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Water availability and the competitive effect of a columnar cactus on its nurse plant

Arturo Flores-Martínez¹, Exequiel Ezcurra², Salvador Sánchez-Colón¹

¹ Departamento de Botánica, Escuela Nacional de Ciencias Biológicas, Instituto Politécnico Nacional. Carpio y Plan de Ayala, C.P. 11340, México D.F., Mexico.

² Centro de Ecología, Universidad Nacional Autónoma de México, Apartado Postal 70-275, C.P. 04510, México D.F., Mexico. Fax 54-5 622 89 95; e-mail afloresm@alquimia.ench.ipn.mx, aflores@miranda.ecologia.unam.mx.

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Abstract – A field study was conducted in a semi-arid tropical ecosystem in Mexico to test whether competition for soil water is the causal mechanism underlying the negative effect of the columnar cactus *Neobuxbaumia tetetzo* on its nurse plant *Mimosa luisana* and to examine how this relationship varies over time. The effect of irrigation was evaluated by recording the production of leaves, modules (i.e. internodes with an axillary bud), inflorescences and fruits in shrubs growing either isolated or associated with juvenile or adult columnar cacti. 4 00l of water, in five doses of 80l each every 15 d, were added to the treatment plants; no water other than rainfall was added to control plants. Additionally, to evaluate how the effect of the columnar cacti on the shrubs may vary among years we made a comparison of the production of plant structures between 2 years of contrasting rainfall. The irrigation treatment increased the production of modules, inflorescences and fruits, but not of leaves. Shrub response to watering was also dependent on class of association: those associated with juvenile cacti showed a higher response to irrigation than any other treatment. Our results show that water addition increases the production of structures and partially reduces the negative effect of the cactus on nurse shrub, thus supporting the hypothesis of competition for water. The negative effect of the cacti on their nurse plants was present during both years of observations, but the intensity of the negative effect varies from relatively wet to dry years. The results are discussed in relation to how temporal changes in resource availability affect the results of competitive interactions and the importance of this mechanism in the structure and dynamics of this dryland community. © Elsevier, Paris

Arid plant communities / plant competition / Mexico / resource availability / Tehuacan Valley

1. INTRODUCTION

The importance of competition in stressful environments in general, and arid land communities in particular, has been a controversial subject [5, 6, 21, 24, 34, 36, 43]. Although the existence of competition has been indirectly inferred (e.g. by analysing the dispersion patterns of species) few experiments have attempted to test the existence of competition between arid-land plants [3, 13; see 8, 18 for reviews of field experiments testing competition in plants].

In some arid land communities the establishment of certain species has been shown to occur mostly beneath the canopy of other plants where micro-environmental conditions are more favourable [2, 15, 23, 27, 38]. It has been suggested that, in this relationship, plants establishing beneath a canopy can negatively affect their nurse plants, so that if the newly-established plant reaches a size comparable to that of the nurse, the latter might eventually be replaced by the nursed individual [26, 27, 39, 40, 44, 45]. However,

evidence supporting this hypothesis of a negative effect on the nurse plant and its eventual replacement comes from indirect observations such as a reduction of plant vigour [45], an increase in the proportion of dead basal area [26, 39], and analyses of the distributional patterns of species [27, 39, 40]. Moreover, the few experimental field studies carried out so far have mainly addressed the question of whether or not competition occurs, rather than attempting to identify what the limiting resources are [19] or evaluating the intensity of competition over time and the consequences of its variation [18, 21].

Results from a previous study [12] showed that the columnar cactus *Neobuxbaumia tetetzo* can negatively affect the growth and fecundity of its nurse plant *Mimosa luisana*, and that this negative effect is more intense in the larger shrubs. As has been suggested by other investigators for similar arid systems, competition for water may be the cause of this negative effect. In this paper we attempt to evaluate this hypothesis by experimentally manipulating the amount of water

available to the shrub and by measuring the resulting effects on its growth and fecundity. We also report how the competitive effects of the cactus on its nurse plant varied between 2 years of contrasting rainfall by comparing a relative dry year (the complete data for this year were reported in [12]) with a relative moist year. If water actually is the limiting resource which the cacti and the shrubs compete for, then artificial irrigation or extraordinary rainy seasons should ameliorate the negative effect of the cactus on its nurse, allowing a relative increase in shrub growth and fecundity.

2. METHODS

2.1. Study site and species

The study was conducted on a hillside at the Botanical Garden of the Instituto Nacional de Ecología (INE), in the semi-arid Valley of Zapotitlán (18°20'N, 97°28'W), a local basin of the Tehuacán Valley in the State of Puebla, Mexico. The climate is semi-arid with a marked rainy season in the summer (June–September). The mean annual rainfall is 380 mm, the mean annual temperature is 21 °C, and the annual evaporative demand is around 1 800 mm [16, 32]. The aridity of this site is due to the rain-shadow cast by the Eastern Sierra Madre (locally known as Sierra de Zongolica) on the predominantly easterly atmospheric circulation. Soils are calcareous lithosols, derived from sedimentary and metamorphic rocks. The main vegetation type is a xerophytic scrub [33] in which giant columnar cacti are dominant elements [46].

