

Evidences for intraspecific competition in the Chilean desert shrubs *Atriplex podocarpa* and *Atriplex deserticola*

Evidencia de competencia intraespecífica en los arbustos del desierto chileno *Atriplex podocarpa* y *Atriplex deserticola*

JULIO R. GUTIERREZ, LORGIO E. AGUILERA and RAUL J. MORENO

Departamento de Biología, Facultad de Ciencias, Universidad de La Serena,
Casilla 599, La Serena, Chile

ABSTRACT

Information on some morphological features of the little known species *Atriplex podocarpa* and *Atriplex deserticola* is presented. Plant dimensional analysis proved to be a good tool to estimate aboveground-dry biomass for both *Atriplex* species. The spatial patterns of two *A. podocarpa* and one *A. deserticola* populations were determined. *A. podocarpa* populations differed in their spatial distribution. The population constituted by large plants showed a random distribution, whereas the population with smaller plants had a clumped distribution. The *A. deserticola* population with the smallest plants of all three populations studied had the greatest level of clumping. The *Atriplex* populations which had a clumped distribution showed a positive correlation between the sum of nearest-neighbor biomasses and the distance separating them which was interpreted as evidence of intraspecific competition in these species.

Key words: Aridlands, *Atriplex*, intraspecific competition.

RESUMEN

Se entrega información de algunos caracteres morfológicos de *Atriplex podocarpa* y *Atriplex deserticola* debido a que estas especies son escasamente conocidas. Se correlacionó el tamaño de las plantas con la biomasa seca que crece sobre el suelo para usarlo como un método no destructivo de estimación de la productividad de estas especies. Se determinó el patrón espacial de dos poblaciones de *A. podocarpa* y una población de *A. deserticola*. La distribución espacial de las poblaciones de *A. podocarpa* cambió con el tamaño de las plantas. La población constituida por individuos grandes presentó una distribución al azar mientras que la población con individuos más pequeños tenía una distribución agrupada. Las plantas de *A. deserticola*, que fueron las de menor tamaño de las tres poblaciones analizadas, tenían el mayor nivel de agregación. Las dos poblaciones de *Atriplex* que tenían distribuciones agrupadas presentaron una correlación positiva entre la suma de las biomasa de las plantas vecinas más cercanas y la distancia de separación entre ellas, lo que fue interpretado como una prueba de que estas especies compiten intraespecíficamente.

Palabras claves: Zonas áridas, *Atriplex*, competencia intraespecífica.

INTRODUCTION

Species of the genus *Atriplex*, which are remarkably adaptable to arid conditions, are typical inhabitants of xeric habitats (Osmond *et al.* 1980). Most of these species, some of which are halophytes, are able to photosynthesize under low soil water availability and high temperatures, thus having a C₄ photosynthetic pathway. In Chile there are 20 species of *Atriplex* distributed north of 30° S (Gastó & Contreras 1972, Badilla 1975). However,

except for studies of *A. repanda* (Gastó & Contreras 1972, Gastó & Caviedes 1976, Acuña *et al.* 1978, Olivares & Johnston 1978, Fernández 1978a, b, c, Johnston & Fernández 1978, 1979, Fernández & Johnston 1978, 1980, Olivares *et al.* 1983, Johnston *et al.* 1983, 1985) the biology of the remaining species is practically unknown. Moreover, the studies on *A. repanda* have been focused on its productivity under artificial conditions and not on its performance in wild populations. Many authors have emphasized that *Atri-*

plex species are able to thrive under extremely dry conditions and therefore are suitable for reclaiming aridlands (Gastó & Contreras 1972). Because these species have a high palatability to livestock, high protein content and ability to recover quickly after severe grazing, they have been extensively used as forage plants (Osmond *et al.* 1980).

In the Atacama Desert, one of the driest deserts of the world, *A. deserticola* is found in dry streams with underground water, in areas close to the coast. Here the soil is sandy and has thick salt layers on the surface. Precipitations are almost absent and most of the humidity comes from coastal fogs. South to the Atacama Desert, in the region called "Norte Chico", where annual rainfall varies from 50 to 200 mm, a second species, *A. podocarpa*, is found at high elevation, ranging from 2000 to 3000 m. This species is exposed to the typical high mountain environment, *i.e.*, to high solar radiation, snowslides and night temperatures frequently below 0°C. The soil is rocky and shows a thin upper horizon.

