Copyright Notice

Effect of *Neobuxbaumia tetetzo* on growth and fecundity of its nurse plant *Mimosa luisana*

ARTURO FLORES-MARTÍNEZ, EXEQUIEL EZCURRA and SALVADOR SÁNCHEZ-COLÓN*

*Centro de Ecología, Universidad Nacional Autónoma de México. Apartado Postal 70-275, C.P. 04510, México D.F. and *Departamento de Botánica, Escuela Nacional de Ciencias Biológicas, Instituto Politécnico Nacional. Carpio y Plan de Ayala C.P. 11340, México D.F., Mexico*

Summary

1 A field study was conducted in a semiarid basin located in the Tehuacán Valley in Central Mexico to determine the effect of the columnar cactus *Neobuxbaumia tetetzo* on the growth and fecundity of its nurse plant *Mimosa luisana*.

2 The production of leaves, modules (internodes), inflorescences and fruits was recorded in shrubs of *M. luisana* growing either in isolation, or associated with small or large cacti. The effect of association with cacti was evaluated for three size-classes of shrubs. To test whether the cactus is likely to replace the nurse plant, a projection matrix was used to estimate the finite growth rates of the canopies of isolated large shrubs and of shrubs growing in association with large cacti.

3 The production of leaves, internodes, inflorescences and fruits of shrubs was negatively affected by the presence of columnar cacti growing beneath the nurses' canopies. The negative effect of the cacti on nurse growth was significant in all cases, but it was more important in larger shrubs. The interaction term was also statistically significant in all cases, implying that the effect of the association varies depending on the size of both the shrub and the cactus. The finite growth rate of the canopy estimated for isolated shrubs implied positive growth ($\lambda = 1.402$), while associated shrubs had negative canopy growth ($\lambda = 0.933$).

4 The results show that large columnar cacti can indeed replace their nurse plants by increasing branch mortality and decreasing the production of canopy parts in the nurse. The importance of this association in the structure and dynamics of arid plant communities is discussed.

Keywords: arid plant communities, competition, population matrices, replacement dynamics, Tehuacán Valley

Journal of Ecology (1994) **82**, 325–330

Introduction

The importance of biotic interactions, and particularly of competition, in the structure and the dynamics of arid plant communities is still a controversial subject (Shreve 1951; Connell 1975; Grime 1979; Fonteyn & Mahall 1981; Kemp 1983; Fowler 1986; Fitter & Hay 1987; Tilman 1988). Barbour (1981) pointed the importance of positive relationships in structuring these communities. The best documented cases, reviewed by Valiente-Banuet (1991), concern the effect of nurse plants which favour the establishment of particular species. For example, in the Sonoran Desert, seedlings of *Larrea tridentata* establish preferentially under *Ambrosia dumosa* shrubs (McAuliffe 1988), whereas *Carnegiea gigantea* seedlings establish mainly beneath *Cercidium microphyllum* (Hutto *et al.* 1986). At the Tehuacán Valley, Mexico, particular associations have been observed for three globose cacti (*Mammillaria colina*, *M. casoi* and *Coriphanta pallida*), and two giant columnar cacti (*Neobuxbaumia tetetzo* and *Cephalocereus hoppendstedtii*; Valiente-Banuet *et al.* 1991a).

Studies of this sort of interspecific association have concentrated on the positive effect of the nurse plant on the species establishing beneath its canopy. This maybe due to amelioration of the physical environment, e.g. lower soil temperatures, reduced desiccation (McAuliffe 1984; Franco & Nobel 1988; Valiente-Banuet & Ezcurra 1991) or to reduction of

326

*Effects of a
columnar cactus on
its nurse plant*

predation risk under the nurse plant (Jaksic & Fuentes 1980; McAuliffe 1986). Though it has been sometimes pointed out that the establishing species may have a negative effect on the nurse plant, little attention has been paid to measuring this effect in the field, although attempts have been made to evaluate it through simulation studies (Franco & Nobel 1988, 1989).

It has been suggested that the negative effects on the nurse plant may be caused either by competition for soil resources such as water (McAuliffe 1984) or by direct mechanical injury (Yeaton & Romero-Manzanares 1986). However, this interpretation has been based on indirect observations such as a reduction in the vigour of nurse plants (Yeaton & Romero-Manzanares 1986), a high proportion of dead basal area in shrubs associated with columnar cacti (Valiente-Banuet *et al.* 1991b), or a higher frequency of dead plants among those associated with large cacti (Hutto *et al.* 1986). However, the occurrence of these patterns does not necessarily imply a cause–effect relationship (Fowler 1986).