Mimosa luisana Brandeg is a perennial deciduous shrub endemic to the Tehuacán Valley, where it occurs with a mean density of 2 400 ind·ha⁻¹, and a mean cover of 2 850 m²·ha⁻¹. *Neobuxbaumia tetetzo* (Coulter) Backeberg is a branched columnar cactus reaching a maximum height of 12 m, and is also endemic to the Tehuacán Valley. Densities of individuals taller than 1 m can reach up to 1 200 plants·ha⁻¹. The root system of *N. tetetzo* is shallow, with considerable lateral spread. Most of the roots occupy the upper 20 cm of the soil. The root system of *M. luisana* is also relatively shallow; most of the roots occupy the first 30 cm of the soil profile, although some roots tap the lower soil horizons penetrating deeper than 1 m when soil conditions allow [39, and our own observations].

2.2. Irrigation experiments

To evaluate how variations in soil water availability modify the competitive effect of *N. tetetzo* on its nurse plant, we selected 32 large shrubs (i.e. shrubs with a canopy volume > 3 m³). These shrubs were classified into three association classes: non-associated shrubs

(shrubs whose closest cactus was at a distance greater than twice the average diameter of the shrub's crown), shrubs associated with juvenile columnar cacti (juvenile cacti were defined as plants between 0.2 and 1.0 m tall) and shrubs associated with large (taller than 1.5 m) columnar cacti. Associated shrubs were defined as those having at least one columnar cactus beneath their canopy. Eleven shrubs (3 non-associated, 3 associated with juvenile cacti, and 5 associated with large cacti) were selected for irrigation treatments (the number of plants selected was limited by the availability of water) and the other 21 were used as controls (5, 5 and 11 respectively for each association category).

Irrigation consisted of the addition of 900 L of water per shrub, applied in 5 successive doses of 80 L each, starting on June 1 and then every second week (except on June 30 when the soil was saturated by a recent rainfall). Water was slowly poured with a bucket under the canopy of the shrub. To avoid surface runoff, the treatment was carried out gradually at intervals during a 30 min period, making sure that the water infiltrated into the soil. The total amount of water applied was approximately equivalent to 100 mm of rain falling over an area of approx. 4 m² beneath each shrub. To prevent any possible interference from neighbouring plants, trenches were carefully dug around each shrub to cut any incoming roots (care was taken not to sever outgoing roots that clearly belonged to the focal plants).

In each irrigated shrub 40 non-ramified terminal branches were randomly chosen and 10 in control shrubs (we selected a higher number of branches in the irrigated plants in order to estimate the branch transition probabilities for another study). These branches were individually marked before leaf production started (April 1991) and the length and number of modules in each one was recorded. Production of leaves, number of modules (a module was defined as an internode with an axillary bud), inflorescences and fruits were periodically recorded for each marked branch during the growing season (May 1991 to January 1992).

2.3. Between-year variation

In 1990 we evaluated the negative effect of the cactus on its nurse plant considering both the sizes of the shrub and of the cactus [12]. In this previous study we found that large shrubs were more susceptible to the competitive effect of the cactus. To evaluate the variability of this effect through time, in 1991 we followed the production of leaves, modules, inflorescences and fruits of the same large shrubs (isolated or associated to juvenile or adult cacti) used in 1990. The evaluation of growth and fecundity was made in a similar manner in both years [12]. The 2 years, how-

ever, were different in rainfall: in 1990 the total annual precipitation was 350 mm (a relatively dry year), whereas 460 mm of rain fell in 1991 (a relatively wet year).

2.4. Statistical analysis

Values of cumulative total production of leaves, modules, inflorescences and fruits per shrub (corrected by the initial number of modules of the shrub) were analysed by means of log-linear models [7, 28], using the GLIM package. Log-linear models were preferred over traditional ANOVAS because the dependent variables were in all cases discrete count data with non-normal errors. In log-linear models, the predicted values are calculated as the exponential transform of a linear function of the independent predictors. The fit of the model (i.e. the significance of the differences between the observed and the fitted values) is evaluated by means of a χ^2 test. The statistical factors considered in the analysis of the irrigation experiments were: (a) irrigation treatment (irrigated vs. control), (b) association class, and (c) the interaction between these.

