

Spatial distribution of *Tephrocactus aoracanthus* (Lem.) Lem. in relation to shrubs in the hyperarid regions of west-central Argentina

MARTÍN ALMIRÓN* AND EDUARDO MARTÍNEZ CARRETERO

Geobotánica y Fitogeografía, Instituto Argentino de Investigaciones de las Zonas Áridas, National Council for Scientific and Technological Research, CC 507, 5500 Mendoza, Argentina (Email: malmiron@lab.cricyt.edu.ar; martinalmiron2000@hotmail.com)

Abstract The spatial intraspecific and interspecific distribution of *Tephrocactus aoracanthus* (Lem.) Lem. was studied using univariate and bivariate point pattern analysis, at landscape scale in four different physiographic units and at microscale in terms of the shrubs found in those units. The influence of shrubs on photosynthetically active radiation and on soil temperature under their canopies was analysed. Results show a high environmental variability in light and temperature under shrubs that generally has no influence on the distribution of *T. aoracanthus*. Apparently, this cactus has great ability to adapt to different conditions of both photosynthetically active radiation and temperature. However, intraspecific distribution was highly clustered in all physiographic units, independently of bushes. Possibly, the mode of seed dispersal and the rooting of cladodes at small scale are the main processes that determine the strong intraspecific clustering of *T. aoracanthus*.

Key words: environmental heterogeneity, intra/interspecific association, Wiegand–Moloney's $O(r)$ statistics.

INTRODUCTION

The importance of interactions between plants in the structure and composition of plant ecosystems is nowadays widely accepted. In the 1970s and 1980s, most reports focused on negative-type interactions (Yeaton & Cody 1976; Yeaton 1978; Conell 1983; Schoener 1983); later, in the 1990s and 2000s, focus changed to positive interactions, where at least one species benefits from the presence of another species (Callaway & Walker 1997; Hacker & Gaines 1997). Probably, both types of interactions coexist simultaneously, resulting in a dynamic balance (Callaway & Walker 1997; Holmgren *et al.* 1997; Tielbörger & Kadmon 2000) which depends also on the life stages of intervening plants (Valiente-Banuet *et al.* 1991; Flores-Martínez *et al.* 1994) and on environmental conditions (Tielbörger & Kadmon 2000; Armas & Pugnaire 2005).

Apparently, facilitation increases in situations of stress, whereas negative interactions prevail under more beneficial conditions (Bertness & Callaway 1994; Callaway & Walker 1997; Tewksbury & Lloyd 2001).

In desert environments, the Cactaceae have been reported to be associated with shrubs that attenuate high solar radiation and soil temperature (Franco & Nobel 1989; Valiente-Banuet & Ezcurra 1991; Valiente-Banuet *et al.* 1991; Leirana-Alcocer &

Parra-Tabla 1999; Carrillo-García *et al.* 2000; Mandujano *et al.* 2002, Almirón & Martínez Carretero 2010), to improve moisture and nutrient content (Carrillo-García *et al.* 2000; Méndez *et al.* 2004), to protect seedlings against herbivory (Valiente-Banuet & Ezcurra 1991) and to provide preferential sites for seed deposition (De Viana *et al.* 2000). On the other hand, allelopathic effects (De Viana *et al.* 2000; Cazón *et al.* 2002) and competition for resources (McAuliffe 1984; Franco & Nobel 1989; Flores-Martínez *et al.* 1994) were detected between shrubs and cacti.

In the Bolivian Prepuna, López and Valdivia (2007) found that the type of growth in cacti determines their dependence on shrubs, suggesting that columnar cacti grow exclusively under shrubs whereas opuntoid cacti, although more successful beneath shrubs, can likewise develop in open areas.

The genus *Tephrocactus* consists of seven species characterized by plants with lax branches formed with several overlapping spherical cladodes connected by fragile joints. This genus is endemic of the central west of Argentina. All species in this genus grow in very dry, rocky or sandy, soils and altitudinally are distributed between 500 and 2500 m (Kiesling 2003).

Tephrocactus aoracanthus (Lem.) Lem., like other opuntoids, has delicately articulated stems that allow its vegetative reproduction through cladode fall and subsequent rooting from areolar meristematic tissue (Bobich & Nobel 2001; Mandujano *et al.* 2007), avoiding the critical germination phase (Mandujano *et al.* 1998; Mauseth 2006).

*Corresponding author.

Accepted for publication March 2012.

No study has thus far addressed the interaction between cacti of the same species; moreover, the spatial distribution pattern of individuals in natural populations of *T. aoracanthus* is likely influenced by density-dependent processes, considering physiographic units and the environmental variability associated with each of them. On this account, the present study was directed to determine both associations (intraspecific and interspecific), using the spatially explicit technique proposed by Wiegand and Moloney (2004).

