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Evidence for intraspecific competition in the *Acacia caven* (leguminosae) savanna of Chile

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SUMMARY

In the Chilean savanna, *Acacia caven* plants exhibit a spatial distribution pattern in which larger individuals tend to be further apart than smaller individuals of this species. Since published models of interspecific competition in plants do not account for the phenomenon as observed in *A. caven*, a new model is developed in which root systems of nearest neighbors are allowed to overlap. It is shown that in these circumstances resources actually available to the plants increase fairly linearly with nearest neighbors distance. The model is shown to predict a positive linear correlation between the sum of squares of the trunk radii of nearest neighbors and the distance separating them. This prediction of the model was tested with *A. caven* and shown able to generate the observed distribution pattern.

RÉSUMÉ

Dans la savane chilienne, *Acacia caven* montre un type de distribution spatiale dans laquelle les grands individus semblent être plus distants les uns des autres que les petits individus de cette espèce. Puisque les modèles publiés jusqu'à présent de la compétition entre espèces de plantes, ne rendent pas compte du phénomène observé chez *Acacia caven*, on a développé un nouveau modèle dans lequel les systèmes racinaires peuvent se chevaucher. On démontre que dans ces circonstances les ressources disponibles pour les plantes augmentent à peu près d'une manière linéaire suivant la distance du voisin le plus proche. Le modèle prévoit une corrélation linéaire positive entre la somme de mètres carrés du tronc des voisins les plus proches et la distance qui les sépare. Cette prévision du modèle a été testée avec *Acacia caven* et se révèle apte à la généralisation pour ce mode de distribution.

INTRODUCTION

Between 27°21' and 36°50' latitude south the Chilean central valley is dominated by an *Acacia caven* savanna (STÖEHR, 1969). In this plant formation the ground is typically covered by annual grasses and the overwhelming majority of plants of shrub to tree-size, belong to the legume species *Acacia caven*. Other woody plants in the savanna are *Prosopis chilensis* and *Prosopis tamarugo*, but their representation in this ecosystem is minimal.

A prominent characteristic of the *Acacia caven* savanna, obvious to even the casual observer, is the suggestively regular spacing of the shrubs (see fig. 1). The aim of this paper is to determine whether this spacing pattern of *Acacia caven* in central Chile can be related to intraspecific competition.

Competition between plants has been traditionally tested by comparing the distribution of individuals in space, with the expectancies from chance (BEALS, 1968; BARBOUR, 1969; WOODCELL *et al.*, 1969; KING and WOODCELL, 1973). By means of

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these methods, evidence for competition is obtained when individuals are found to be more regularly spaced than expected by chance. On the other hand, clumped or random distributions are not taken as evidence of intraspecific competition (MAC ARTHUR and CONNELL, 1966).

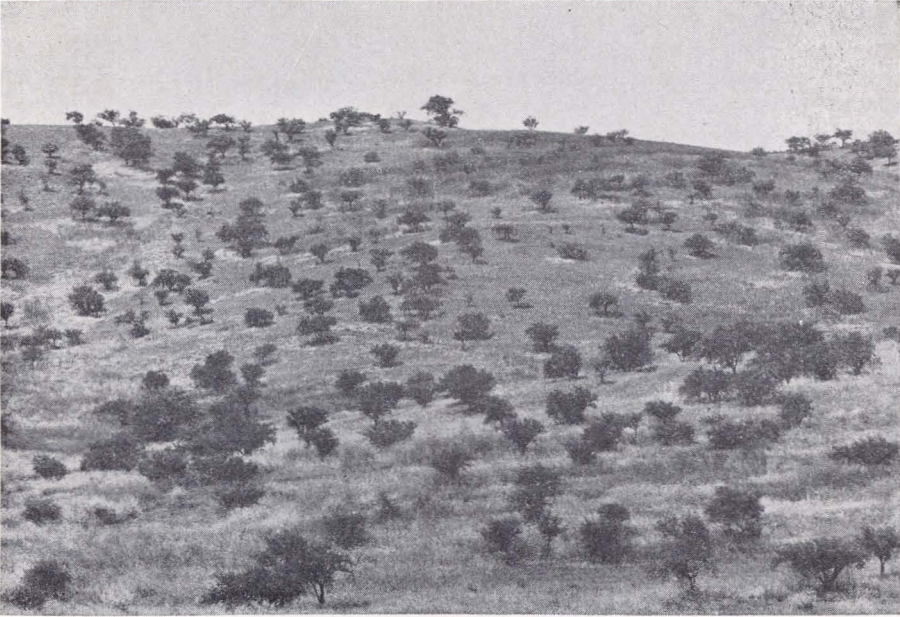


FIG. 1. — Aspect of the *Acacia caven* savanna in central Chile. Shrubs shown are *Acacia caven*, herb cover is constituted by several species of annuals. Notice the fairly regular spacing pattern of the shrubs.

