Seedling habitat structure in dry Chaco forest (Argentina)

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We hypothesized that seedlings of different dominant species in the dry Chaco forests of Córdoba Province were restricted to patches with particular microenvironmental conditions. To test this hypothesis, the seedling habitat was characterized by measuring physical and biotic microhabitat variables such as incident light, distance to the nearest neighbour, and herb, thallophyte, and litter cover. Seedlings of the different dominant species established in different patches representing a broad range of microhabitat conditions. Open, arid microsites with high percentages of incident light were occupied by *Cercidium praecox*, *Larrea divaricata* and *Prosopis* spp. seedlings. These species colonize open patches in the forest, taking advantage of the low competition environment and establishing during the brief favourable period before the dry season. In contrast, seedlings of *Celtis pallida*, *Capparis atamisquea*, *Mimozyganthus carinatus* and *Acacia furcatispina* tend to establish in closed, canopied microsites, with lower incident light and better moisture and nutrient conditions. These species may benefit from the conditions underneath the canopies. Distance to the nearest neighbour did not restrict seedling establishment when the neighbours were herbs, but the nearest shrub exerted a strong influence, depending on the seedling species as well as the shrub species. Facilitation could be an important mechanism in the regeneration of species in the dry Chaco forests.

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Introduction

Abiotic and biotic factors that characterize a particular site act as filters conditioning germination and seedling survival from the viable seeds available at that site (Harper, 1977). Microsite conditions such as percentage of incident light (Augspurger, 1984; Fenner, 1985; MacDougall & Kellman, 1992; Schmitt & Wulff, 1993), distance to the nearest neighbour (Goldberg & Werner, 1983; Silander & Pacala, 1985; Goldberg, 1987; Fowler, 1988), litter cover and depth (Facelli & Pickett, 1991*a,b*), may restrict seedling abundance and establishment. In arid and semi-arid environments, where spatial and temporal variation of water and nutrient availability may be extreme, tree and shrub dominant plants can generate complex changes in microclimate and soil conditions (Wilson & Agnew, 1992). This may represent a potential mechanism by which trees and shrubs forming vegetation patches dominated by different species can

alter seedling establishment (Burton & Bazzaz, 1991). In these patches, the coupled effects of canopy and litter cover result in microhabitat amelioration via an increase in water and nutrient availability, thus favouring seedling and herb growth (e.g. Franco & Nobel, 1989; Valiente-Banuet & Ezcurra, 1991; Vetaas, 1992; Gutiérrez et al., 1993; Pugnaire et al., 1996a,b; Moro et al., 1997). Facilitation, i.e. the modification of the environment by one species that makes it more suitable for other species (Bertness & Callaway, 1994), could be an important mechanism in the regeneration of species in semi-arid environments (Pugnaire et al., 1996a). In this context, proximity to the nearest neighbour can be viewed not only as a source of potential competitive relationships (Yeaton & Cody, 1976), but also as potentially beneficial for establishing seedlings.

These factors may be considered in the context of the regeneration niche approach (Grubb, 1977). The analysis of the seedling regeneration niche is scale dependent and needs to be based on quantification of relevant variables for different plant species (Gibson & Good, 1987). The characteristics of the microenvironment surrounding the seedlings and its effects upon seedling survival, are critical in determining seedling population dynamics (Harper, 1977; Fowler, 1988).

Based upon field observations on seedling spatial distribution in the dry Chaco forests of Córdoba Province, and studies done in the same forest showing an increase in soil nutrient availability under certain type of tree and shrub canopies (Mazzarino et al., 1991a,b), we hypothesized that seedlings of different species were restricted to patches with particular microenvironmental conditions. To test this hypothesis, we characterized the seedling habitat by measuring physical and biotic microhabitat variables such as incident light, distance to the nearest neighbour, and herb, moss, and litter cover, following the individual plant approach used by Mann & Shugart (1983), Collins & Good (1987) and Gibson & Good (1987).