The factors included in the analysis of the inter-annual variation were: (a) association class, (b) season (1990 or 1991), and (c) the interaction terms among these. In this case, we used a repeated-measurement analysis because the same shrubs were followed over the 2 years. As the response variables were frequencies whose errors should follow a Poisson distribution, we analysed the data following a split-unit design [29] but keeping the log-linear approach. For this, we followed the procedure suggested by Von Ende [42] to first test the pooled effects of the main factor (i.e. association class) independently of time, and then to test for the effect of time within shrubs, and the corresponding interactions.

When the residual deviance of a log-linear model is significantly higher than the residual degrees of freedom, the data points are over-dispersed, i.e. there is a significant residual variation that is not explained by the model. Over-dispersion commonly arises from the tendency of the error values in certain data sets to follow a negative binomial distribution rather than the expected Poisson distribution [7]. As there was evidence of over-dispersion in all our analyses, we re-scaled the deviance of the models in order to obtain residual deviance that were not statistically significant. This procedure accordingly reduced the significance levels of all factors included in the models, thus taking into account the background statistical noise in the data and making the test of hypotheses more conservative.

3. RESULTS

3.1. Irrigation experiments

The irrigation treatment produced a significant increase in the number of stem modules, inflorescences and fruits produced by *M. luisana*, but did not produce a significant increase in the number of leaves (table 1). The response pattern, however, was affected by the association class of the shrub.

Module production (a measure of branch elongation and therefore of shrub growth) was significantly affected by shrub association class and by water addition. Shrubs associated with columnar cacti always produced fewer modules than non-associated shrubs. On the other hand, irrigated shrubs always produced more modules than control shrubs of the same association class. No significant interaction was found between irrigation and shrub association class. It is

Table 1. Analysis of the χ^2 deviance of the log-linear models for the production of leaves, modules, inflorescences and fruits of *Mimosa luisana* shrubs in the irrigation experiments; *** = $P < 0.001$, n.s. = $P > 0.1$.

Source of variation	Scaled deviance	d.f.	P
LEAVES			
Model	4.77	5	n.s.
Irrigation	1.04	1	n.s.
Association	1.47	2	n.s.
Irrigation \times Assoc.	2.562	2	n.s.
Residual	38.62	26	
MODULES			
Model	15.27	5	0.009
Irrigation	6.97	1	0.008
Association	7.56	2	0.023
Irrigation \times Assoc.	0.74	2	n.s.
Residual	37.53	26	
INFLORESCENCES			
Model	16.82	5	0.005
Irrigation	3.21	1	0.073
Association	5.90	2	0.052
Irrigation \times Assoc.	7.71	2	0.021
Residual	37.69	26	
FRUITS			
Model	29.33	5	***
Irrigation	21.18	1	***
Association	2.53	2	n.s.
Irrigation \times Assoc.	5.62	2	0.060
Residual	37.88	26	

important to point out that irrigated shrubs associated with juvenile or large cacti did not differ significantly from non-watered, non-associated shrubs, in relation to module production (respectively: $t=0.684$, $P=0.50$; $t=1.68$, $P=0.104$); the increase in module production brought forth by watering the shrubs balanced the negative effect of the cactus.

In shrubs associated with large cacti and in non-associated shrubs, inflorescence production was not significantly affected by irrigation. By contrast, in shrubs associated with juvenile cacti, the number of inflorescences produced under irrigation was significantly higher than that of control shrubs (figure 1). This pattern, however, was not reflected in fruit production (figure 1). Non-associated irrigated shrubs, and irrigated shrubs associated with juvenile cacti,

produced significantly more fruits than non-watered shrubs of the same association class. Fruit production of shrubs associated with large cacti was increased to a lesser amount, but also significantly ($t=2.68$, $P=0.012$), by irrigation.

3.2. Between-year variation

Leaf production did not differ significantly among shrubs of different association class (table II). However, it decreased significantly during the wetter year, especially in the non-associated shrubs, and in shrubs associated with large cacti (table II, figure 2). By contrast, there were significant differences in module, inflorescence and fruit production for shrubs of different association class over the two-year period.