However, PIELOU (1960) has shown that if plants are not represented by dots in a plane but by circles, thus allowing for different sizes and ages, the above methods are not adequate to infer competition. PIELOU suggested instead, that in a competitive situation the individual's resource utilization should be positively correlated with distances between nearest neighbors. Thus using *Pinus ponderosa*, she showed that the logarithm of the sum of the trunk circumferences is positively correlated with distance between neighboring plants. The reason for this test being that in her model with circular root systems, where neighbors do not overlap, the sum of the circumferences is correlated with interplant distance. The logarithmic transformation was used to correct for skewness.

Later, YEATON and CODY (1976) have used an extension of PIELOU's method to determine the competition structure on shrub species-assemblages in the Mohave desert. YEATON and CODY showed that photosynthetic area (a measure of the individual's resource requirements) is positively correlated with distance between neighbors.

In this paper we will relax one of PIELOU's assumptions and thus generate a different expected correlation. We will show that when the plant rooting systems are allowed to overlap (incomplete competitive exclusion), it is the sum of the squared radii of trunk of neighboring plants that should be positively correlated with their

distance. We will then exhibit evidence that the distribution of *Acacia caven* conforms to this modified competition model.

THE MODEL

Following PIELOU's model we assumed root systems are circular and proportional to the radius of the trunk. Furthermore, trunk radius and canopy surface, and hence resource demands by the plant, were also assumed to be positively correlated. From our field experience we feel that these assumptions are approximately correct. From these assumptions it is reasonable to infer that in a homogeneous patch of ground, resources actually available to a particular plant should be proportional to the fraction of the plant's root system that does not overlap with its nearest neighbor. (For simplicity we will further assume that only these interact.) The question we will attempt to answer now, is how root overlap varies with distance between plants if radii are kept constant. That is, we will search for the resource supply function as distance between neighbors varies.

In general for nearest neighbors T_1 , and T_2 , of trunk radii r_i , and r_j , and if T_2 is larger than T_1 , all possible situations will satisfy:

$$0 \leq r_i/r_j \leq 1.$$

Thus, in an effort to simplify calculations, and in order to bracket the supply function for intermediate cases, we analyzed overlap as a function of distance for the two limiting cases: $r_i/r_j = 0$, and $r_i/r_j = 1$, with $r_i > 0$. Calculating the integrals for a fixed d value and $r_i/r_j = 1$, the overlap area is (see fig. 2 a):

$$4 \int_{x_0}^r (r^2 - x^2) dx = 6.28 r^2 - 2d(r^2 - x^2/4)^{1/2} - 4r^2 \sin^{-1}(d/2r),$$

whereas when $r_i/r_j = 0$, and $r_i > 0$ overlap is (see fig. 2 b):

$$2 \int_{x_0}^{r_i} (r_i^2 - x^2) dx = 3.14 r_i^2 - 2(d - r_j)(r_i^2 - (d - r_j)^2)^{1/2} - 2r_i^2 \sin^{-1}(d - r_j/r_i).$$

The behavior of these equations was simulated for different values of d with the aid of a desk calculator. It was thus apparent that in spite of the relatively complex mathematical functions involved, in both cases percent overlap decreases fairly linearly with distance (fig. 3).

This result suggests that for fixed radii, resources available should *increase* linearly with distance between neighbors. The same should therefore also occur with the size of the plants.

In an analogous as we showed the relation between overlap and distance for fixed radii, it can be shown that for a fixed distance, overlap increases with the square of the radii.

From this model we expected, in a competitive situation, a positive correlation between the sum of squared radii and the distance to the nearest neighbor. This is the competition test which we used with *Acacia caven*.

