

Asymmetrical growth of the crowns of neighbouring desert shrubs

Garry F. Rogers*

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To study the influence of nearest neighbours on the geometry of crown growth I calculated the difference between the distances from the centres of the base and crown of a plant to the base centre of the nearest neighbour. The calculations were replicated in two populations of the desert shrub *Ambrosia deltoidea* [(Torr.) Payne]. In both, the difference was positive, indicating that neighbouring plants grew apart. As a consequence, the dispersion of crown centres was greater than the dispersion of base centres. Also, the correlation of proximity and summed sizes of nearest neighbours was greater when proximity was measured between crown centres rather than base centres. Least squares regression analysis indicated partial dependence of the difference between base- and crown-centre distance on neighbour size and proximity. Previous studies of the dispersion of desert shrubs that used nearest-neighbour crown-centre distances might have erroneously concluded that greater dispersion of larger plants was due to proximity-dependent mortality when it was actually due to asymmetrical crown growth.

Introduction

Observation of almost any patch of plants shows that neighbours grow away from one another (Harper, 1985). Numerous studies of plant competition that used one-time observations of spatial pattern and plant size have suggested that greater distance between large plants was due to mortality of near neighbours (e.g. Phillips & MacMahon, 1981; Yeaton *et al.*, 1985; McCanny & Cavers, 1987). Alternative explanations are usually discussed (e.g. Wright & Howe, 1987), but asymmetrical growth of plant crowns has not been considered. If the distance between plants is measured between crown centres rather than base centres, then asymmetrical growth of neighbours away from one another would increase the distance between them. The resulting increased dispersion of large plants might be interpreted to be a result of density-dependent mortality. This mistake is independent of errors in distinguishing ramets and genets (Ebert & McMaster, 1981; King & Woodell, 1987), and it is not avoided by analyzing the dispersion of circles rather than points (Simberloff, 1979; Cox, 1987). I test for asymmetrical crown growth using two sets of observations of naturally occurring populations of desert shrubs, and I evaluate effects of asymmetry on the dispersion and correlation of distance and summed size of nearest neighbours.

*2997 S. Connor St., Salt Lake City, UT 84109, U.S.A.

Materials and methods

Asymmetrical growth was evaluated using observations of *Ambrosia deltoidea* [(Torr.) Payne], a perennial shrub that typically lives less than 100 years (Goldberg & Turner, 1986), and that is common and sometimes dominant throughout the Arizona Upland subdivision of the Sonoran Desert (Shreve & Wiggins, 1964). *Ambrosia* crowns are usually oblate ellipsoidal or hemispherical, less than 1 m³ in size, and are composed of numerous thin, woody shoots radiating from a meristematic cushion at or near the ground surface. Smaller shoots tend to be unbranched, and larger shoots reach 5th or 6th order wherein the diameter of the shoot system exceeds its length. The branching pattern is simple dendritic with branching angles of about 45°. Flowers appear near the ends of almost all branches. Above-ground modules are short lived, and throughout the plant's life dead leaves and shoots are abundant in the crown. Crown shape appears to be influenced by solar azimuth, and better performance of modules on south sides of crowns of plants grown apart from neighbours results in a small southerly shift of crown centres.

To measure directional plant growth relative to nearest neighbours, I used a geometric reference framework defined by the axis joining the two landmarks provided by the base centres of a plant and its nearest neighbour. The two members of nearest-neighbour pairs of plants are referred to as the *object plant*, the plant from which measurements were made to find the nearest neighbour, and the *neighbour*. The response of the object plant to the neighbour is defined as the difference between the distances from the object plant base and crown centres to neighbour base centre. This measure is referred to as *DVAS*. Centres are found for polygons formed by projecting base and crown outlines onto a two-dimensional plane (Zarkos & Rogers, 1987). The measure responds to divergence of the object plant's crown centre from its base centre when the divergence changes the distance to the neighbour base centre.

Observations were made in two permanent quadrats located near the base of Tumamoc Hill, the site of the former Carnegie Institution's Desert Laboratory in Tucson, Arizona, U.S.A. Observation differed for the two quadrats. In one, bases and crowns were mapped on graph paper using tape measures, and in the other an electronic distance measurer was used to obtain polar coordinates for the base centres and perimeters of plant crowns. The first quadrat is approximately 100 m², and the second is 50 m². The plots are protected from livestock grazing, but rodent herbivory might sometimes occur. Rodent herbivory was not mentioned by the surveyors when the first quadrat was mapped, and evidence of herbivory was not found when plants of the second quadrat were measured.