Because both biotic and abiotic factors contribute to environmental heterogeneity in arid ecosystems (Zavala-Hurtado 1982), and as spatial distribution is the long-term result of intraspecific and interspecific interactions, the objective of this study was to analyse the intraspecific interactions among individuals of the opuntoid cactus species *T. aoracanthus* and the interspecific interactions between *T. aoracanthus* and all shrub species observed within four different physiographic units (geotopes) in the central Monte desert, attempting to elucidate the following question: how environmental heterogeneity affects, at mesoscale (physiographic unit) and microscale (shrub species), the spatial distribution pattern of *T. aoracanthus*.

METHODS

Study area

The study was conducted at the Matagusanos locality (31°13'17"S 68°39'7"W) San Juan Province, Argentina. Average annual precipitation is 116.5 mm, 72% occurring during the summer period. Mean annual temperature is 17.2°C, with an absolute maximum of 42.8°C and an absolute minimum of -7.3°C (Servicio Meteorológico Nacional 1958). The shrubland is the dominant physiognomy, with an average plant cover of 20%. Dominant species are *Larrea cuneifolia* Cav., *Bulnesia retama* (Gillies ex Hook. & Arn.) Griseb., *Zuccagnia punctata* Cav., *Larrea divaricata* Cav., *Bougainvillea spinosa* (Cav.) Heimerl, *Lycium tenuispinosum* Miers and *Cercidium praecox* (Ruiz & Pav.) Burkart & Carter, among others.

At the working scale, the landscape is heterogeneous with sandy and rocky plains and hillsides with east and west exposure, both affected significantly by water erosion.

Sampling design

To analyse the effect of environmental heterogeneity, the spatial distribution of *T. aoracanthus* was assessed in four physiographic units (at geotope level): alluvial plain (AP), sandy plain (SP), east-exposed hillside (EH) and west-exposed hillside (WH).

In each physiographic unit, five plots of 6 × 10 m were randomly established. Each plot was split into 1500 squares

of 20 × 20 cm to obtain the Cartesian coordinates for each cactus as well as the shape, position and size of each shrub, following the methodology of Wiegand *et al.* (2006) for spatial point pattern analysis for objects of finite size and irregular shape.

Results of the five plots (in each physiographic unit) have been combined in one average graphic function, using the 'combine replicates tool' included in the Programita software. Theoretical issues are developed in Appendix A included in Raventós *et al.* (2010).

Each cactus was considered as one entity when it had at least one rooted cladode and was independent of other individuals.

To analyse the microenvironment under shrubs, photosynthetically active radiation (PAR) was measured with a digital radiometer: QMSS-S, Apogee, and temperature (Temp) 7 cm above ground was recorded using rapid response alcohol thermometers. All data have been always recorded on the same shrubs. Measurements were taken at midday and at three positions on the projection of the shadow of bushes: centre, middle and edge of the shadow projection, throughout 1 day in the middle of the spring, summer, autumn and winter periods.

Simultaneously, PAR and Temp were recorded for bare soil in four random points of each plot; the average of these values was taken as reference value.

In each geotope, height and higher and lower diameters of shrub canopies have been measured on all shrubs found within each plot, and the average shrub for each species was established.

Nomenclature of plant species follows that by Zuloaga and Morrone (1999).

Data analysis

To establish a benchmark for comparison, and to eliminate variation in the readings due to the time elapsed between one plot and another, the values of PAR and Temp recorded under the bushes were subtracted from the average reference value of PAR and Temp recorded for bare soil, on each plot, in each geotope and by season. Thus, one Δ PAR and one Δ Temp value was obtained for each combination of factors (species, geotope and shade position). Subsequently, the average annual value was calculated per shrub species and position in each geotope. In each physiographic unit, the effect of the two factors (shrub species and positions beneath shrubs) on Δ PAR and Δ Temp and the interaction between them were analysed by using ANOVA factorial and mean separation with Tukey test ($P < 0.05$).

Using the Programita software, we analysed the intraspecific distribution pattern of *T. aoracanthus* in each geotope, comparing the values from the empirical Wiegand-Moloney's $O_{11}(r)$ statistics with a null model of complete spatial randomness distribution (Wiegand & Moloney 2004). To determine 95% confidence bands, 99 Monte Carlo simulations (Bailey & Gatrell 1995; Haase 1995) were performed, taking the 5th highest and 5th lowest values as confidence limits (Wiegand *et al.* 2000). Graphically, if the empirical distribution falls within the confidence limits it is assumed that there are no significant differences with respect to the theoretical distribution model; values distributed above the

upper confidence limit indicate spatial aggregation and values below the lower limit indicate a regular (uniform) spatial pattern (Diggle 1983).

The relationship between *T. aoracanthus* and shrubs (intraspecific relationship) was analysed using the null model 'Toroidal shift' (Wiegand *et al.* 2006), in order to preserve the possible intraspecific distribution pattern of *T. aoracanthus*, as well as the shape, size and position of the bushes.

RESULTS

Composition, height and average coverage of shrub species found on the plots were different in all four geotopes (Table 1).