Little is known about the dynamics of this association. Although it is thought that the nurse plant is affected by the growth of the nursed seedlings in such a way that the initial commensalism gradually becomes an ammensalism or even a competitive relationship (Valiente-Banuet *et al.* 1991b), there is no sound evidence supporting this idea. It has also been suggested that the nursed plant eventually replaces its nurse and then when it dies the space so released is occupied by a radiation-tolerant nurse plant, thus starting the cycle again (Yeaton 1978; McAuliffe 1988; Valiente-Banuet *et al.* 1991b). Thus, the dynamics of this association should be reflected in the dynamics of the whole community. This hypothesis of replacement in arid plant communities has been put forward several times (Yeaton 1978; McAuliffe 1988) and has been used as a basis for modelling the dynamics of these systems either as an analogue of predator-prey systems (Vandermeer 1980) or using Markovian models (McAuliffe 1988).

In the Zapotitlán de las Salinas Basin, part of the Tehuacán Valley in Central Mexico, it has been observed that the establishment of several species of cactus, including the columnar cactus *Neobuxbaumia tetetzo*, occurs mostly beneath the canopy of perennial shrubs, where their survivorship is also higher (Valiente-Banuet *et al.* 1991a; Valiente-Banuet & Ezcurra 1991). As in similar systems (Yeaton & Romero-Manzanares 1986; McAuliffe 1988), it is thought that as *Neobuxbaumia tetetzo* grows it affects its nurse plant *Mimosa luisana* negatively, eventually causing its death and replacement by the cactus (Valiente-Banuet *et al.* 1991b).

We carried out a detailed analysis of this interaction from the point of view of the nurse plant *Mimosa luisana*. We evaluated changes in the growth and fecundity of the nurse plant when *Neobuxbaumia tetetzo* grows beneath or inside its canopy. In addition,

a matrix model of population growth is presented as a basis for testing the hypothesis that the nurse plant is replaced by the nursed cactus. This model describes the growth of the shrub canopy as the result of the dynamics of a population of branches differing in size, survival probability and 'fecundity' (i.e. capacity to produce new branches).

Methods

STUDY SITE AND SPECIES

The study was conducted on a hillside at the Botanical Garden of the Instituto Nacional de Ecología (INE), in the semiarid 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 semiarid with a marked monsoon-type rainy season in summer. The mean annual rainfall is 380 mm and the mean annual temperature is 21°C (García 1981). The aridity of this locality is due to the rain-shadow cast by the Eastern Sierra Madre (locally known as Sierra de Zongolica). Soils are calcareous lithosols, derived from sedimentary and metamorphic rocks. The main vegetation type is a xerophytic scrub (Rzedowski 1978) in which giant columnar cacti constitute the dominant elements (Zavala-Hurtado 1982). The most important species are the columnar cacti *Neobuxbaumia tetetzo* and *Cephalocereus hoppenstedtii*, the agaves *Agave marmorata* and *Agave karwinski*, and the shrubby legumes *Mimosa luisana*, *Acacia constricta*, *Cercidium praecox* and *Caesalpinia melanadenia*.

Mimosa luisana Brandeg. is a perennial deciduous shrub endemic to the Tehuacán Valley, where it occurs at a mean density of 2400 individuals per ha, and a mean cover of 2850 m² ha⁻¹ (28.5%). *Neobuxbaumia tetetzo* (Coulter) Backeberg is a branched columnar cactus, also endemic to the Tehuacán Valley. It reaches densities of up to 1200 individuals taller than one metre per hectare, and a maximum height of 12 m. Valiente-Banuet *et al.* (1991a,b) have studied the spatial relationship between the two species and have examined their root systems. They found that while most of the smaller individuals of *N. tetetzo* are spatially associated with *M. luisana*, the distribution of the larger cacti is independent of the nurse shrubs. The root system of *N. tetetzo* is shallow; all of the roots occupy the upper horizon of the soil profile and the area explored by the roots increases as a quadratic function of cactus height. The root system of *M. luisana* is also relatively shallow; our observations confirm that most of the roots occupy the first 30 cm of the soil profile. Some of the *Mimosa* roots, however, tap the lower soil horizons, penetrating deeper than one metre when the soil conditions allow.