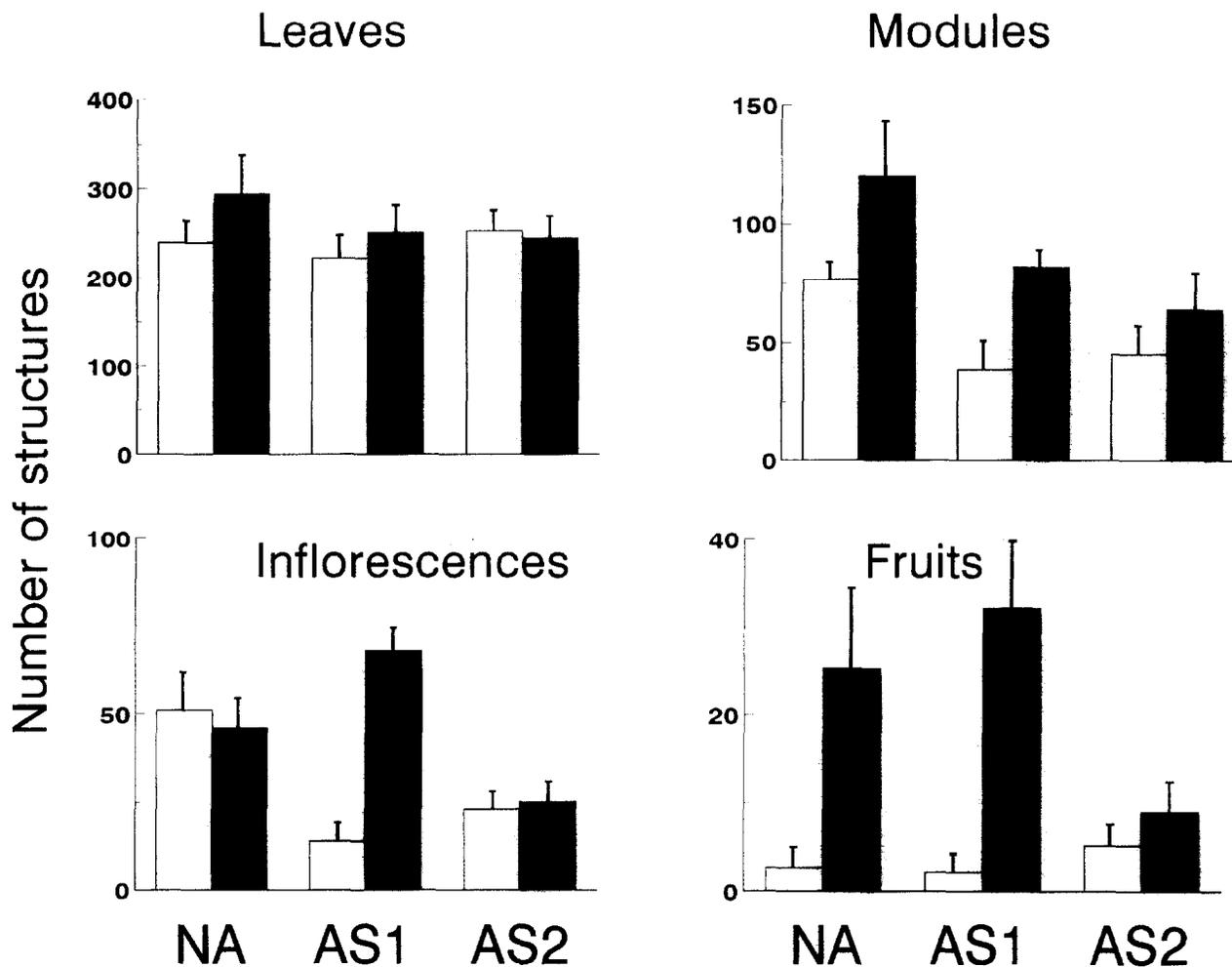


Figure 1. Total Average production of leaves, modules, inflorescences and fruits by *Mimosa luisana* shrubs. Empty bars, control shrubs; solid bars, irrigated shrubs. NA = Non-associated shrubs, AS1 = Shrubs associated with juvenile cacti, and AS2 = Shrubs associated with large cacti. Vertical lines represent one standard error.

Table II. Analysis of the χ^2 deviance of the log-linear models for the production of leaves, modules, inflorescences and fruits of *Mimosa luisana* shrubs for 2 years, considering the effect of repeated measurements as a split-units design; *** = $P < 0.001$, n.s. = $P > 0.05$.

Source of Variation	Scaled deviance	d.f.	P
LEAVES			
Between-subjects			
Association	2.918	2	n.s.
Residual	14.74	15	
Within-subjects			
Time	4.398	1	0.0359
Association \times Time	4.439	2	n.s.
Residual	8.8223	15	
MODULES			
Between-subjects			
Association	18.51	2	***
Residual	14.186	15	
Within-subjects			
Time	0.299	1	n.s.
Association \times Time	24.33	2	***
Residual		15	
INFLORESCENCES			
Between-subjects			
Association	25.37	2	***
Residual	14.081	15	
Within-subjects			
Time	1.57	1	n.s.
Association \times Time	29.81	2	***
Residual	8.074	15	
FRUITS			
Between-subjects			
Association	8.305	2	0.0157
Residual	22.88	15	
Within-subjects			
Time	4.43	1	0.0353
Association \times Time	11.512	2	0.0214
Residual	15.24	15	

Large shrubs associated with juvenile cacti produced significantly more modules in the second, wetter year (*table II, figure 2*). Inflorescence production showed a different pattern, decreasing in the second year for non-associated shrubs, increasing in shrubs associated with juvenile cacti, and remaining almost constant in shrubs associated with large columnar cacti. Fruit production followed a pattern similar to inflorescences, but shrubs associated with large columnar cacti showed a reduction in fruit production.