At low-slope sites (AP and SP), ANOVA showed significant differences for Δ PAR and Δ Temp between the factors 'species' and 'position' (Tables 2,3

Table 1. Characterization of physiographic units and shrub species found on the plots

Physiographic unit	Shrub species	H	HD	LD	C	Specific relative frequency (%)
Alluvial plain (AP)						
Slope: 3%	<i>Bulnesia retama</i>	1.90	3.80	3.40	10.15	3.80
Soil: rocky	<i>Bougainvillea spinosa</i>	1.00	1.80	0.95	1.51	3.60
Shrub cover: 25%	<i>Lycium tenuispinosum</i>	0.86	1.28	0.80	0.80	1.90
	<i>Larrea cuneifolia</i>	0.80	1.18	0.92	0.97	90.70
Sandy plain (SP)						
Slope: 2–3%	<i>B. retama</i>	2.43	3.57	3.15	8.79	12.50
Soil: fine sands	<i>Cercidium praecox</i>	1.90	3.00	1.80	4.24	4.20
Shrub cover: 14%	<i>L. cuneifolia</i>	0.85	1.03	0.70	0.60	12.50
	<i>Larrea divaricata</i>	0.95	1.13	1.00	1.00	70.80
East hillside (EH)						
Slope: 50%	<i>C. praecox</i>	1.40	5.20	1.80	7.35	3.00
Soil: heterometric clasts	<i>L. cuneifolia</i>	0.71	1.14	0.88	0.90	84.80
Shrub cover: 15%	<i>Zuccagnia punctata</i>	1.47	2.03	1.63	2.68	12.20
West hillside (WH)						
Slope: 50%	<i>L. cuneifolia</i>	0.98	1.42	1.06	1.29	55.60
Soil: rocky with gravels	<i>Z. punctata</i>	1.62	2.23	2.00	3.74	44.40
Shrub cover: 36%						

H (height), HD (high crown diameter) and LD (low crown diameter) are expressed in metres. C (shrub cover) is expressed in square metres.

Table 2. ANOVA of Δ Temp and Δ PAR in the four physiographic units, with respect to the factor shrub species

Shrubs in each physiographic unit	\bar{X} Δ Temp ($^{\circ}$ C)	\bar{X} Δ PAR (μ mol m^{-2} s^{-1})
Alluvial plain	(<i>F</i> : 24.19; <i>P</i> < 0.0001)	(<i>F</i> : 3.25; <i>P</i> < 0.022)
<i>Larrea cuneifolia</i>	1.55	1022.52
<i>Lycium tenuispinosum</i>	1.77	847.04
<i>Bougainvillea spinosa</i>	2.33	838.02
<i>Bulnesia retama</i>	4.89	1389.21
Sandy plain	(<i>F</i> : 19.33; <i>P</i> < 0.0001)	(<i>F</i> : 3.81; <i>P</i> < 0.01)
<i>L. cuneifolia</i>	1.53	929.06
<i>Larrea divaricata</i>	1.69	924.33
<i>Cercidium praecox</i>	2.55	967.46
<i>B. retama</i>	3.56	1201.56
East hillside	(<i>F</i> : 10.18; <i>P</i> < 0.0001)	(<i>F</i> : 1.64; <i>P</i> = 0.19)
<i>L. cuneifolia</i>	1.17	1076.05
<i>Zuccagnia punctata</i>	2.14	1187.8
<i>C. praecox</i>	2.33	935.04
West hillside	(<i>F</i> : 8.81; <i>P</i> < 0.0032)	(<i>F</i> : 0.64; <i>P</i> = 0.42)
<i>L. cuneifolia</i>	2.01	1002.62
<i>Z. punctata</i>	2.56	1041.94

Different letters indicate significant differences for Tukey test (*P* < 0.05). PAR, photosynthetically active radiation; Temp, temperature.

Table 3. ANOVA of Δ Temp and Δ PAR in the four physiographic units, with respect to the factor position beneath shrubs

Position beneath shrubs in each physiographic unit	\bar{X} Δ Temp ($^{\circ}$ C)	\bar{X} Δ PAR ($\mu\text{mol m}^{-2} \text{s}^{-1}$)
Alluvial plain	($F: 3.07; P < 0.0484$)	($F: 13.48; P < 0.0001$)
Edge	2.04 a	623.62 a
Middle	2.92 b	1030.52 b
Centre	2.95 b	1418.45 c
Sandy plain	($F: 12.54; P < 0.0001$)	($F: 31.41; P < 0.0001$)
Edge	1.41 a	559.95 a
Middle	2.59 b	1068.80 b
Centre	3.00 b	1388.04 c
East hillside	($F: 6.41; P = 0.0019$)	($F: 21.15; P < 0.0001$)
Edge	1.08 a	634.19 a
Middle	2.16 b	1121.29 b
Centre	2.40 b	1443.41 c
West hillside	($F: 30.43; P < 0.0001$)	($F: 115.60; P < 0.0001$)
Edge	1.35 a	535.59 a
Middle	2.41 b	1084.82 b
Centre	3.09 c	1446.42 c

Different letters indicate significant differences for Tukey test ($P < 0.05$). PAR, photosynthetically active radiation; Temp, temperature.

respectively). The interaction between factors was not significant in the low-slope sites (AP: Δ PAR = $F: 0.66$; $P = 0.6798$; Δ Temp = AP: $F: 0.43$; $P = 0.8587$; SP: Δ PAR = $F: 1.19$; $P = 0.3102$; Δ Temp = AP: $F: 0.46$; $P = 0.8344$).