EFFECT OF *Neobuxbaumia tetetzo* ON *Mimosa luisana*

To evaluate the effect of *N. tetetzo* on its nurse plant *M. luisana*, we selected 21 individual shrubs which

were grouped into three size categories: small shrubs (with a canopy volume, estimated as the product of each plant's height, largest diameter and smallest diameter, of less than 1.5 m³), intermediate shrubs (canopy volume between 1.5 and 3.0 m³), and large shrubs (canopy volume > 3.0 m³). The shrubs were also classified into three association types: 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 (between 0.2 and 1.0 m high) and shrubs associated with large columnar cacti (taller than 1.5 m). Associated shrubs were defined as those having at least one columnar cactus beneath the shrub canopy. Intermediate types, i.e. nonassociated nurse plants with cacti nearer than twice the crown diameter, were not included in the study. To prevent any possible interference from neighbouring plants, trenches were dug around each shrub in order to cut any invading roots.

Ten nonramified terminal branches were randomly chosen on each shrub. These branches were individually marked before leaf production started (April 1990) and the length and number of modules in each one was recorded (a module was defined as an internode with an axillary bud). The number of leaves, modules, inflorescences and fruits were recorded periodically (every fortnight from May to August and then every 20 days) for each marked branch throughout the growing season.

Values of cumulative total production of leaves, modules, inflorescences and fruits per shrub (corrected for the initial number of modules of the shrub) were analysed by means of log-linear models (McCullagh & Nelder 1983) in which the logarithm of the number of structures produced was modelled as a function of the size class of the shrub, the type of association with *N. tetetzo* and the interaction between these two factors. The fit of the model (also known as the deviance, see McCullagh & Nelder 1983), was measured by the *G*-statistic, which is distributed as χ^2.

CANOPY GROWTH

In order to test the hypothesis that the nurse plant is replaced by the nursed cactus, the finite growth rate of the canopy of large shrubs associated with large *N. tetetzo* was estimated and compared with that of non-associated shrubs of similar size. The growth rate of the shrub was estimated by considering the canopy as a population of branches differing in size (Maillette 1982; Huenneke & Marks 1987). In April 1990, one month before the onset of the summer rains, 10 branches were individually marked on each of five associated and four nonassociated shrubs. The marked branches were classified into four size categories: branches with 5–9 modules, with 10–13 modules, with 14–16 modules, and branches with more than 16 modules.

For each marked branch we recorded the number and size of the new branches produced during the growing season (May–December 1990) that survived the drought season (January–May 1991). The survivorship of the original marked branches was also recorded.

With these data, 4 × 4 projection matrices summarizing the demographic features of the populations of branches constituting the canopies of associated and nonassociated shrubs were built, following Maillette (1982). The dominant eigenvalue (λ) of these matrices represents the finite growth rate of the branch populations that form the shrub canopies. A growth rate of less than 1.0 implies that the canopies had negative growth during the observation period and therefore that the number of live branches tended to decrease. Similarly, values of λ greater than 1.0 imply that the canopies had positive growth during the observation period and that the number of live branches tended to increase. Thus, if the replacement hypothesis were true, it should be expected that λ in associated plants would be less than 1.0 (i.e. nurse plant canopies should tend to decrease), while it should show values higher than unity in non-associated shrubs (i.e. the canopies of cactus-free plants should tend to increase).

Results

EFFECTS ON GROWTH AND FECUNDITY

Association with *N. tetetzo* produced a significant negative effect on the growth and fecundity of *Mimosa luisana*. Leaf production, which requires a lower energy investment than the production of branches, was comparatively unaffected. Although differences induced by association with cacti were statistically significant ($\chi_2^2 = 31.0$, $P < 0.0001$), the differences in leaf production between associated and nonassociated shrubs were quantitatively unimportant and not always in the same direction (Fig. 1). Shrub size had no significant effect on leaf production ($\chi_2^2 = 2.2$, $P = 0.3328$).