Materials and methods

Study area

The study site is the Chancaní Park (Central Argentina, 65·26′ W, 31·22′ S), — a Chaco forest reservation. The climate is semi-arid, with mean annual rainfall ranging from 350 to 550 mm, concentrated in hot summer months, and a dry period during the cool winter months. Summer mean maximum and minimum temperatures are 35°C and 20°C. Vegetation is classified as Occidental Chaco Forest (Luti et al., 1979). Tree canopy reaches 15 m, and the shrub layer is well developed. The forest dominant species (Luti et al., 1979), were chosen as study species. Selected trees were *Aspidosperma quebracho-blanco* SCHLECHT. (Apocynaceae); *Prosopis* spp., *Geoffrea decorticans* (H.et A.) BURK., *Cercidium praecox* (Ruiz et Pavón) Harms (Leguminosae), and shrub species were *Celtis pallida* TORREY (Ulmaceae); *Mimozyganthus carinatus* (GRIS.) BURK., *Acacia furcatispina* BURK.(Leguminosae); *Capparis atamisquea* D.K. (Capparidaceae); and *Larrea divaricata* CAV. (Zygophyllaceae).

Microhabitat characterization

In June 1996, 30 one- to three-year-old seedlings of each species were located randomly on 10 line randomly located transects of 200 m each (three seedlings/transect). Eight habitat variables (Table 1) were recorded inside of a 24 cm^2 circle centred on each seedling. Cover variables were visually estimated. Thallophyte cover was the per cent soil covered by non-vascular cryptogams, i.e. mosses, algae and lichens (xeric thallophytes, Box, 1981), including *Selaginella selowii* (Selaginellaceae). Litter depth was measured adjacent to a seedling by inserting a wire probe down to the soil surface.

Table 1. *Variables considered in microhabitat seedling description of dominant species present in Chaco forest*

Variable	Measurement
Thallophyte cover★	Percentage of soil covered by moss, algae and *Selaginella selowii*
Herb cover★	Percentage of soil covered by herbs
Litter cover★	Percentage of soil covered by litter
Litter depth★	Mean ($n = 5$) of litter layer depth
Nearest neighbour	Seedling distance to the nearest neighbour (cm)
Nearest shrub	Seedling distance to the nearest shrub stem (cm)
Light†	Percentage of the maximum Photosynthetically Photon Flux Density (PPFD) in open areas
Canopy type†	Canopy type above each seedling, 1 = tree 2 = shrub 3 = without canopy. Types 1 and 2 were classified by species providing the canopy

★ Recorded inside of a 24 cm² circle centred on each seedling.
† Recorded immediately above each seedling.

Distance from the seedling to its nearest neighbour was recorded considering the nearest plant and the nearest shrub. In this latter case the species of shrub was recorded. Light immediately above each seedling was measured with a LiCor PPFD (Photosynthetically Active Photon Flux Densities) sensor. The measurements, taken between 11:00 and 13:00 h on sunny days, were expressed as a percentage of ambient light, measured in an open neighbouring area. The species providing the canopy above the seedling was recorded for tree and shrub canopy types.

Data analysis

Parametric analyses were used whenever data structure made it possible, otherwise, nonparametric equivalent analyses were used.

One-way ANOVA was used to analyse the effect of canopy type on five of the habitat variables (thallophyte cover, litter cover and litter depth, herb cover and percentage of light). The same analysis was done considering the species providing the tree and shrub canopy, using a Kruskal-Wallis test and a posteriori comparison of medians (Dunn, 1964). For each seedling species, influence of nearest neighbour was analysed using the Kruskal-Wallis test. The distance to the nearest shrub without specifying shrub species, was analysed with a chi-square test. The same analysis, this time considering the shrub species, was done using one-way ANOVA followed by Fisher's independence test (Montgomery, 1991). Habitat data were also subjected to principal component analysis and canonical discriminant analysis. To present the relationship between habitat variables and seedling species graphically, an ordination of results obtained from the previous discriminant analysis was done (Brewer & Platt, 1994). Results from discriminant analysis were based on untransformed values of all dependent variables. Efficiency of the classification matrix was evaluated with the Cohen's Kappa statistic (Titus *et al.*, 1984). The ordination was based on the first two canonical axes. Ordination scores for each dependent variable were Pearson correlations with canonical axes, weighted by the eigenvalues associated with these canonical axes. The centroids for each seedling species were superimposed upon the ordination of dependent variables (Jongman *et al.*, 1987). In this ordination diagram, the direction of each vector in relation to the location of each seedling species centroid indicates the degree of association between

the corresponding variable and that particular seedling species. An acute angle between two vectors indicates that the two corresponding variables are related similarly to a particular seedling species, whereas an obtuse angle indicates that the two variables are related to the species in opposite ways. A right angle indicates that the two variables are not related with the presence of that seedling species. The length of each vector is proportional to the total amount of variation accounted for by its corresponding variable.