At high-slope sites (EH and WH), only the factor 'position' was significant for Δ PAR and Δ Temp (Table 3), while the factor 'species' was significant for Δ Temp and not significant for Δ PAR (Table 2). No significant interaction was observed between factors in the high-slope sites (EH: Δ PAR = $F: 0.10$; $P = 0.98$; Δ Temp = AP: $F: 1.13$; $P = 0.34$; WH: Δ PAR = $F: 0.02$; $P = 0.97$; Δ Temp = AP: $F: 1.07$; $P = 0.34$).

In all four environments, a gradient of Δ PAR and Δ Temp was observed, which decreased from the centre of the bushes towards the edge of the shadow projection (Table 3). When comparing differences in PAR and Temp between bushes, the soil under *B. retama* in the low-slope geotopes (AP and SP) was significantly colder and shadier (Table 2).

At the two high-slope sites (EH and WH), where no *B. retama* occurred, the shrub casting the most shade was *Zuccagnia punctata*, although with no significant differences from the partner species (Table 2). With regard to Δ Temp observed under bushes on 'WH', *Z. punctata* had the highest value, and was significantly different from the codominant species *L. cuneifolia*. On 'EH', the species with the greatest shadow was *C. praecox*, followed by *Z. punctata*, both significantly different from *L. cuneifolia* (Table 2).

Intraspecific spatial distribution

Tephrocactus aoracanthus was found in all geotopes with densities of 2.28 individuals per square metre in 'SP',

0.87 individuals per square metre in 'AP', 1.66 individuals per square metre on 'EH' and 0.59 individuals per square metre on 'WH'.

The significant differences observed between the empirical spatial distribution and the null model (complete spatial randomness) in all the physiographic units (Fig. 1) indicate that the probability of finding individuals of *T. aoracanthus* around another is greater than expected by chance.

Tephrocactus aoracanthus forms dense clusters of individuals between different spatial scales (AP: 0–60 cm, SP: 0–100 cm, EH: 0–80 cm and WH: 0–60 cm). From these maximum distances, the absence of significant differences between real data and the theoretical model suggests a random distribution.

Interspecific spatial distribution

The spatial distribution of *T. aoracanthus* in relation to shrubs showed no significant differences from the Poisson random distribution (Fig. 2). In the 'AP', the density of *T. aoracanthus* was lower than expected by chance for two shrubs: with *B. retama* between 20 and 100 cm and *L. tenuispinosum* between 0 and 200 cm. Beneath the canopies of these shrubs (*B. retama* and *L. tenuispinosum*), no individuals of *T. aoracanthus* were found in any of the plots in the AP, which demonstrates the negative interaction between these shrubs and cacti. *Tephrocactus aoracanthus* was positively associated only with *Z. punctata* on 'WH' between 0 and 80 cm, although on 'EH' the empirical distribution of *T. aoracanthus* with respect to this shrub was within the confidence interval and therefore can not reject the random distribution of *T. aoracanthus* with respect to *Z. punctata* in 'EH' (Fig. 2).