Association with cacti had a markedly negative effect on the production of modules (Fig. 1; $\chi_2^2 = 125.44$, $P < 0.0001$). In comparison to non-associated shrubs, nurses growing close to columnar cacti produced fewer and smaller branches. This effect was particularly noticeable in large shrubs, where nonassociated plants produced nearly 80% more modules than those associated to columnar cacti.

Association with *N. tetetzo* resulted in a marked reduction in the number of inflorescences produced by *M. luisana* except in small shrubs (Fig. 1; $\chi_2^2 = 239.0$, $P < 0.0001$). Shrub size had a significant effect on flower production ($\chi_2^2 = 141.2$, $P < 0.0001$). Fruit production followed a similar pattern (Fig. 1). It was significantly affected by association ($\chi_2^2 = 101.3$, $P < 0.0001$), and by shrub size ($\chi_2^2 = 134.2$, $P < 0.0001$). Quantitatively, the effect of shrub size was more important than the effect of association,

328

*Effects of a
columnar cactus on
its nurse plant*
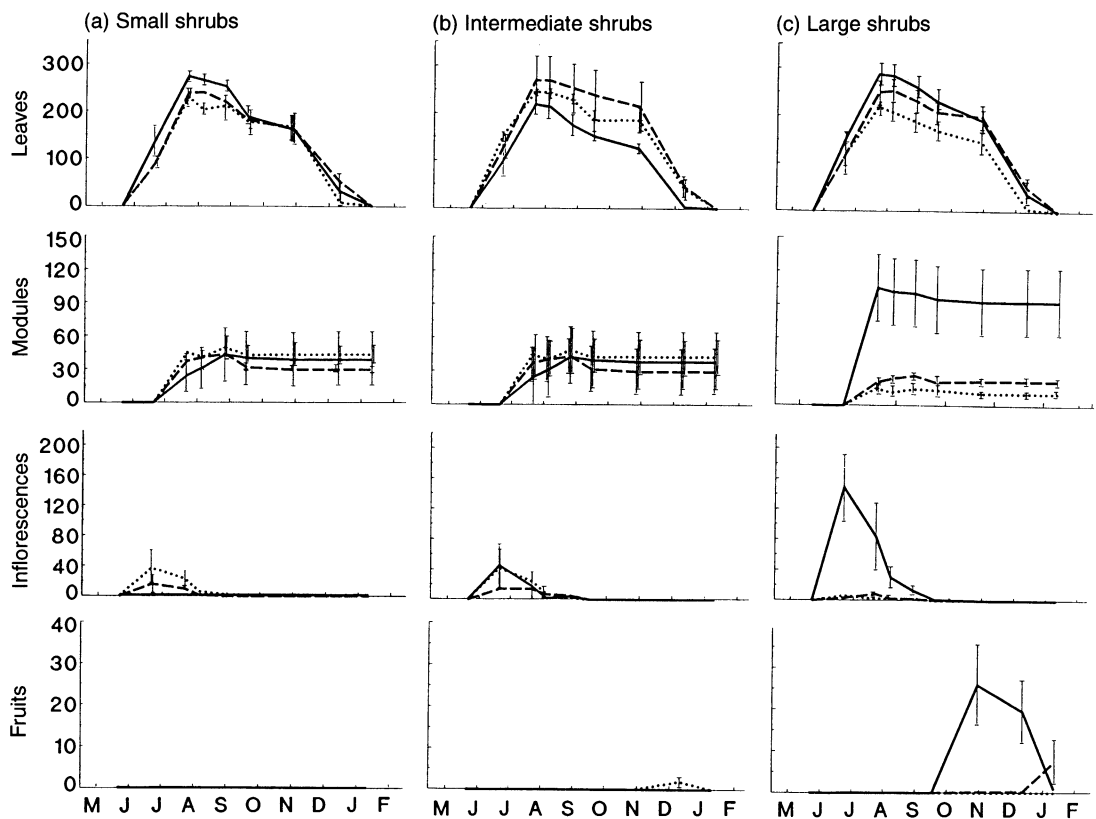
Fig. 1 Production of leaves, modules, inflorescences and fruits by *Mimosa luisana* (May 1990 to February 1991) in isolation (solid line), associated with juvenile columnar cacti (dotted line), and associated to large columnar cacti (dashed line). (a) Small shrubs, (b) intermediate shrubs and (c) large shrubs. Each data point represents the average ± 1 SE.

while the opposite was true for flower production (Table 1).

