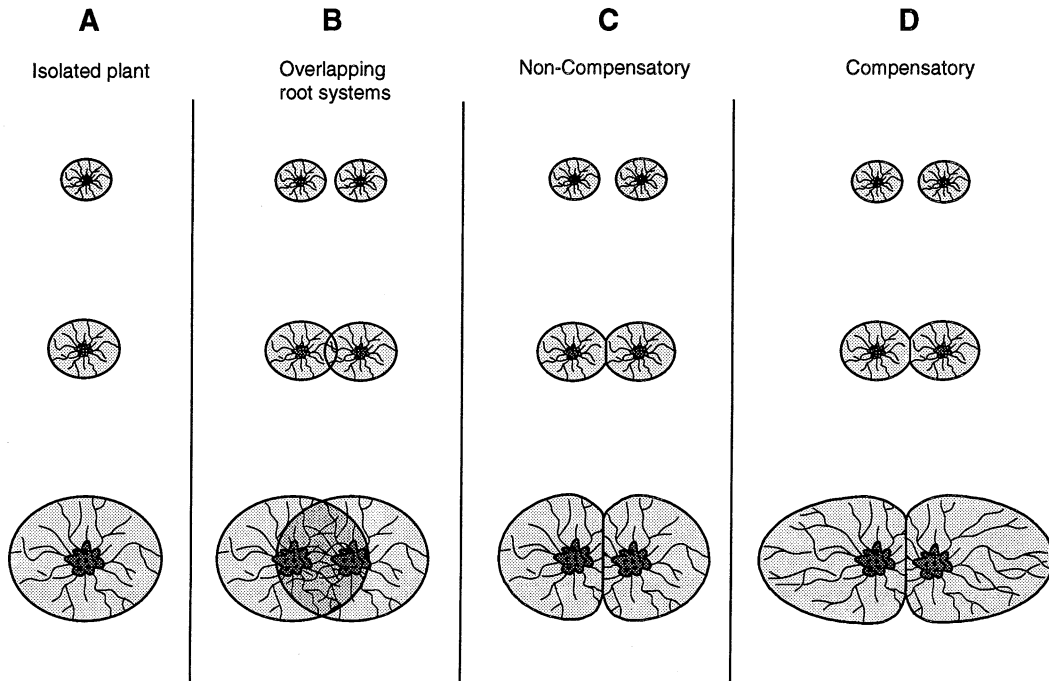| **A**	**B**	**C**	**D**
Isolated plant	Overlapping root systems	Non-Compensatory	Compensatory

FIG. 6. Conceptual models of root growth response to interaction with a neighbor. (A) Plant grown in isolation. In absence of neighbors, its root system grows to optimal size. (B) Overlapping root systems. (C) Non-compensatory model: deficit of roots at zone of contact is not compensated, so that overall surface area of the root system is reduced compared with the optimal size, possibly affecting plant performance. (D) Compensatory model: deficit of roots at zone of contact is compensated by growth in region free of neighbors. The surface area of the root system stays optimal despite the proximity of the neighbor.

growth of the plant and its overall performance. The closer the neighbor, the more negative the effect. The non-compensatory model is consistent with several concepts in competition theory: the inverse correlation between distance between neighbors and their combined size, or any predictions based on the concept of "area of influence."

With compensatory plants (Fig. 6D), growth is also inhibited where the root systems meet. However, the plant responds by investing in root growth away from the competitive pressure, or simply in zones free of neighbors, resulting in displacement away from the competitive pressure. In contrast with non-compensatory plants, the volume of soil explored by the plant is the same as if the plant was isolated, and the interaction with the neighbor does not translate into a decreased performance: two plants can be close to each other and not compete. Competition in the population is for space and only occurs when a plant root system is crowded on all sides. In the compensatory model, the advantage to the plant is obvious: it can partially escape the fate of a sessile organism by selectively growing its roots in areas free of competition. There is not necessarily an inverse correlation between distance to nearest neighbor and size, and consequences for population attributes like spatial distribution remain unclear.

Both non-compensatory and compensatory models

suppose that root growth is impaired at the zone of contact between neighboring root systems. This is supported by a recent experimental study showing that growth of roots of two neighboring creosotebush seedlings, grown in pots, ceases when they come into proximity, presumably due to the effect of chemical compounds released in the soil (Mahall and Callaway 1991). Because of this response, overlap between active parts of the root system of neighboring plants should be reduced. The fact that we found a significant amount of overlap of root polygons in our population may only reflect the inaccuracy of our measure of occupation of space. While closed-angle root polygons are very simple to determine and give a good estimate of the relative shape and size of the area of influence of a plant, they tend to overestimate the surface occupied and, consequently, the overlap between neighbors. An open-angle polygon would more closely follow the outline of the root system but would greatly complicate the analysis. Also, our measure of the partitioning of space is two dimensional, when in fact the nature of root exploration is three dimensional. Lateral roots occur in a narrow range of depth in our population, a situation also reported elsewhere for creosotebush (Singh 1964, Chew and Chew 1965). However, some of the roots that appear to overlap when projected on a map are, in fact, vertically separated by 10 cm or more. Mapping and analyzing root systems as volumes rather

than surfaces would be more accurate but again would represent a formidable task. Despite the limitation in our representation of root systems, we found much less overlap than expected, in support of the two models. We should note, however, that we did occasionally find roots of different shrubs very closely overlapping, as Cannon (1911) also observed, a situation that may occur when young active roots cross older less active roots.

The difference between the two models is in the response in root investment in regions free of neighbors. This distinction may translate into significant differences in spatial and size patterns in creosotebush populations. The inverse relation between distance of two neighbors and their combined size in creosotebush populations (Yeaton et al. 1977, Phillips and MacMahon 1981, Biehl 1984) and the occasional regular distribution reported (Woodell et al. 1969, Fonteyn and Mahall 1981, Phillips and MacMahon 1981) favor the non-compensatory model, although they are not necessarily inconsistent with the compensatory model. On the other hand, it is common in creosotebush populations to find very close individuals that are apparently thriving well, which is more consistent with the compensatory model.

In theory, it should be possible to distinguish between these models by the study of the spatial organization of the root systems of neighboring plants. As shown in Fig. 6, the size and displacement of a root system are larger in the compensatory model, for a given distance apart and plant size. Unfortunately, it appears impossible to differentiate between the models using excavation data of plants grown in natural conditions. Other factors, such as grazing or soil heterogeneity, may also affect root system sizes. Multiple interactions further complicate the situation. One way to test the models would be to grow pairs of neighbors of the same age at varying distances apart under tightly controlled conditions (e.g., Solangaarachchi and Harper 1989). It should also be noted that these two models do not necessarily represent two absolute and conflicting processes, but rather two opposite ends of a continuum. A plant may show plasticity in root investment in response to interaction with neighbors (as in the compensatory model), but by doing so it may have to pay a physiological cost that reduces its overall performance (as in the non-compensatory model). The question remains as to where in this continuum the real plant response exists. We are presently developing a neighborhood model that simulates competitive interaction according to both our non-compensatory and compensatory models, in order to evaluate their respective effect on plant population attributes such as spatial and size distribution.

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