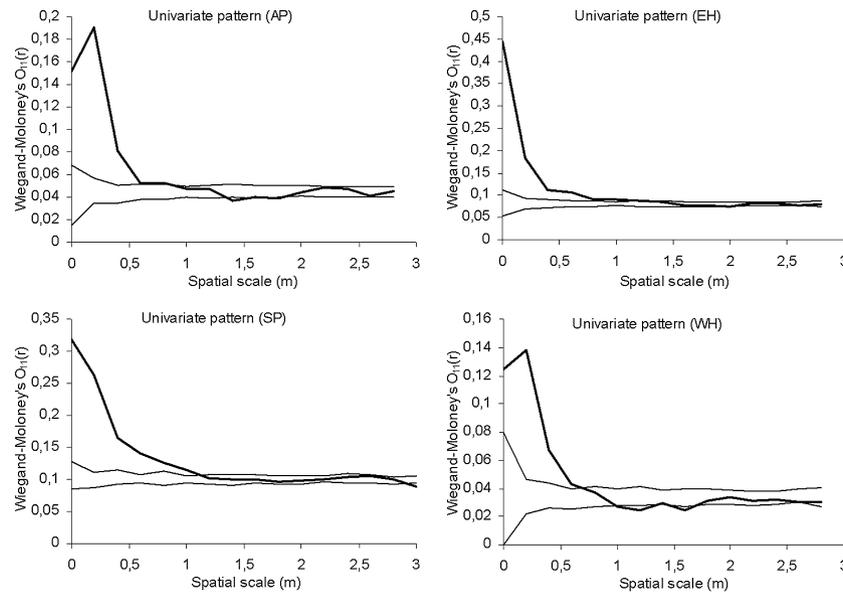


Fig. 1. Analysis of the univariate spatial pattern of *Tephrocactus aoracanthus* in all physiographic units: alluvial plain (AP), sandy plain (SP), west hillside (WH) and east hillside (EH). Bold line shows the empirical function Wiegand–Moloney's $O_{11}(r)$ and thin lines show the confidence interval generated by the 5th highest and 5th lowest values of 99 Monte Carlo simulations of random Poisson null model.

DISCUSSION

Prior studies addressing interactions between plants in arid and semiarid systems have proposed that landscape-scale heterogeneity determines different host species assemblages due primarily to terrain physical variables, such as accumulation of fine sediments and slope, which affect rainwater runoff and infiltration (Yeaton & Cody 1976; Zavala-Hurtado 1982; Yeaton & Romero Manzanares 1986). On a lower scale, some authors (Turner *et al.* 1966; Franco & Nobel 1989; Valiente-Banuet & Ezcurra 1991; Mandujano *et al.* 2002; Méndez *et al.* 2004; Almiron & Martínez Carretero 2010) have proposed that shrubs produce a favourable environment regarding bare soil, thus favouring the establishment of cacti. This study provides evidence of the simultaneous relationship between landscape-level perception and diversity of physiographic units that include the environmental variability generated by each shrub species.

Some shrubs, such as species of the genus *Larrea* that have small evergreen leaves and of *B. spinosa* and *L. tenuispinosum* with tiny leaves that fall early, affected very little the photosynthetically active solar radiation and temperature beneath their canopies. These plants are relatively small both in height (<1 m) and area covered (<1.5 m²) (Table 1) and possess a network of fine branches, generally stunted.

On the other hand, species like *Z. punctata*, *B. retama* and *C. praecox*, of greater height and area covered, have numerous densely imbricate stems that

prevent the entry of light under their canopies and further reduce soil temperature.

Similarly as found by Yeaton (1978), the studied shrubs were hemispherical, and a light and temperature gradient was observed under them which decreased from the middle to the border of the crown projection area, constituting another source of environmental variation in the microscale system, in keeping with the results obtained by Franco and Nobel (1989).

Despite the marked differences in solar radiation and temperature between shrubs and bare soil, the distribution of *T. aoracanthus* was in general not associated with shrubs. It was only negatively associated with *B. retama* and *L. tenuispinosum* in the AP and positively related to *Z. punctata* on WH.

In the AP, under *B. retama*, the soil was cooler and darker (Table 2), likely due to the shape (Table 1) and decumbent position of its dense imbricate stems. Franco and Nobel (1989) proposed that CO₂ assimilation in cacti is drastically reduced by some nurse plants that attenuate PAR, consequently affecting host plant fitness. Probably, the exclusion of *T. aoracanthus* under *B. retama* in the AP is the long-term result of a competitive effect for light or temperature, similar to the spatial dissociation of *Lophophora diffusa* (Cactaceae) from the colder and shadier environment observed under the canopy of *Celtis pallida* (Zuñiga *et al.* 2005).

Instead, the presence of *T. aoracanthus* under *B. retama* in the SP can be a product of a better-lighted