With the exception of fruit production, in all other cases the interaction between shrub size and association was the factor that accounted for the greatest proportion of the deviance (Table 1). This means that the effect of the association with *N. tetetzo* depends on the size of both the shrub and the cactus. In large shrubs, the association with juvenile or adult columnar cacti drastically reduces the capacity to produce new branches, inflorescences and fruits (Fig. 1). By contrast, for middle-sized shrubs the association with columnar cacti had little effect on leaf and module production, but the production of flowers and fruits was significantly reduced. Finally, in small shrubs, the association with cacti (regardless of their size) did not affect significantly either growth or fecundity. In all cases they presented little growth and produced very few branches and inflorescences.

CANOPY GROWTH

The matrices that summarize the demographic characteristics of the populations of branches for associated and nonassociated shrubs are shown in Table 2. The finite population growth rate (λ) estimated for the crown of nonassociated shrubs was 1.402. This means that the cactus-free *Mimosa* canopies increased in size during the observation period.

By contrast, the estimated λ of associated shrubs was 0.933, which means that the canopy of these shrubs had, for this year, a negative growth and therefore tended to decrease in size. This result is consistent with the hypothesis of the replacement of the nurse plant by nursed cacti.

To investigate the sensitivity of shrub growth to variations in mortality, the matrices were modified by altering survival values until λ became equal to 1.0. We found that with a survival 72% lower than that observed for the study year, the canopy of nonassociated shrubs would still show a positive growth rate. By contrast, an increase of 8% in the survival rate of the branches of associated shrubs would be needed to achieve a positive growth rate.

Discussion and conclusions

Cody (1986) suggested that species with different life-forms can avoid competitive effects by occupying different niches. However, our results show that *N. tetetzo* has a significant negative effect on the growth and fecundity of its nurse plant *M. luisana*, which is particularly noticeable in larger shrubs. The fact that this effect depends on the size of both the shrub and the columnar cactus leads to a complex type of dynamics in which the final outcome may vary both in magnitude and in character. It is likely that for *N. tetetzo* the interaction with *M. luisana* changes

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

Source of Variation	Deviance	d.f.	P	r^2
Leaves				
Model	67.816	8	***	0.4139
Size	2.207	2	0.3317	0.0135
Association	31.04	2	***	0.1895
Size × Ass.	34.57	4	***	0.2110
Residual	96.01	12		
Modules				
Model	281.280	8	***	0.4479
Size	2.500	2	0.2865	0.0040
Association	125.44	2	***	0.1997
Size × Ass.	153.36	4	***	0.2442
Residual	346.74	12		
Inflorescences				
Model	786.256	8	***	0.6081
Size	141.20	2	***	0.1092
Association	239.01	2	***	0.1849
Size × Ass.	407.01	4	***	0.3148
Residual	505.75	12		
Fruits				
Model	282.540	8	***	0.6776
Size	134.19	2	***	0.3218
Association	101.31	2	***	0.2429
Size × Ass.	47.04	4	***	0.1128
Residual	134.46	12		

*** $P < 0.0001$.

through time from a beneficial relationship during the critical seedling stage, to a negative interaction in the juvenile stage when the two species probably compete for soil resources and when the shade of the shrub canopy reduces the amount of PAR that is available to the cactus (Valiente-Banuet *et al.* 1991b). For *M. luisana*, the interaction with seedlings of *N. tetetzo* might be neutral at first, but would become negative as the cactus grows. The cactus may produce direct mechanical damage to the shrub canopy and/or expose it to a greater desiccation stress (Yeaton & Romero-Manzanares 1986). This negative effect of *N. tetetzo* on *M. luisana* is non-linear; it is very intense in big shrubs, negligible in small ones, and only slightly noticeable in nurse plants of intermediate size. Because the root system of columnar cacti is extensive and extremely shallow (Nobel 1988; Valiente-Banuet *et al.* 1991b), and because of their capacity to absorb and to store large amounts of water in a short period

(Nobel 1988), it is likely that *N. tetetzo* affects negatively *M. luisana* through competition for soil water similarly to the way that *Carnegiea gigantea* has been reported to affect *Cercidium microphyllum* (McAuliffe 1984).