Log-linear models (*table II*) show that the interaction terms association class \times time were statistically significant for most of the variables examined. This means that the effects of the association class significantly varied from one year to the next. These results are indicative of a significant variability over time in the intensity of competition between these two species. Particularly important in this respect is the fact that shrub growth (module production) and fecundity showed important qualitative differences over the 2 years: while module production increased in the second (moister) year, the production of inflorescences and fruits decreased.

4. DISCUSSION

So far, two main hypotheses have been put forward to account for the negative effect of the cacti on their nurse plants in arid environments: competition for water [26, 39] and mechanical injury [45]. The results obtained in our experiments support the hypothesis that competition is the likely causal mechanism behind nurse plant decline, and that water availability plays a fundamental role in this process. It is important to bear in mind, however, that we measured the consequences of potential competition for water through external variables such as branch, leaf, flower and fruit production. However, water stress may also affect other variables, such as the water-use efficiency, leaf-area index, leaf size or intercellular leaf CO_2 concentration [9, 10, 22, 35].

The results of the irrigation experiments clearly show that watering increases the production of modules and fruits in all shrubs, and of inflorescences in shrubs associated with juvenile cacti. This result is consistent with the hypothesis that water is the most limiting resource in desert ecosystems [31]. Leaf production, in contrast, was not affected by watering. This is possibly due to the fact that leaves can be produced either as axillary leaves in long shoots (i.e. new modules) or in verticils on short shoots [1]. The production of axillary leaves is always accompanied by the metabolically costly production of long internodes, whereas the production of verticillate leaves implies a minimal cost in shoot production. Thus, leaves can be produced at very different costs, and the total number of leaves may not necessarily reflect the differential physiological effort invested in their production.

As suggested by the module production data, canopy growth increased with higher water availability induced either by experimental irrigation or by natural rainfall. In 1990 (a relatively dry year) large shrubs associated with juvenile individuals of *N. tetetzo* produced only about 15 % of the number of modules that were produced by non-associated shrubs. In 1991 (a relatively wet year) their production increased to 52 %