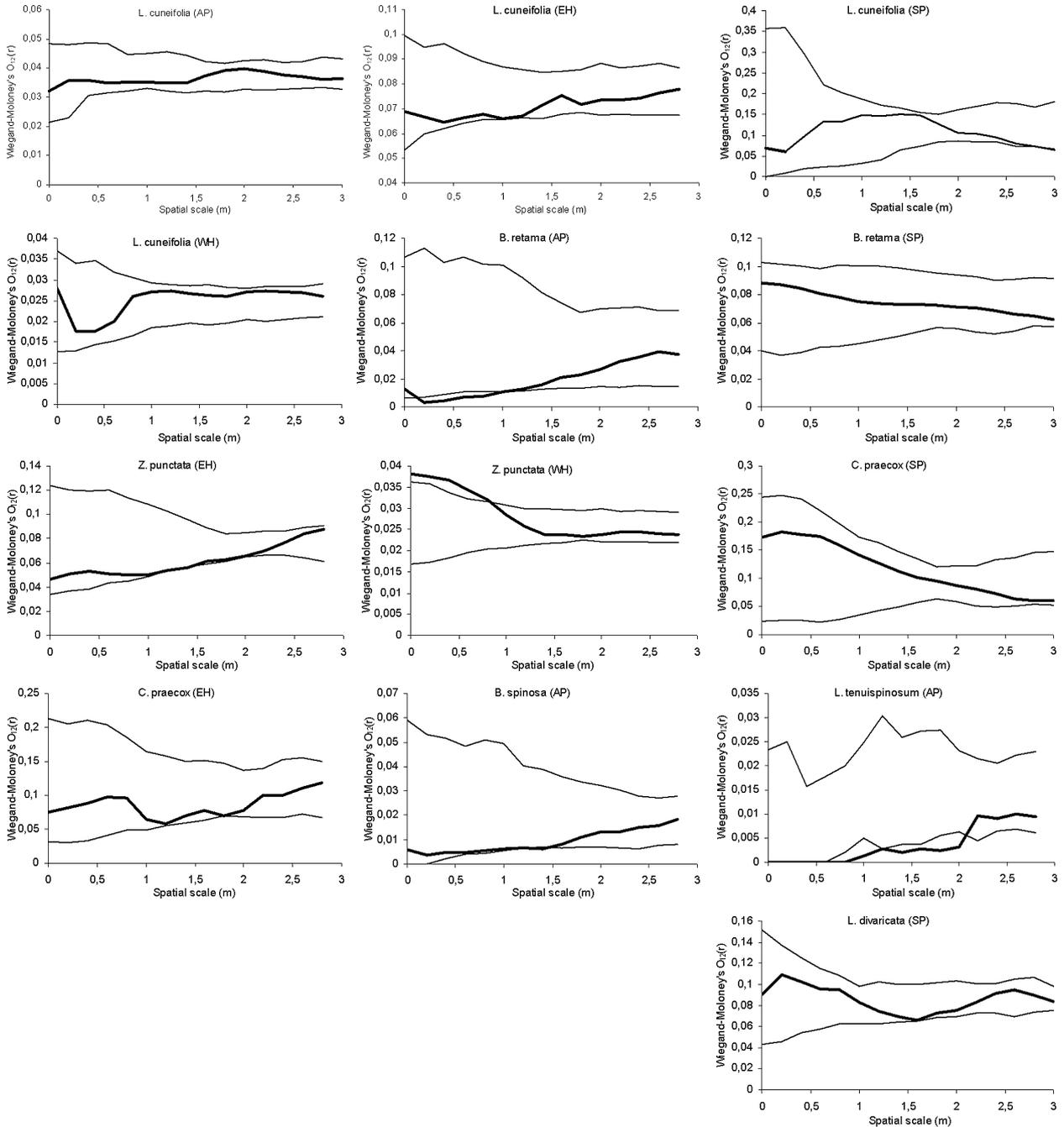


Fig. 2. Analysis of the spatial distribution of *Tephrocactus aoracanthus* with respect to shrubs found in all physiographic units: alluvial plain (AP), sandy plain (SP), west hillside (WH) and east hillside (EH). Bold line shows the empirical function Wiegand–Moloney’s $O_{12}(r)$ and thin lines show the confidence interval generated by the 5th highest and 5th lowest values of 99 Monte Carlo simulations of ‘Toroidal shift’ null model. *B. retama*, *Bulnesia retama*; *B. spinosa*, *Bougainvillea spinosa*; *C. praecox*, *Cercidium praecox*; *L. cuneifolia*, *Larrea cuneifolia*; *L. divaricata*, *Larrea divaricata*; *L. tenuispinosum*, *Lycium tenuispinosum*; *Z. punctata*, *Zuccagnia punctata*.

and warmer environment provided by the greater height and lower cover of shrubs (Table 1) and by the upward orientation of their main stems.

The negative association with *L. tenuispinosum* can be mediated by the low architecture of dense spiny stems,

which root upon reaching the ground surface generating new plants of agamic origin (Gonzalez Loyarte 1983), and which could act as a physical barrier to fragile seedlings and/or cladodes since this shrub slightly changes radiation and temperature conditions.

The results show *Z. punctata* as a shrub that neither generated different radiation and temperature microenvironments nor had different sizes on each of the hill-sides (west and east). Possibly, some other variables not analysed in this study (e.g. nutrient content, root interactions, differential water availability) can influence interspecific interactions between *T. aoracanthus* and this shrub.

On a general level, the distribution of *T. aoracanthus* was mostly independent of shrubs, which concurs with other authors like Reyes-Olivas *et al.* (2002), Méndez *et al.* (2004) and López and Valdivia (2007) who postulate that cacti of the opuntoid type can become established on bare soil.

Nonetheless, studies so far conducted on Cactaceae have focused on the relationships between this group and the shrubs that compose the landscape (Valiente-Banuet *et al.* 1991; Mandujano *et al.* 1998, 2002; de Viana *et al.* 2000; Méndez *et al.* 2004; López & Valdivia 2007; López *et al.* 2007), but without the methodological tools used (tests: χ^2 and G) allowing detection of intraspecific interactions. In this study it was determined that *T. aoracanthus* presents a strong and positive intraspecific association in all physiographic units studied and on scales lower than 1 m. From this distance, up to 3 m, the intraspecific distribution of cacti was random.