Because both *A. deserticola* and *A. repanda* grow under severe environmental constraints, several factors could be limiting the survival and growth of individual plants. Under these conditions intraspecific competition could be important (King & Woodell 1984). Competition among plants has been traditionally tested by comparing the distribution of individuals in space, with the expectancies from chance. Regular spacing of plants has been considered as indicative of plant competition in arid and semiarid zones (Beals 1968, Barbour 1969, Woodell *et al.* 1969, King & Woodell 1973, 1984). Failure to find this pattern would occur in non-even-aged plant populations and in environments where the limiting resources are not evenly distributed (Anderson 1971, Gutiérrez & Armesto 1978).

Pielou (1960) proposed an alternative model to test for plant competition. Her model predicts a positive linear relationship between the sum of the sizes of nearest neighbors and the distance separating them, and has been useful to study competition in desert shrub assemblages (Yeaton & Cody 1976, Yeaton *et al.* 1977).

The aim of this work is to investigate the evidences for intraspecific competition in populations of *A. podocarpa* and *A.*

deserticola using each of the two analytical approaches described above.

Species Description

A. podocarpa and *A. deserticola* are spheroidal-shaped shrubs reaching up to 1.5 m in height. They present green puberulent ascendent branches and have two kinds of root system. One is a taproot system which may have several meters in depth and the another is an extended shallow root system, consisting of a dense mat of fine roots.

Study Sites

One population of *A. podocarpa* was sampled at Doña Ana Mountain (29°50' S, 70°05' W; 2700 m elevation) on the Andean Range, 120 km E of Vicuña. The soil was rocky and poorly developed. *A. podocarpa* was the dominant species coexisting with herbs and stunted shrubs of other species. A second *A. podocarpa* population was sampled in the same area (29°55' S, 70°10' W), but at 2200 m on an alluvial fan where the soil was relatively deeper. Data from El Indio Mine Co. Weather Station (29°55' S, 69°59' W; 3900 m) show that the average annual rainfall and snowfall in the area were 115 mm and 225 cm respectively, from 1981 through 1984.

Sampling of a population of *A. deserticola* was carried out at Canto del Agua (28°07' S, 70°55' W; 300 m elevation), in the Atacama Desert, 50 km NW of Vallenar. *A. deserticola* was the only shrub species present in this area. The population was at the bottom of a dry streambed with humid, sandy-loamy soil, and with a thick salt layer outcropping the surface. Climatic data are unavailable for this area, but in Vallenar (470 m elevation) average annual precipitation is 10 mm (Di Castri & Hajek 1976).

METHODS

Spatial distributions of the three populations were determined using the quadrat method (MacArthur & Connell 1966). An area of 450 m² was subdivided into fifty 9 m² quadrats. Plant frequency was recorded and compared to the expected Poisson frequency distribution and the same sampling was used to determine

plant density in each population. The selected quadrat size allowed to get empty quadrats as well as quadrats with more than one individual. Since the same quadrat size was used in all three populations the determined spatial distributions are comparable.

The nearest-neighbor analysis developed by Pielou (1960) was used to test for evidence of plant competition within *A. podocarpa* (at 2700 m) and *A. deserticola* populations. At each population, two orthogonal canopy diameters (in cm) and height (in cm) of randomly selected individuals and their nearest neighbors were measured. Simultaneously, the distances between nearest neighbors were measured. Plant dimensions of eleven plants from just outside the study areas were used to obtain information on the relationship between plant size and biomass. For both species, individuals were selected to cover the entire range of size variation within the populations.

Only the aboveground parts of the plants were harvested, because of the hard labour involved in getting plant roots. However, excavation around some *Atriplex* plants suggests that there is a positive correlation between below and aboveground biomass. Therefore, we can make inferences about root sizes by knowing the aboveground biomass. The plants removed were oven-dried at 60°C for 72 h and then weighed to the nearest gram. Plant sizes were determined assuming an upper-half prolate spheroid volumen for both species since they are very similar in shape (details of this procedure in Ludwig *et al.* 1975). Regressions between plant size and aboveground dry-weight (biomass hereafter) were calculated for each species. Logarithmic transformations of the biomass and plant sizes were used to correct for skewness. In the analysis of competition, the sum of the biomasses of nearest-neighbor plants was used instead of sizes, because biomass reflects better productivity and resource use by the plants (Whittaker 1975).