Although the results obtained with the matrix models of canopy growth suggest that the negative effect of the cacti on their nurse plants could be strong enough for replacement to occur, we do not consider this evidence yet to be conclusive. The hypothesis could be true if the negative effect occurred continuously as the cactus grows, leading eventually to the replacement of the shrub when the cactus reaches a certain height (2 to 3 metres according to Valiente-Banuet *et al.* 1991b). However, this is contradicted by the common occurrence in the field of large shrubs growing side by side with columnar cacti taller than five meters. This pattern could be due to the fact that the negative effect of *N. tetetzo* on *M. luisana* is not constant either in time or magnitude, and so may not invariably lead to replacement in the short term. Fonteyn & Mahall (1981) found that interference between two shrubs, *Larrea tridentata* and *Ambrosia dumosa*, occurs only in dry years. If competition for water is in fact the causal mechanism in our system, the occasional occurrence of wet years could delay or even reverse the replacement process, making it slow and difficult to observe.

Vandermeer (1980) suggested that the dynamics of species replacement in arid plant communities could be represented by an analogue of a predator-prey model. Although Vandermeer's model might be useful for describing the phenomenon in general terms, it is evident that it is conceptually simplistic, as it does not allow for variations of the parameters in time. Our results show that the interactions between nurse and nursed species do not remain constant through time either in magnitude or in nature. A nonautonomous system in which the sign and magnitude of the interactions can change with time might would probably provide a more adequate representation of this phenomenon.

McAuliffe (1988) used a Markovian model to simulate the dynamics of an arid plant community in the Arizona desert. The replacement pattern there seems to be quite clear-cut: *Larrea tridentata* establishes mostly under the canopy of the small shrub *Ambrosia dumosa* and eventually replaces it. The *Neobuxbaumia–Mimosa*

Table 2 Transition matrices of the branch populations forming the canopies of isolated and associated *Mimosa luisana* shrubs

Isolated					Associated			
0.800	0.130	0.400	0.460		0.500	0.143	0.333	0.429
0.200	1.070	0.000	0.133		0.000	0.857	0.000	0.000
0.000	0.000	1.000	0.133		0.000	0.000	0.933	0.000
0.200	0.000	0.066	1.133		0.000	0.000	0.000	0.929

$\lambda = 1.402$ (Isolated) $\lambda = 0.933$ (Associated)

330

*Effects of a
columnar cactus on
its nurse plant*

system seems to be more complex since the dynamics of the association between a particular pair of plants will depend on the stage in the nurse shrub's life-cycle at which the cactus establishes. McAuliffe (1988) suggests that replacement might take place even in the absence of competition if seedlings become established under a mature shrub that has already entered the senile stage. Changes in the growth rate of cacti and shrubs may also be related to spatial heterogeneity or temporal changes in resource availability (e.g. seasonal rainfall patterns), and to large-scale events (e.g. droughts and sequences of unusually wet years) which can play a very important role in vegetation change (Turner, 1990). There are therefore many possibilities which must be explored before we understand the dynamics and the patterns found in arid plant communities. At present we are making longer-term studies of the effect of *Neobuxbaumia tetetzo* on *Mimosa luisana*, and particularly of the response to changes in resource availability, in order to establish the time-course of the replacement process.

Acknowledgements

References

Barbour, M.G. (1981) Plant–plant interactions. *Arid-Land Ecosystems*, Vol. 2 (eds D. W. Goodwall & R. A. Perry), pp. 33–49. Cambridge University Press, Cambridge.

Cody, M.L. (1986) Structural niches in plant communities. *Community Ecology* (eds J. Diamond & T. J. Case), pp. 381–405. Harper & Row Publications, New York.

Connell, J.H. (1975) Some mechanisms producing structure in natural communities: A model and evidence from field experiments. *Ecology and Evolution of Communities* (eds M. L. Cody & J. L. Diamond), pp. 460–490. Harper & Row, New York.

Fitter, A.H. & Hay R.K.M. (1987) *Environmental Physiology of Plants*, 2nd edn. Academic Press. London.

Fonteyn, P.J. & Mahall B.E. (1981) An experimental analysis of structure in a desert plant community. *Journal of Ecology*, **89**, 883–896.

Fowler, N. (1986) The role of competition in plant communities in arid and semiarid regions. *Annual Review of Ecology and Systematics*, **17**, 89–110.