It is likely that in the assemblage of these populations there predominate distance-dependent processes, such as agamic propagation by gravitational fall and by rooting of cladodes which is typical in opuntoids (Bobich & Nobel 2001; Mandujano *et al.* 2007) and in this species in particular (Kiesling 1984). In addition, the permanence of seeds on the ground near the parent plant for time periods exceeding 1 year enhances the relevance of future studies explaining the dispersal mechanisms of this species at different scales, from clusters formation and dynamics to colonization of new environments from a landscape perspective.

The method of analysis proposed by Wiegand and Moloney (2004) affords the possibility of detecting relationships among groups of plants occurring in an explicit spatial context with different environmental variables; therefore, its use is suggested for prospective studies related to interactions between plants and their biophysical environment.

ACKNOWLEDGEMENTS

Thanks to M. Ariza, J. Cáceres and J. Aguilera for assistance in field, N. Horak for the English version and T. Wiegand, PhD for comments.

REFERENCES

- Almirón M. & Martínez Carretero E. (2010) *Echinopsis leucantha* (Gilles ex Salm-Dick) Walp. (Cactoideae). Interacciones con plantas nodrizas en el Desierto Central Argentino. *Multequina* **19**, 77–87.
- Armas C. & Pugnaire F. (2005) Plant interactions govern population dynamics in a semiarid plant community. *J. Ecol.* **93**, 978–89.
- Bailey T. & Gatrell A. (1995) *Interactive Spatial Data Analysis*. Longman Scientific and Technical, Harlow.
- Bertness M. & Callaway R. (1994) Positive interactions in communities. *Trends Ecol. Evol.* **9**, 191–3.
- Bobich E. & Nobel P. (2001) Biomechanics and anatomy of cladode junctions for two *Opuntia* (Cactaceae) species and their hybrid. *Am. J. Bot.* **88**, 391–400.
- Callaway R. & Walker L. (1997) Competition and facilitation: a synthetic approach to interactions in plant communities. *Ecology* **78**, 1958–65.
- Carrillo-García A., Bashan Y. & Bethlenfalvay G. (2000) Resource-island soil and the survival of the gigante cactus, cardón of Baja California Sur. *Plant Soil* **218**, 207–14.
- Cazón A., De Viana M. & Gianello J. (2002) Comparación del efecto fitotóxico de aleloquímicos de *Baccharis boliviensis* (Asteraceae) en la germinación de *Trichocereus pasacana* (Cactaceae). *Ecol. Austral* **12**, 73–8.
- Conell J. (1983) On the prevalence and relative importance of interspecific competition: evidence from field experiment. *Am. Nat.* **122**, 661–96.
- De Viana M., Suhring S. & Manly B. (2000) Application of randomization methods to study the association of *Trichocereus pasacana* (Cactaceae) with potential nurse plants. *Plant Ecol.* **156**, 193–7.
- Diggle P. (1983) *Statistical Analysis of Spatial Point Patterns*. Academic Press, London.
- Flores-Martínez A., Ezcurra E. & Sánchez-Colón S. (1994) Effect of *Neobuxbaumia tetetzo* on growth and fecundity of its nurse plant *Mimosa luisiana*. *J. Ecol.* **82**, 325–30.
- Franco A. & Nobel P. (1989) Effect of nurse plants on the microhabitat and growth of cacti. *J. Ecol.* **77**, 870–86.
- Gonzalez Loyarte M. (1983) Estudios sobre la erosión en la Formación El Zampal. *Serie Científica* **29**, 13–15.
- Haase P. (1995) Spatial pattern analysis in ecology based on Ripley's K-function: introduction and methods of edge correction. *J. Veg. Sci.* **6**, 575–82.
- Hacker S. & Gaines S. (1997) Some implications of direct positive interactions for community species diversity. *Ecology* **78**, 1966–75.
- Holmgren M., Scheffer M. & Huston M. (1997) The interplay of facilitation and competition in plant communities. *Ecology* **78**, 1966–75.
- Kiesling R. (1984) Estudios en Cactaceae de Argentina: *Maihueniopsis*, *Tephrocactus* y géneros afines (Opuntioideae). *Darwiniana* **25**, 171–215.
- Kiesling R. (2003) *Flora de San Juan. República Argentina*, Vol. **II**. Estudio Sigma, Buenos Aires.
- Leirana-Alcocer J. & Parra-Tabla V. (1999) Factors affecting the distribution, abundance and seedling survival of *Mammillaria gaumeri*, an endemic cactus of coastal Yucatán, Mexico. *J. Arid Environ.* **41**, 421–8.
- López R. & Valdivia S. (2007) The importance of shrub cover for four cactus species differing in growth form in an Andean semi-desert. *J. Veg. Sci.* **18**, 263–70.