Plant height-class distributions for each population were compared using histograms. Because both *A. podocarpa* and *A. deserticola* have similar growth-forms, we also assumed that plant height reflects plant age.

RESULTS AND DISCUSSION

Dimensional analysis has been recommended as a rapid, non-destructive method to estimate plant biomass considering the labour invested in measuring productivity and the need to preserve arid ecosystems (Ludwig *et al.* 1975). The double-logarithmic plot of aboveground dry-weight (B) and volume (V) fits well to a linear regression for both *Atriplex* species (Fig. 1). The regression equations for *A. podocarpa* ($\log B = -1.84 + 0.77 \log V$; $r = 0.96$; $P < 0.001$) and *A. deserticola* ($\log B = -2.0 + 0.78 \log V$; $r = 0.98$; $P < 0.001$) do not differ either in slope ($F_{(1,18)} = 0.053$; $P > 0.25$) or in intercept ($F_{(1,19)} = 3.83$; $P > 0.05$), *i.e.* similar volumes represent equivalent amounts of aboveground biomasses regardless of the species. The high regression coefficients (R^2 over 0.90) show that

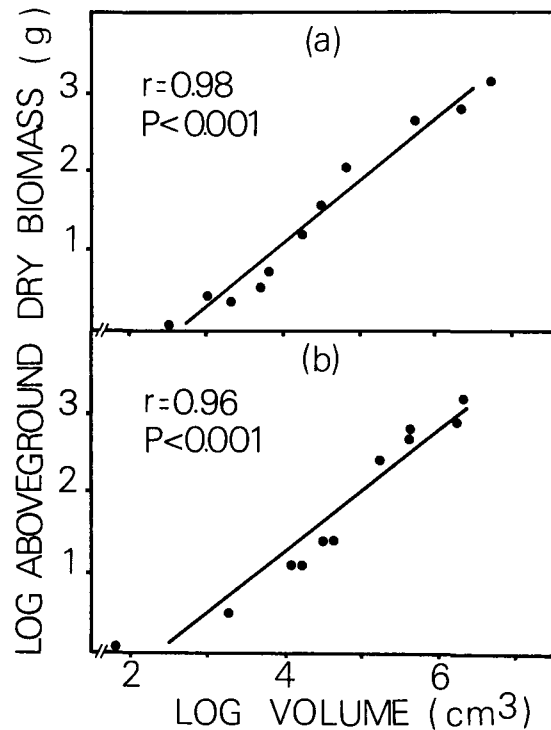


Fig. 1: Dimensional analysis for (a) *Atriplex podocarpa* and (b) *Atriplex deserticola*. For both species there is a significant, positive correlation between the logarithm of aboveground dry-biomass and the logarithm of volume.

Análisis dimensional de (a) *Atriplex podocarpa* y (b) *Atriplex deserticola*. En ambas especies hay una correlación positiva, significativa entre el logaritmo de la biomasa seca sobre el suelo y el volumen de las plantas.

canopy volumen is a good stimator of aboveground biomass in these species and therefore these equations may be useful tools for predicting purposes. Similar findings have been reported for eight Chihuahuan desert shrubs (Ludwig *et al.* 1975) and for *A. repanda* in the Chilean Desert (Azócar *et al.* 1981).

Spatial distribution of *A. podocarpa* was clumped at 2700 m whereas it was random at 2200 m (Table 1). Average height of individuals was higher at 2200

m than at 2700 m (Fig. 2), but the opposite was true in regard to density (Table 2). In other words, the larger and less abundant plants were more segregated in space than the smaller and more abundant ones. This change in the spatial pattern of one species with age or size has been reported for other shrub species (Gutiérrez & Armesto 1977, Schlesinger & Gill 1978, Phillips & MacMahon 1981) and interpreted as a result of thinning due to intraspecific competition.

TABLE 1

Spatial pattern of *Atriplex podocarpa* and *Atriplex deserticola* in three study sites. Expected number of quadrats with x plants was determined using the Poisson frequency distribution. χ^2 : chi-square; * : $P < 0.01$.

Distribución espacial de *Atriplex podocarpa* y *Atriplex deserticola* en tres sitios de estudio. El número esperado de cuadrados con x plantas se determinó usando la distribución de frecuencias de Poisson. χ^2 : chi-cuadrado; * : $P < 0.01$.