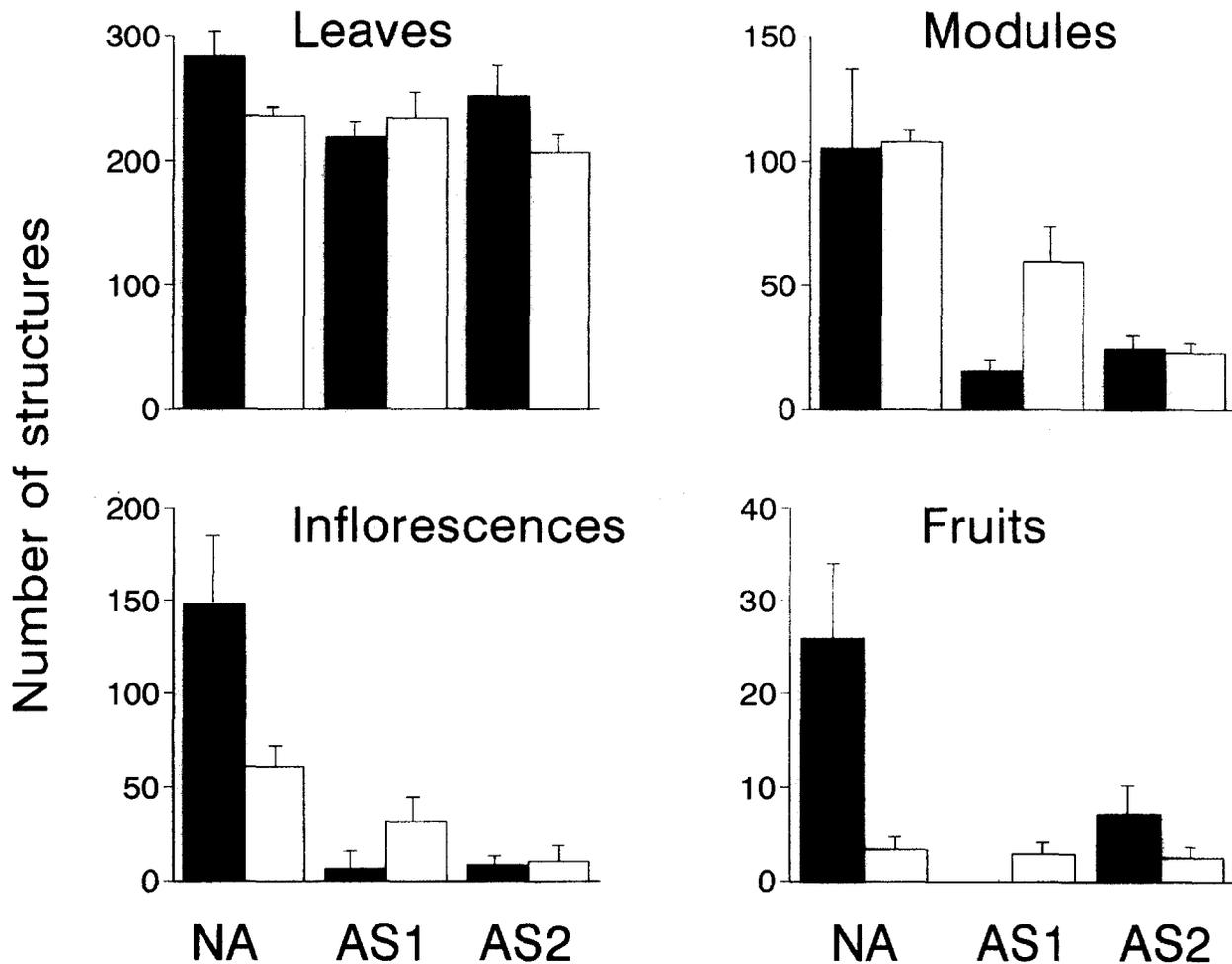


Figure 2. Production of leaves, modules, inflorescences and fruits by *Mimosa luisana* (May 1990 to February 1992) in isolation (NA), associated with juvenile columnar cacti (AS1), and associated with large columnar cacti (AS2). Solid bars, May 1990 to January 1991; empty bars, May 1991 to January 1992. Vertical lines represent one standard error.

of that of non-associated individuals. Similarly, irrigation caused individuals of this same association class to increase their growth from around 50 % to almost 70 % of the growth of similar non-associated plants. These results suggest that increasing water availability ameliorates the negative effect of the cactus on the shrub. Shrubs associated with large cacti showed no conspicuous differences between 1990 and 1991. In both years these shrubs produced only some 25 % of the modules produced by non-associated shrubs. However, under experimental irrigation this group reached a module production of about 50 % of that of non-associated shrubs. Although under experimental irrigation shrubs associated with large cacti did show a reduction of the negative effect of the cactus, it seems unlikely that 1 year could occur with sufficient rainfall to completely offset the competitive effect of the

cactus. These results are possibly a product of the extremely high efficiency of cacti for soil water uptake [3, 30].

The role of competition in the structure of arid plant communities has been widely debated [14]. One of the most controversial points concerns the question: under what condition (i.e. low or high resource availability) is competition most important for living organisms? For *M. luisana* the most intense competitive effect (*sensu* [17]) on shrub growth (i.e. module production) was observed in the drier year. Fonteyn and Mahall [13] and Knoop and Walter [25] also found that the strongest negative effect of plants upon their neighbours occurred under conditions of low resource availability.

The effect of water availability on shrub fecundity was less clear-cut than in module production. During

1991 flower and fruit production were lower than in the drier 1990. Irrigation, however, caused an important increase in the production of these structures. This counter-intuitive finding (moister years produced less flowers and fruits, but irrigation increased them) is possibly due to the fact that flower and fruit production may not depend only on the total amount of water but also on its distribution in time [8, 11], on the events of physiological stress undergone by the individual plant during flower and fruit formation [4], or on stored resources from the previous season [35]. In 1991, a single rain event accounted for 40 % of the total annual rainfall, whereas the water supply of the experimentally irrigated shrubs was more constant. We cannot discard the possibility, however, that the cause of this contrasting behaviour may be due to environmental or climatic queues other than precipitation. Nevertheless, in terms of fruit production (one of the most important estimators of reproductive success) it may be concluded that (a) non-associated shrubs in the field produce significantly more fruits than associated shrubs during years of high fruit production, and that (b) in years of low fruit production, a constant supply of additional water may significantly increase the fruit count in non-associated plants and in plants associated with juvenile cacti, but may not be enough to significantly increase the number of pods in shrubs associated with large cacti.

The largest differences between years in relative module production were observed in shrubs associated with juvenile cacti. A similar result was observed in fruit production between irrigated and non-irrigated shrubs: plants associated with juvenile cacti responded markedly to watering, while those associated with large cacti did not. This suggests that the outcome of the interaction during this stage of the relationship (i.e. nurse shrub - juvenile cactus) is highly dependent on the amount of rainfall and, therefore, on the water supply to the soil. As the associated cacti grow to their adult size, the negative effect on the nurse shrub becomes more permanent and varies little within the normal range of rainfall. Years wetter than 1991 have a probability of occurrence of *c.* 0.20, and seasons with more rainfall than that simulated by the irrigation experiment have a probability of occurrence lower than 0.05 [37].