The data for the first quadrat consists of a map (scale = 1:39) of 248 *Ambrosia*, 41 of which are rooted outside the quadrat. Population dynamics within the plot are described by Goldberg & Turner (1986). Eighteen *Ambrosia* had nearest neighbours of other species. *Ambrosia* crowns covered 20.9 m² within the quadrat, and other species covered 6.9 m². The field methods used to map the quadrat are described by Goldberg & Turner (1986). A 1-m grid of tape measures was used as a guide while transferring crown outlines and base positions to graph paper. Convex arcs were used to connect points along crown outlines, and this would have tended to obscure *DVAS* whenever straight boundaries were longest on the same side of a crown as the nearest neighbour. I calculated area using measurements of major and minor crown axes in the standard formula for an ellipse. Crown centre locations were found using averages of visual estimates made by two observers.

The second quadrat was established to provide a more accurate set of observations. Polar coordinates for crown outlines and base centres were recorded directly using a Nikon electronic distance measurer (EDM), model number NTD-4. The EDM was placed near a level site dominated by *Ambrosia*, and coordinates were obtained by aiming the EDM at a reflecting prism held directly above (using a bubble level) points on crown perimeters and base centres. Crown-perimeter points were chosen so that no portions of the true crown margin were farther than 4 cm from imaginary lines connecting each point. This produced a total of 3 to 8 points for each crown outline. For analysis, polar coordinates were

transformed to rectangular coordinates, and crown area and centre of mass of each plant was found using a Stokes' Theorem transformation of the appropriate surface integrals to line integrals on the crown perimeters. Compass bearings of the quadrat boundaries were used in converting interplant polar coordinates to obtain compass directions from the object plant base centre to its crown centre and to its neighbour's base centre. Plants were larger in the second plot than the first, and total cover was 18 m².

Plants rooted outside the boundary of the second quadrat, or nearer the boundary of the first quadrat than another plant, were not used as object plants because their nearest neighbours might not have been recorded. I also excluded *Ambrosia* plants having nearest neighbours of other species, plants having crown margins farther than 10 cm from their nearest neighbour's crown margin, and plants separated from their nearest neighbour by the crowns of other plants. *Ambrosia* crowns appeared to respond to other species, but interspecific pairs were not numerous and were excluded to simplify interpretations.

Predictions

The following predictions were tested using statistical methods: For plants whose crowns are close enough to influence one another either by physically training and pruning one another's modules, or by altering essential resource distributions in the space available to each other's modules, *DVAS* should increase with the size of the nearest neighbour, and the increase should be greatest when base-centre distance is small. As asymmetrical growth occurs, the distance between crown centres will increase while base-centre distance remains fixed. Thus, the dispersion of crown centres will be greater than base centres (cf. Ishizuka, 1984), and the correlation between summed sizes and distance between nearest neighbours, a technique used to test for competition (Pielou, 1960; Phillips & MacMahon, 1981), will be greatest when distance is measured between crown centres.

Statistical analysis

Using *DVAS* to measure above-ground interaction requires knowledge of compass directions. Directional factors such as solar azimuth, wind and frost can influence both crown growth and the location of establishment of neighbour plants. The coordinate system I used was directional, enabling randomness tests for the directions of displacement of crown centres from base centres, and of the direction to neighbours. To distinguish the influence of neighbours from other factors, the compass directions to neighbours must be random (uniform). I used the Rayleigh test (Davis, 1986) for uniformity and modality of the directions between object-plant base and neighbour-base centres. The test presumes that the directions are not bimodal. Visual inspection of the data indicated that they were not, and no plausible reason for bimodality could be imagined. The Rayleigh test indicated that within the *Ambrosia* populations studied, neighbour-base centres were randomly distributed about object plant base centres ($p < 0.001$). A comparison of directions to the nearest neighbour and to additional neighbours showed they were not the same, indicating that *DVAS* is a measure of response to the nearest neighbour.

Regression was used to test the predictions that *DVAS* was independent of object plant size and dependent on neighbour proximity and size. I used crown area to represent size, and the distance between object plant and neighbour base centres to represent proximity. Thus, multiple regression was performed using area and distance as independent variables to predict *DVAS*. The variables' size and proximity are not independent (Phillips & MacMahon, 1981). For additional regression analysis a composite independent variable was created by dividing neighbour size by the square of base-centre distance. Use of this

ratio to predict *DVAS* does not violate the assumptions of least squares regression (Zar, 1984). Also, it seems appropriate because of the exponential increase of crown area in contact as the distance between the plants decreases linearly (imagine the changing area of the intersecting plane between two spheres merging into one another). I also performed regressions using nearest-neighbour size over distance unsquared, and achieved almost identical results.