Study Sites	Species	Number of plants per quadrat (x)	Number of quadrats with x plants		χ^2
			Observed	Expected	
Doña Ana at 2700 m	<i>A. podocarpa</i>	0	14	9.0	11.95*
		1	20	15.4	
		2	6	13.2	
		3	3	7.6	
		≥ 4	7	4.8	
Doña Ana at 2200 m	<i>A. podocarpa</i>	0	30	28.5	0.78
		1	14	16.0	
		≥ 2	6	4.6	
Canto del Agua	<i>A. deserticola</i>	0	10	22.5	29.84*
		1	16	18.0	
		≥ 2	24	9.4	

TABLE 2

Elevation, slope aspect and plant density in the study sites.
Altitud, orientación de laderas y densidad de plantas en los sitios de estudio.

Study Sites	Elevation (m)	Slope Aspect	Plant Density (plants/m ²)
Doña Ana	2700	15° Polar-facing slope	1.72
Doña Ana	2200	5° Polar-facing slope	0.56
Canto del Agua	300	Bottom of a dry streambed	2.54

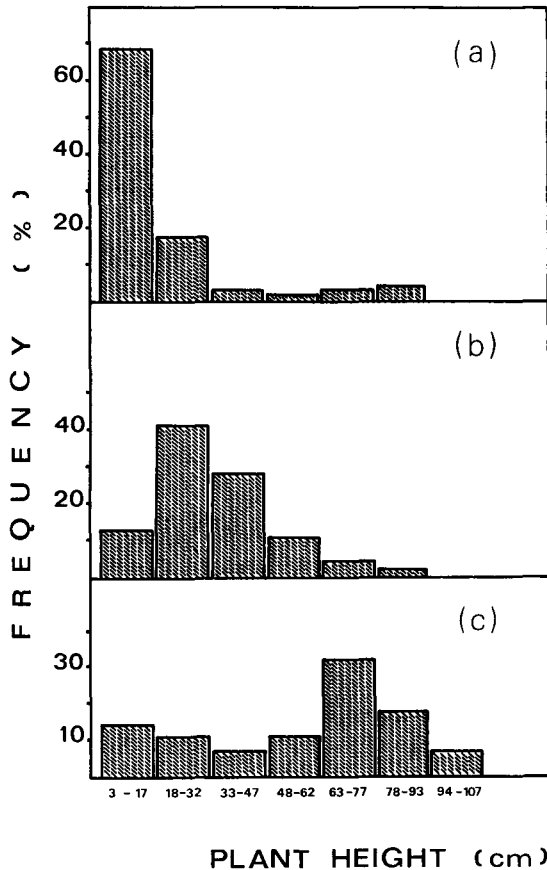


Fig. 2: Plant height-class distribution for (a) *Atriplex deserticola*; (b) *Atriplex podocarpa* at 2700 m; (c) *A. podocarpa* at 2200 m.

Distribución de clases de alturas de plantas en (a) *Atriplex deserticola*; (b) *Atriplex podocarpa* a 2700 m; (c) *A. podocarpa* a 2200 m.

The population of *A. deserticola* which had the smallest individuals (Fig. 2) and the highest density of all three populations studied (Table 2) showed the greatest level of clumping (Table 1). King and Woodell (1973, 1974) point out that in arid habitats dominated by a single woody species, a clumped pattern of small individuals may give rise by selective mortality to a random or regular distribution of larger individuals. However, in large mature *Acacia caven*, a common leguminous shrub of the Chilean savanna, for which there are good evidences of intraspecific competition, this pattern sequence has not been found (Gutiérrez & Fuentes 1979).

In arid systems, where plants usually have a small canopy and are sparsely distributed, light is not likely to be a limiting factor, but competition for the temporary water supply and for scarce nutrients is highly probable. Nitrogen and presumably other macronutrients are distributed in patches in arid ecosystems (West & Klemmenson 1978, Parker *et al.* 1982, Brown 1983), therefore the spatial distribution of seedlings or juvenile plants may be reflecting the heterogeneous resource distribution. Unfortunately, we do not have soil data in this study to confirm or reject this hypothesis.