Our results show that the competitive effect of the cactus on its nurse plant (except for leaf production) was statistically significant and quantitatively important throughout the 2 year observation period. Although this supports the idea that competition may be permanent in time, the fact that the interaction between association class and time was also statistically significant for almost all the variables tested (except leaf production) indicates that the intensity of competition varies between years, as a result of

changes in water availability. These complex temporal variations in the intensity of competition render the system difficult to model with precision, as any model that attempts to explain not only the outcome of the interaction but also the time necessary for the process to occur should incorporate the potentially strong effect of temporal variability. Previous models simulating the replacement process in desert ecosystems without considering this phenomenon (e.g. [27, 40, 41]) should be revised under the light of these results.

In conclusion, our investigation shows that water is a limiting factor on shrub canopy growth, and that increased water availability lessens the competitive effect of the cactus on the shrub. Competition varies according to the size of the cactus, and it also varies over time; it is more intense during the drier periods and it potentially plays a major role as a force structuring plant communities in dry environments.

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REFERENCES

- [1] Bell A.D., *Plant form: an illustrated guide to flowering plant morphology*, Oxford University Press, Oxford, 1991.
- [2] Belsky A.J., Amundson R.G., Duxbury J.M., Rhia J.H., Ali A.R., Mwonga S.M., The effects of trees on their physical, chemical and biological environments in a semi-arid savanna in Kenya, *J. Appl. Ecol.* 26 (1989) 1005-1024.
- [3] Briones V.O., *Competencia en plantas desérticas: Inferencias del patrón de distribución y evidencias experimentales de los efectos de la competencia en tres formas de vida del Desierto Chihuahuense*, Ph. D. Thesis. Universidad Nacional Autónoma de México. México, 1992.
- [4] Chiarello N.R., Gulmon S.L., Stress effects on plant reproductions, in: Mooney H.A., Winner W.E., Pell E.J. (eds), *Response of Plants to Multiple Stresses*, Academic Press, 1991, pp. 161-188.
- [5] Cody M.L., Structural niches in plant communities, in: J. Diamond, T.J. Case (eds), *Community Ecology*, Harper & Row Publications, New York, 1986, pp. 381-405.
- [6] Connell J.H., Some mechanisms producing structure in natural communities: a model and evidence from field experiments, in: M.L. Cody, J. Diamond (eds), *Ecology and Evolution of Communities*, Harvard University Press, Cambridge, 1975, pp. 460-490.
- [7] Crawley M.J., *GLIM for Ecologists*, Blackwell Scientific Publications, 1993, Oxford.
- [8] Dittommaso A., Aarssen L.W., Resource manipulation in natural vegetation: a review, *Vegetatio* 84 (1989) 9-29.