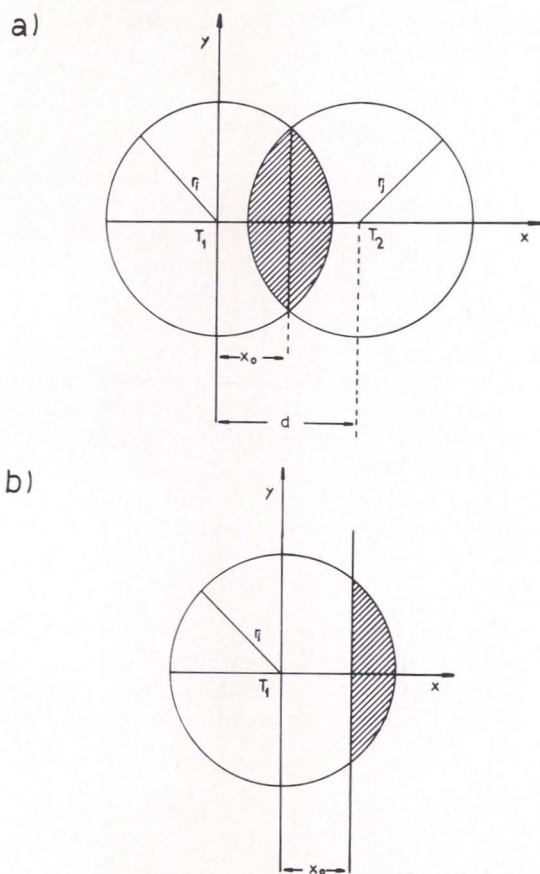


FIG. 2. — Models of root overlap: (a) root overlap between 2 nearest neighbors of the same size. T_1 and T_2 are the centers of the two root systems, r_i and r_j are their root radii and d the distance separating them. x_0 is the point on the abscissa where the two circles intersect; (b) root overlap between plants of extremely different sizes. In fact only one of them (T_1) is assumed to have a finite root radius, the second plant (T_2) is assumed to have an infinite radius. T_2 has its center infinitely far to the right and therefore the observable segment of its circumference is represented by a straight line. See the text for further discussion. Symbols as in figure 2 a.

RESULTS

Three sites were chosen where *Acacia caven* individuals were of grossly different sizes.

Site A: Is located by Los Domínicos on the outskirts east of Santiago. This site is on the more xeric north facing slope of the valley (MANN, 1964; PARSONS, 1976). Here mean *Acacia caven* density is 230 ha, and shrubs are about 1 to 1.5 m tall.

Site B: This site is also by Los Domínicos, but in the flat, and has a slightly wetter aspect than site A. Thus for example, soil samples dried in the oven, showed that at least in the month of July, site B is significantly wetter than site A ("t" test = 3.87, $P < .01$). (For more general references on dry-wet slopes in Chile see PARSONS,

1976.) At site *B* mean *Acacia caven* density is 305 ha and the shrubs are on the average about 2 m tall.

Site C: Is located by Peñuelas close to Valparaíso. Here mean rainfall is 448.7 mm whereas in Santiago close to Los Domínicos it is only 356.2 mm (HAJEK and DI CASTRI, 1975). *Acacia caven* individuals by Peñuelas are about 5 m tall and close to each other. Mean distance to nearest neighbor is 8.07 m ($SE = 1.11$) and mean canopy diameter is 3.68 m ($SE = 0.17$).

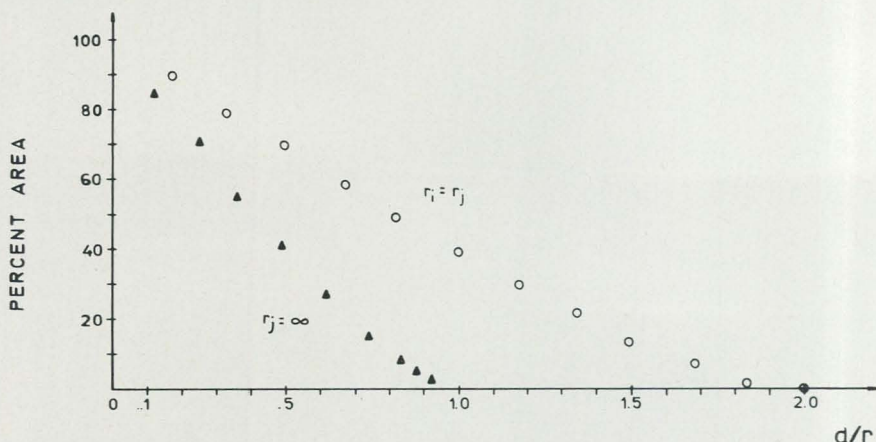


FIG. 3. — Distance versus overlap. Percent area of overlap (ordinate) is shown against a normalized distance between nearest neighbors (abscissa). Distance was normalized dividing by the radius of T_1 . Light dots exhibit the simulated pattern for plants of the same root radius. Black triangles refer to the case of the second plant being infinitely larger than the first. Notice that in both cases percent overlap decreases fairly linearly with distance. See the text for discussion.

It can be seen that as sites vary from xeric to mesic (sites *A* to *C*) the size of *Acacia caven* individuals increases.

Results of the correlation tests between sum of squared radii and distance are shown in figure 4. It can be seen that as expected from the model at all three sites there is a positive correlation between the two variables. An analysis of covariance on the data in figure 4, shows that the intercepts are different ($F_{(1,117)} = 206.54$, $P < .001$), but slopes are not ($F_{(1,116)} = 7.41 \times 10^{-6}$, $P > .999$). That is, plants are larger at the progressively more mesic sites, as we mentioned above, but the increment in distance required for similar increments in plant sites is not statistically different at the three sites.