The two *Atriplex* populations which showed a significant departure from a random pattern were tested for intraspecific competition using Pielou's (1960) model. This analysis revealed significant correlations ($r = 0.74$ and 0.80 ; $P < 0.001$, for *A. podocarpa* and *A. deserticola* respectively) between the sum of nearest-neighbor biomasses and the distance separating them (Fig. 3). This means that the growth of an individual would be retarded by the presence of a large neighbor, but these effects were not in evidence by the Poisson-quadrat method.

Fuentes and Gutiérrez (1981) suggested that the slope of the regression line could be considered as an experimental measure of the importance of competitive interactions, *i.e.*, the greater the slope the stronger the resource-release associated with a unitary distance increment between plants. Accordingly, intraspecific competition should be greater in the *A. podocarpa* population at 2700 m whose slope is 4.6 than in the *A. deserticola* population whose slope is 3.1 ($F_{(1,90)} = 4.78$; $P < 0.05$). *A. podocarpa* individuals are larger and therefore might have larger root systems than *A. deserticola* individuals which could account for this result. A large root system entails ample root overlap between nearest neighbors and consequently less resources available for plant growth. This would also account for the decrease in density observed in populations of large individuals. In addition to plant sizes, intraspecific competition could affect other plants characters such as seed production, seed quality, leaf chemical defenses and so on. If this is so, the total effect of intraspecific competition upon the population fitness would be greater than that estimated on plant

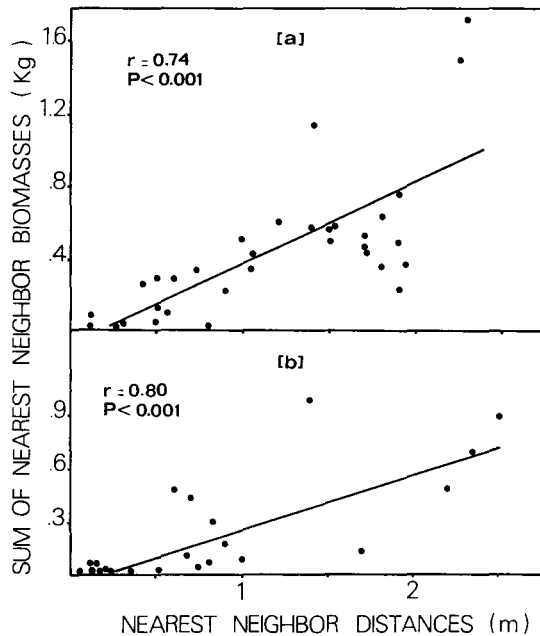


Fig. 3: Intraspecific biomass-distance pattern for (a) *Atriplex podocarpa* and (b) *Atriplex deserticola*. For both species there is a significant positive correlation between the sum of the aboveground dry biomasses of the two nearest neighbors and the distance separating them.

Patrón intraespecífico de biomasa y distancia en (a) *Atriplex podocarpa* y (b) *Atriplex deserticola*. En ambas especies hay una correlación positiva que es significativa entre la suma de la biomasa seca sobre el suelo de los dos vecinos más cercanos y la distancia de separación entre ellos.

size only. Further research is needed to verify this hypothesis.

In Chile, studies on intraspecific (Gastó & Caviedes 1976) and interspecific competition (Acuña *et al.* 1979) in *A. repanda* have attempted to relate competition with population density. However, this study clearly shows that individuals of *A. podocarpa* and *A. deserticola*, which are similar in morphology and live within the same geographical range as *A. repanda*, do not compete for resources with all the other members of the population, as suggested by the above mentioned studies, but only with a small number of neighboring plants. Hence, the intensity of competition experienced by each individual will vary according to the size and spatial arrangement of neighbors. Even at a constant density, competition effects between plants could differ in populations with different size and plant spatial distribution. In equilibrium populations, com-

peting individuals would tend to maximize exploitation of resources, and therefore spacing among individuals would reflect the optimal spatial arrangements given the different plant sizes in the population. These findings should be taken into account for a better management of the Chilean arid systems.

A. podocarpa and *A. deserticola* live in very harsh environments and therefore they could be characterized as stress-tolerant species (*sensu* Grime 1977) subjected to several sources of mortality such as abrupt daily temperature fluctuations, freezing-temperatures, high soil salinity and so on. This study has shown, however, that intraspecific competition can not be ruled out as a factor affecting the fitness of these species.

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