Franco, A.C. & Nobel P.S. (1988) Interaction between seedlings of *Agave deserti* and the nurse plant *Hilaria rigida*. *Ecology*, **69**, 1731–1740.

Franco, A.C. & Nobel P.S. (1989) Effect of the nurse plant on the microhabitat and growth of cacti. *Journal of Ecology*, **77**, 870–886.

García, E. (1981) *Modificaciones al Sistema Climático de Köppen*, Instituto de Geografía Universidad Nacional Autónoma de Mexico. Mexico.

Grime, J.P. (1979) *Plant Strategies and Vegetation Processes*, John Wiley & Sons, Chichester.

Huenneke, L.F. & Marks P.L. (1987) Stem dynamics of the shrub *Alnus incata* spp. *rugosa*: transition matrix models. *Ecology*, **68**, 1234–1242.

Hutto, R.L, McAuliffe J.R & Hogan L. (1986) Distributional associates of the saguaro (*Carnegiea gigantea*). *Southwestern Naturalist*, **31**, 469–473.

Jaksic, F.M. & Fuentes E.R. (1980) Why are native herbs in the Chilean Matorral more abundant beneath bushes: microclimate or grazing? *Journal of Ecology*, **68**, 665–669.

Kemp, P.R. (1983) Phenological pattern of Chihuahuan Desert Plants in relation to the timing of water availability. *Journal of Ecology*, **71**, 427–436.

Maillette, L. (1982) Structural dynamics of silver birch II. a matrix model of the bud population. *Journal of Applied Ecology*, **19**, 219–238.

McAuliffe, J.R. (1984) Sahuaro nurse tree associations in the Sonoran Desert: Competitive effect of sahuaro. *Oecologia (Berlin)*, **64**, 319–321.

McAuliffe, J.R. (1986) Herbivore-limited establishment of a Sonoran Desert cacti tree, *Cercidium microphyllum*. *Ecology*, **67**, 276–280.

McAuliffe, J.R. (1988) Markovian dynamics of simple and complex desert plant communities. *American Naturalist*, **131**, 459–490.

McCullagh, P & Nelder J.A. (1983) *Generalized Linear Models*. Chapman & Hall, London.

Nobel, P.S. (1988) *Environmental Biology of Agaves and Cacti*. Cambridge University Press, New York.

Rzedowski, J. (1978) *Vegetación de México*, Limusa, Mexico.

Shreve, F. (1951) Vegetation of the Sonoran Desert, *Carnegie Institute Washington Publications*, **591**, 1–192.

Tilman, D. (1988) *Plant Strategies and the Structure and Dynamics of Plant Communities*. Princeton University Press, Princeton, New Jersey.

Turner, R.M. (1990) Long-term vegetation change at a fully protected Sonoran Desert site. *Ecology*, **71**, 464–473.

Valiente-Banuet, A. (1991) *Dinámica del establecimiento de cactáceas: Patrones generales y consecuencias de los procesos de facilitación por plantas nodriza en desiertos*. PhD thesis, Universidad Nacional Autónoma de México, Mexico.

Valiente-Banuet, A., Bolongaro-Crevena A., Briones O., Ezcurra E., Rosas M., Nuñez H., Bernard G. & Vazquez E. (1991a) Spatial relationship between cacti and nurse shrubs in a semi-arid environment in central México. *Journal of Vegetation Science*, **2**, 15–20.

Valiente-Banuet, A., Vite F. & Zavala-Hurtado J.A. (1991b) Interaction between the cactus *Neobuxbaumia tetetzo* and the nurse *Mimosa luisana*. *Journal of Vegetation Science*, **2**, 11–14.

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, Mexico. *Journal of Ecology*, **79**, 961–971.

Vandermeer, J. (1980) Sahuaro and nurse trees: a new hypothesis to account for population fluctuations. *Southwestern Naturalist*, **25**, 357–360.

Yeaton, R.I. (1978) A cyclical relationship between *Larrea tridentata* and *Opuntia leptocaulis* in the northern Chihuahuan Desert. *Journal of Ecology*, **66**, 651–656.

Yeaton, R.I. & Romero-Manzanares A. (1986) Organization of vegetation mosaics in the *Acacia schaffneri – Opuntia streptocantha* association southern Chihuahuan Desert Mexico. *Journal of Ecology*, **74**, 211–217.

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**, 1.