The density of plants rooted in the quadrats ($2.1/m^2$ for both quadrats), was used to calculate *R*, the nearest-neighbour statistic (Clark & Evans, 1954). *R* was used to test the idea that the centres of plant crowns are farther apart than their base centres (cf. Ishizuka, 1984). This was done by comparing *R* calculated for nearest neighbours determined by the distance between base centres, with *R* calculated for nearest neighbours determined by the distance between crown centres. I also compared correlation coefficients (Zar, 1984: 313, 320) calculated for the same two groups of nearest neighbours to test the idea that the correlation of summed sizes of nearest neighbours and distance (Pielou, 1960; Yeaton *et al.*, 1985) increases when distance is measured between crown centres rather than base centres. Spearman's correlation coefficient was used for the comparisons because size and distance were not normally distributed, and transformations (Zar, 1984) were ineffective in correcting this. Although the data from the two quadrats do not represent random observations of *Ambrosia*, statistical significance is reported for comparative purposes.

Results

DVAS was approximately normally distributed for both plots (Table 1). It was not dependent simply on growth. As regression showed, its dependence on object plant size was too small to be measured for either quadrat.

The dimensional nature of *DVAS* permits the use of least squares regression analysis to measure neighbour influences. The regression models using nearest-neighbour area over squared distance predicted 10% of the variation of *DVAS* for the first quadrat and 24% for the second quadrat (Table 2). Part of the increase of *DVAS* (Table 2) might be due to more

Table 1. Statistical characteristics of *DVAS* in the two quadrats, and *t*-test of the null hypothesis that the mean value was zero. The distribution of values in both quadrats was considered sufficiently normal for regression analysis

Quadrat	<i>N</i>	<i>X</i> (cm)	<i>t</i>	SD	range (cm)	Skew	Kurtosis
First (map)	121	4.0	8.94***	0.05	29.0	0.82	0.68
Second (EDM)	67	9.0	9.03***	0.08	39.0	0.42	0.30

*** $p < 0.001$.

Table 2. Results from regression analysis with *DVAS* entered as dependent variable, and the ratio of neighbour size (m^2) over the square of distance (m) between base centres as independent variable

Quadrat	Model	R^2	<i>F</i>	<i>p</i>
First (map)	$0.01 + 0.07 \text{ size/distance}^{2***}$	0.10	13.0	0.0005
Second (EDM)	$0.05 + 0.01 \text{ size/distance}^{2***}$	0.24	21.0	0.0001

*** $p < 0.001$.

Table 3. Values of the nearest-neighbor dispersion index (R) for distances (m) measured between base centres and crown centres (r_A = actual mean distance; r_E = expected mean distance)

	N	r_A	r_E	R
Distance measured between base centres				
First (map)	121	0.31	0.35	0.90*
Second (EDM)	67	0.31	0.35	0.88 ^{NS}
Distance measured between crown centres				
First (map)	121	0.35	0.35	1.00 ^{NS}
Second (EDM)	67	0.40	0.35	1.16**

^{NS} $p > 0.05$; * $p < 0.05$; ** $p < 0.01$.

Table 4. Coefficients of Spearman rank-order correlations (R_s) of summed cover of pairs of nearest neighbours with distances measured between base centres and between crown centres

	N	R_s Distance between base centres	R_s Distance between crown centres
First (map)	121	0.58***	0.66***
Second (EDM)	67	0.60***	0.79***

*** $p < 0.001$.

accurate measurements in the second quadrat; as mentioned earlier, the use of convex arcs for mapping the first plot would have tended to obscure DVAS. The most likely cause, however, was the greater total cover in the second quadrat which increased the contacts between crowns. Plots of residuals showed that the assumptions of homoscedasticity, normal error distribution, and error means of zero were met for each model.

The dispersion index (Clark & Evans, 1954) increased when measurements were made between crown centres rather than base centres (Table 3). As Ishizuka (1984) observed among forest trees, dispersion shifted toward regularity when distance was measured between crown centres. Also, when distance between crown centres was used, the correlation of summed size and distance increased substantially (Table 4). These results suggest that intercrown distances represent distance relevant to interaction better than interbase distances. As near neighbours become larger and grow apart, base-centre distance becomes a poorer measure of interaction distance. In all analyses, the results for the two quadrats were similar except that the indices were larger for the 1985 quadrat.

Discussion

The values of DVAS observed for *Ambrosia*, and their statistical relationships with size and proximity of the nearest neighbour are small. Most of the displacement of crown centres from base centres is accounted for by other factors. Despite this, DVAS in a population of small scattered shrubs in an arid habitat suggests that above-ground interaction may have broad ecological importance. It is not surprising that the *Ambrosia* values of DVAS are small; it is surprising that they occur at all. In benign habitats where

plant crowns are more dense, the stimulus for horizontal asymmetry must be much stronger.