- López R., Valdivia S. & Quintana N. (2007) The role of nurse plants in the establishment of shrub seedlings in the semi-arid subtropical Andes. *Oecologia* **152**, 779–90.
- McAuliffe J. (1984) Sahuaro-nurse tree associations in the Sonoran Desert: competitive effects of Sahuaros. *Oecologia* **64**, 319–21.
- Mandujano M., Flores-Martinez A., Golubov J. & Ezcurra E. (2002) Spatial distribution of three globose cacti in relation to different nurse-plant canopies and bare areas. *Southwest. Nat.* **47**, 162–8.
- Mandujano M., Golubov J. & Huenekke L. (2007) Effect of reproductive modes and environmental heterogeneity in the population dynamics of a geographically widespread clonal desert cactus. *Popul. Ecol.* **49**, 141–53.
- Mandujano M., Montaña C., Méndez I. & Golubov J. (1998) The relative contribution of sexual reproduction and clonal propagation in *Opuntia rastrera* from two habitats in the Chihuahuan Desert. *J. Ecol.* **86**, 911–21.
- Mauseth J. (2006) Structure–function relationships in highly modified shoots of Cactaceae. *Ann. Bot.* **98**, 901–26.
- Méndez E., Guevara J. & Estevez O. (2004) Distribution of cacti in *Larrea* spp. shrublands in Mendoza, Argentina. *J. Arid Environ.* **58**, 451–62.
- Raventós J., Wiegand T. & de Luis M. (2010) Evidence for the spatial segregation hypothesis: a test with nine-year survivorship data in a Mediterranean fire-prone shrubland. *Ecology* **91**, 2110–20.
- Reyes-Olivas A., García-Moya E. & López-Mata L. (2002) Cacti-shrub interaction in the coastal desert of northern Sinaloa, Mexico. *J. Arid Environ.* **52**, 431–45.
- Schoener T. (1983) Field experiments on interspecific competition. *Am. Nat.* **122**, 240–85.
- Servicio Meteorológico Nacional (1958) Estadísticas climatológicas 1941–1950. Publicación B1.
- Tewksbury J. & Lloyd J. (2001) Positive interactions under nurse-plants: spatial scale, stress gradients and benefactor size. *Oecologia* **127**, 425–34.
- Tielbörger K. & Kadmon R. (2000) Temporal environmental variation tips the balance between facilitation and interference in desert plants. *Ecology* **81**, 1544–53.
- Turner R., Alcorn S., Olin G. & Booth J. (1966) The influence of shade, soil and water on Saguaro seedling establishment. *Bot. Gaz.* **127**, 95–102.
- Valiente-Banuet A., Bolognaro-Cravenna A., Briones O. *et al.* (1991) Spatial relation between cacti and nurse shrubs in a semi-arid Environment in central Mexico. *J. Veg. Sci.* **2**, 15–20.
- Valiente-Banuet A. & Ezcurra E. (1991) Shade as a cause of the association between the cactus *Neobuxbaumia tetetzo* and the nurse plant *Mimosa luisana* in the Tehuacán Valley, México. *J. Ecol.* **79**, 961–71.
- Wiegand K., Florian J. & Ward D. (2000) Do spatial effects play a role in the spatial distribution of desert-dwelling *Acacia raddiana*. *J. Veg. Sci.* **11**, 473–84.
- Wiegand T., Kissling W., Cipriotti P. & Aguiar M. (2006) Extending point pattern analysis to objects of finite size and irregular shape. *J. Ecol.* **94**, 825–37.
- Wiegand T. & Moloney K. (2004) Rings, circles and null-models for point pattern analysis in ecology. *Oikos* **104**, 209–29.
- Yeaton R. (1978) A cyclical relationship between *Larrea Tridantata* and *Opuntia Leptocaulis* in the Northern Chihuahuan Desert. *J. Ecol.* **66**, 651–6.
- Yeaton R. & Cody M. (1976) Competition and spacing in plant communities: the Northern Mohave Desert. *J. Ecol.* **64**, 689–96.
- Yeaton R. & Romero Manzanares A. (1986) Organization of Vegetation Mosaics in the *Acacia Schaffneri-Opuntia Strep-tacantha* association, Southern Chihuahuan Desert, Mexico. *J. Ecol.* **74**, 211–17.
- Zavala-Hurtado J. A. (1982) Estudios ecológicos en el valle semiárido de Zapotitlán, Puebla. I. Clasificación numérica de la vegetación basada en atributos binarios de presencia o ausencia de las especies. *Biotica* **7**, 99–120.
- Zuloaga F. & Morrone O. (1999) *Catálogo de las Plantas Vasculares de la República Argentina. II. Dicotyledoneae (Acanthaceae-Euphorbiaceae) y (Fabaceae-Zygophyllaceae)*. Missouri Botanical Garden, St. Louis.
- Zuñiga B., Malda G. & Suzán M. (2005) Interacciones Plantanodrizas en *Lophophora diffusa* (Cactaceae) en un desierto subtropical de México. *Biotrópica* **37**, 351–6.