- [9] Donovan L.A., Ehleringer J.R., Carbon isotope discrimination, water use efficiency, growth and mortality in a natural shrub population, *Oecologia* 100 (1994) 347-354.
- [10] Ehleringer J.R., Intraspecific competitive effects on water relations, growth and reproduction in *Encelia farinosa*, *Oecologia* 63 (1984) 153-158.
- [11] Evenari M., Synthesis, Goodall D.W., Perry R.A. (eds), *Arid-Land Ecosystems*. Cambridge University Press, 1981, pp. 555-591.
- [12] Flores-Martínez A., Ezcurra E., Sánchez-Colón S., Effect of *Neobuxbaumia tetetzo* on growth and fecundity of its nurse plant *Mimosa luisana*, *J. Ecol.* 82 (1994) 325-330.
- [13] Fonteyn P.J., Mahall B.E., An experimental analysis of structure in a desert plant community, *J. Ecol.* 89 (1981) 883-896.
- [14] Fowler N., The role of competition in plant communities in arid and semi-arid regions, *Ann. Rev. Ecol. System.* 17 (1986) 89-110.
- [15] Franco A.C., Nobel P.S., Effect of the nurse plant on the microhabitat and growth of cacti, *J. Ecol.* 77 (1989) 870-886.
- [16] García E., Modificaciones al Sistema Climático de Köppen, Instituto de Geografía UNAM, México, 1981.
- [17] Goldberg D.E., Components of Resource Competition in Plant Communities, in: Grace J.B., Tilman D. (eds), *Perspectives on Plant Competition*, Academic Press, 1990, pp. 27-49.
- [18] Goldberg D.E., Barton A.M., Patterns and consequences of interspecific competition in natural communities: a review of field experiments with plants, *Am. Nat.* 139 (1992) 771-801.
- [19] Grace J.B., On the relationship between plant traits and competitive ability, in: Grace J.B., Tilman D. (eds), *Perspectives on Plant Competition*, Academic Press, 1990, pp. 51-56.
- [20] Grime J.P., *Plant Strategies and Vegetation Processes*, John Wiley & Sons, 1979.
- [21] Gurevitch J., Collins S.L., Experimental manipulation of natural plant communities, *Trends Ecol. Evol.* 9 (1994) 94-98.
- [22] Harrington R.A., Fownes J.H., Meinzer F.C., Scowcroft P.G., Forest growth along a rainfall gradient in Hawaii: Acacia koa stand structure, productivity, foliar nutrients, and water -and nutrient-use efficiencies, *Oecologia* 112 (1995) 227-284.
- [23] Jaksic F.M., Fuentes E.R., Why are native herbs in the Chilean Matorral more abundant beneath bushes: microclimate or grazing? *J. Ecol.* 68 (1980) 665-669.
- [24] Kemp P.R., Phenological pattern of Chihuahuan Desert plants in relation to the timing of water availability, *J. Ecol.* 71 (1983) 427-436.
- [25] Knoop W.T., Walker B.H., Interaction of woody and herbaceous vegetation in a Southern African Savannah, *J. Ecol.* 73 (1985) 235-253.
- [26] McAuliffe J., Sahuaro nurse tree associations in the Sonora Desert: competitive effects of sahuaros, *Oecologia* 64 (1984) 319-321.
- [27] McAuliffe J., Markovian dynamics of simple and complex desert plant communities, *Am. Nat.* 131 (1988) 459-490.
- [28] McCullagh, P., Nelder J.A., *Generalized Linear Models*, Chapman & Hall, London, 1983.
- [29] Mead R., *The design of experiments*, Cambridge University Press, New York, 1988.
- [30] Nobel P.S., *Environmental Biology of Agaves and Cacti*, Cambridge University Press, 1988.
- [31] Noy-Meir I., Desert Ecosystem: environment and producers, *Ann. Rev. Ecol. System.* 5 (1973) 25-51.
- [32] Peters E., *Variaciones microclimáticas de un desierto intertropical en el centro de México: algunas implicaciones sobre la vegetación*. B. Sc. Thesis, Universidad Nacional Autónoma de México, México, 1993.
- [33] Rzedowski J., *Vegetación de México*, Limusa, Mexico, 1978.
- [34] Shreve F., *Vegetation of the Sonora Desert*, Carnegie Institute Washington Publications 591 (1951) 1-192.
- [35] Schulze E.D., Plant life forms and their carbon, water and nutrient relations, in: Lange O.L., Nobel P.S., Osmond C.B., Ziegler (eds), *Physiological Plant Ecology II: Water relation and carbon assimilation*, Springer-Verlag, Berlin, 1982, pp. 615-676.
- [36] Tilman D., *Plant strategies and the structure and dynamics of plant communities*, Princeton University Press, Princeton NJ, 1982.
- [37] Valiente L., *Patrones de precipitación en el valle semiárido de Tehuacán, Puebla México*. B. Sc. Thesis, Universidad Nacional Autónoma de México, México, 1991.
- [38] Valiente-Banuet A., Bolongaro-Crevena A., Briones O., Ezcurra E., Rosas M., Nuñez H., Bernard G., Vazquez E., Spatial relationship between cacti and nurse shrub in a semi-arid environment in central México, *J. Veg. Sci.* 2 (1991a) 15-20.
- [39] Valiente-Banuet A., Vite F., Zavala-Hurtado J., Interaction between the cactus *Neobuxbaumia tetetzo* and the nurse *Mimosa luisana*, *J. Veg. Sci.* 2 (1991b) 11-14.
- [40] Vandermeer J., Sahuaro and nurse trees: a new hypothesis to account for population fluctuations, *Southwest. Nat.* 25 (1980) 357-360.
- [41] Vega E., *Empleo de modelos de simulación para el estudio de la dinámica de reemplazamiento y los patrones de disposición espacial en una comunidad vegetal del valle de Zapotitlán Salinas, Puebla*, B. Sc. Thesis, Universidad Nacional Autónoma de México, México, 1992.
- [42] Von Ende C.N., Repeated-measures analysis: Growth and other time-dependent measures, in: Scheiner S.M., Gurevitch J. (eds), *Design and Analysis of Ecological Experiments*, Chapman & Hall, New York, 1993, pp. 113-137.
- [43] Went F.W., The ecology of desert plants, *Sci. Am.* 192 (1955) 68-75.
- [44] Yeaton R.I., A cyclical relationship between *Larrea tridentata* and *Opuntia leptocaulis* in the Northern Chihuahuan Desert, *J. Ecol.* 66 (1978) 651-656.
- [45] Yeaton R.I., Romero-Manzanares A., Organization of vegetation mosaics in the *Acacia shaffneri* - *Opuntia streptacantha* association, Southern Chihuahuan Desert, Mexico, *J. Ecol.* 74 (1986) 211-217.
- [46] Zavala-Hurtado J., *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*, *Biótica* 7 (1982) 99-120.