DVAS can be influenced by numerous factors other than interaction with the nearest neighbour. *Ambrosia* growth can be influenced by herbivores, micro climate, additional neighbour plants, solar azimuth, and soils. Herbivory on the contact zone between crowns might increase *DVAS*. Herbivory, desiccation, frost, and additional neighbours on the opposite side of the object plant from the neighbour might reduce *DVAS*. Branch pruning by rabbits sometimes occurs on the unprotected margins of *Ambrosia*. I have not observed comparable contact-zone pruning, but cumulative effects of modest use by rabbits or smaller organisms might be difficult or impossible to detect without continuous surveillance. The same uncertainty applies to desiccation and frost opposite the neighbour. The position of additional neighbours can be observed, however, but in the data sets used for the analysis the number of plants directly opposite the neighbour was small. *Ambrosia* crowns grow south, but this does not influence *DVAS* in the plant populations studied here, because directions to neighbours were random.

If root growth patterns influence crown growth, soil heterogeneity might tend to reduce *DVAS*. Centrifugal growth of roots of plants on outer margins of a benign soil patch would be restricted, and centripetal growth into the patch, the most likely direction of the nearest neighbour, would be favored.

The factors that would reduce *DVAS* appear more likely to occur than those that would increase *DVAS*. Thus, the results obtained for *Ambrosia* should be conservative, because they underestimate rather than overestimate the effect of above-ground interaction between nearest neighbours.

Studies of desert plant community ecology have generally assumed that below-ground interactions are reflected in the position and size of above-ground plant parts (e.g. Ehleringer, 1985: 167; Wright & Howe, 1987). Desert shrubs are often widely spaced, and they are typically oblate spheroidal with dominantly horizontal rather than vertical axes. Thus, they appear unlikely to compete for light, and it is not surprising to find that previous studies of dispersion did not consider above-ground interaction and its role in determining plant position. Adding to this, most studies of crown interaction have been conducted in benign habitats, and have focused on mechanisms such as leaf arrangement and vertical crown development (e.g. Hallé *et al.* 1978). Although the studies were conducted at sites where vegetation is dense and lateral interactions intense, plant capabilities for horizontally asymmetrical growth were usually ignored.

In desert competition studies, plant position is usually defined as a dimensionless point (Cox, 1985), but the location of the point relative to crown and base positions is often undefined (e.g. Wright & Howe, 1987). The four most likely positions are crown margins, crown centres, trunk margins, and base centres (trunk centres). Personal correspondence received from seven authors indicates that base centres have been used most often, but that exceptions and inconsistencies exist. This study of *Ambrosia* shows that the results of analysis of dispersion or correlation of distance and summed sizes of neighbouring plants can vary according to definitions of position. Because of the tendency of adjacent crowns to grow apart, the use of crown centres to define plant position will invariably produce measures of dispersion and correlations of summed size and distance that increase with the size of the plants being observed. Increased dispersion with age and size would be due to above-ground interference rather than the mortality of close neighbours.

Looking beyond desert habitats, the capability for asymmetrical growth might be related to adaptive traits involved in plant-community organization. For instance, the rapid module turnover common to competitive plants (Grime, 1979) should increase capabilities for rapid asymmetrical growth to avoid neighbours or to exploit resources. As with other competitive traits, the importance of this capability should vary temporally during succession, and spatially along gradients of habitat benignity and niche density. For instance, the abundance of basal meristems and sprouts among oblate spheroidal shrubs that dominate Mediterranean and desert environments should confer increased

plasticity, and might be partially a response to lateral above-ground interactions as well as other environmental factors such as fire.

Overall crown shape is a product of the growth, replication, and interaction of individual modules. Harper (1981) referred to intracrown shading as 'narcissistic competition', to describe the internecive behavior of a crown's modules. Just as selection appears to have favored developmental rules that minimize intracrown shading (Niklas, 1986), intracrown architectural rules that separate modules and minimize internecive training and pruning might also be favored. Thus, the evolution of branching and rotation angles that produce a central axis with separate layers of branches (Niklas, 1986) might be a consequence of other forms of interaction as well as the need for light. Avoidance of internecive interaction and reduced growth efficiency might appear in fossil sequences and across contemporary taxa of varying age as gradual shifts of mean branching angles, or as canalization of angles. Perhaps the apparently random branching that occurs in *Ginkgo biloba* L. is typical of earlier plants.

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