DISCUSSION AND CONCLUSIONS

Our results with *Acacia caven* support the hypothesis that populations of the species are affected by intraspecific competition. As expected from our model of circular overlapping roots, resources available to the plants, and hence plant biomass, tend to increase fairly linearly with distance between nearest neighbors.

As we mentioned above, methods suggested in the literature in relation to competition, were not very useful in explaining the distribution of *Acacia caven* plants. Thus, PIELOU's expected correlation between the logarithm of the summed trunk circumferences and distance did not denounce competition at site *C*, where plants are

largest and closest to each other, and where we expected competition to be keenest (GUTIÉRREZ, 1977). On the other hand, the Poisson quadrat-method (MAC ARTHUR and CONNELL, 1966) did not indicate the presence of competition at either site A or B, whereas the other methods clearly indicated a competition effect.

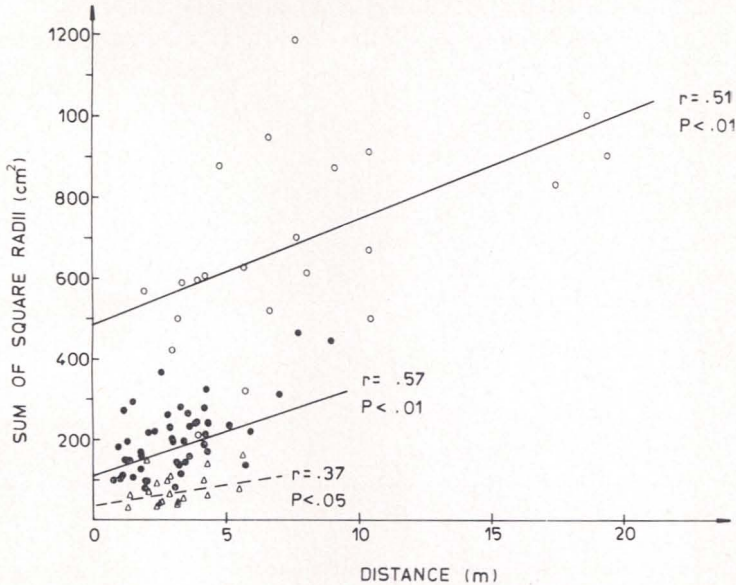


FIG. 4. — Spacing patterns at three sites. Light dots refer to Peñuelas, dark dots to site B and light triangles to site A at Los Domínicos. At all three sites there is a significant positive correlation between the sum of square radii of neighboring plants (ordinate) and distance separating them (abscissa). See the text for further explanations.

It is important to emphasize that our model requires only overlap of circular *areas of influence* and not of root systems. Unfortunately at present we still do not know the detailed root morphology of *Acacia caven* although it is known to at least have a tapping root (BURKART, 1952; STÖEHR, 1969). This point undoubtedly requires more research.

Could intraspecific competition account for the spacing pattern of *Acacia caven*? The evidence on competition offered suggests that resource acquisition could diminish and plant growth be retarded by the presence of a large neighbor. Thus, if chances of survival were related to growth rate, as for example when herbivores eat plantules, or when young plants are relatively more vulnerable to desiccation, delayed growth could generate *Acacia caven*-free spaces around the larger plants. The dimensions of these open spaces would depend of the competitive effect and therefore of the size of the nearby plant, as is suggested by the model.

Unfortunately, at present we do not know the relative importance of the above two mortality sources. Conceivably though, the usual 6 months of summer-drought in central Chile (DI CASTRI, 1968; DI CASTRI and HAJEK, 1976) could favor plantules exhibiting fast growth which would allow them to reach deep water sources. Slow growing plantules would be less favored in these circumstances. On the other hand, domestic animals (goats and sheeps) as well as rabbits eat small *Acacia caven* (A. Hoffmann, personal communication, and unpublished observations). Both,

climatic factors and herbivores, or a combination of both of them could thus interact with competition in generating the spacing of *Acacia caven* in the Chilean savanna. However, more research on the actual importance of these effects is pending.

It is interesting to mention that other postulated causal relations in plant spacing, namely allelopathy by means of canopy substances (MULLER *et al.*, 1964), and seed predation (JANZEN, 1970) do not seem to be important in the case of *Acacia caven*. GUTIÉRREZ (1977) has shown that leaf extracts of *Acacia caven* do not show an intraspecifically significant effect on seed germination or seedling growth. On the other side, the seed predation hypothesis for plant spacing also lacks support. GUTIÉRREZ (1977) showed that the overwhelming majority of the large *Acacia caven* pods fall directly under the canopy and no pods at all fall beyond the area of two times canopy radius. Moreover, GUTIÉRREZ found no evidence for post-dispersal predation of seeds as required by JANZEN's hypothesis. The evidence available at this point tends to support the hypothesis of intraspecific competition as an explanation for the pattern shown in figure 1.

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