Results

Microhabitat characterization

Five microhabitat variables differed between canopy types, thallophyte cover ($F = 2.79$, $p < 0.01$), litter cover ($F = 11.99$, $p < 0.001$), litter depth ($F = 2.98$, $p < 0.01$), and light ($F = 2.06$, $p < 0.01$). Herb cover, in contrast, did not differed with canopy type ($F = 1.16$, $p > 0.05$). The same variables varied depending on the species providing the canopy (Fig. 1). Thallophyte cover was significantly lower in open sites and under *Prosopis* spp. canopy than under *M. spinosa* and *A. furcatispina* canopies (Kruskal Wallis $H = 23.53$, $p < 0.05$) (Fig. 1(a)). Herb cover did not differ significantly between canopy types (Kruskal Wallis $H = 10.71$) (Fig. 1(b)). Litter cover differed significantly (Kruskal Wallis $H = 96.51$, $p < 0.001$), with higher values under *C. pallida*, *G. decorticans*, *Prosopis* spp., *A. quebracho-blanco* and *A. furcatispina* canopies than under *L. divaricata*, *M. carinatus* and *C. microphylla*. Sites without canopy cover showed low values of litter cover (Fig. 1(c)). Litter depth was significantly different (Kruskal Wallis $H = 52.72$, $p < 0.001$), with lower values in open sites and under *L. divaricata* and *C. microphylla* canopies than under *C. atamisquea*, *C. praecox*, *Prosopis* spp., and *A. quebracho-blanco* (Fig. 1(d)). Percentage of light was significantly different between sites with different canopy types (Kruskal Wallis $H = 96.49$; $p < 0.001$). Sites under *M. spinosa*, *A. furcatispina*, *C. pallida*, *G. decorticans*, *Prosopis* spp. and *A. quebracho-blanco* canopies showed significantly lower values of light than open sites (Fig. 1(e)).

Distance to the nearest neighbour (which was the herb *Deinacanthon urbanianum* MEZ (Bromeliaceae) in 93% of cases) was not significant (Kruskal Wallis $H = 12.56$, $p > 0.05$) (Fig. 2). In contrast, *A. quebracho-blanco*, *C. pallida* and *C. atamisquea* seedlings were closer to the nearest shrub (medians 50–60 cm) than *A. furcatispina*, *C. praecox*, *L. divaricata*, *M. carinatus*, and *Prosopis* spp. seedlings (medians 90–110 cm) ($\chi^2 = 36.63$, df. = 21, $p < 0.05$) (Fig. 3). Considering the species of the nearest shrub, distance was significant for *A. quebracho-blanco* ($F = 4.48$, $p < 0.01$), *L. divaricata* ($F = 3.55$, $p < 0.05$), and *Prosopis* spp. ($F = 2.95$, $p < 0.05$) seedlings. Distances to *Trichomaria usillo* (GILL.) HOOK et ARN. and *C. atamisquea* were significantly greater for *A. quebracho-blanco* seedlings. *L. divaricata* seedlings were significantly more distant to conspecific shrubs. *Prosopis* spp. seedlings were significantly more distant to *C. atamisquea* shrubs (Fig. 4). The species of the nearest shrub did not affect shrub distance to seedlings of *A. furcatispina* ($F = 1.16$, $p > 0.05$), *C. atamisquea* ($F = 1.83$, $p > 0.05$), *C. pallida* ($F = 0.75$, $p > 0.05$), *C. praecox* ($F = 0.86$, $p > 0.05$), and *M. carinatus* ($F = 0.88$, $p > 0.05$) (Fig. 4).

Microhabitat of established seedlings

Principal component analysis of the seedlings microhabitat data set produced three factors with significant chi-square values, describing 97% of the overall variation in the data (Table 2). Based on Cohen's Kappa statistic the discriminant classification matrix
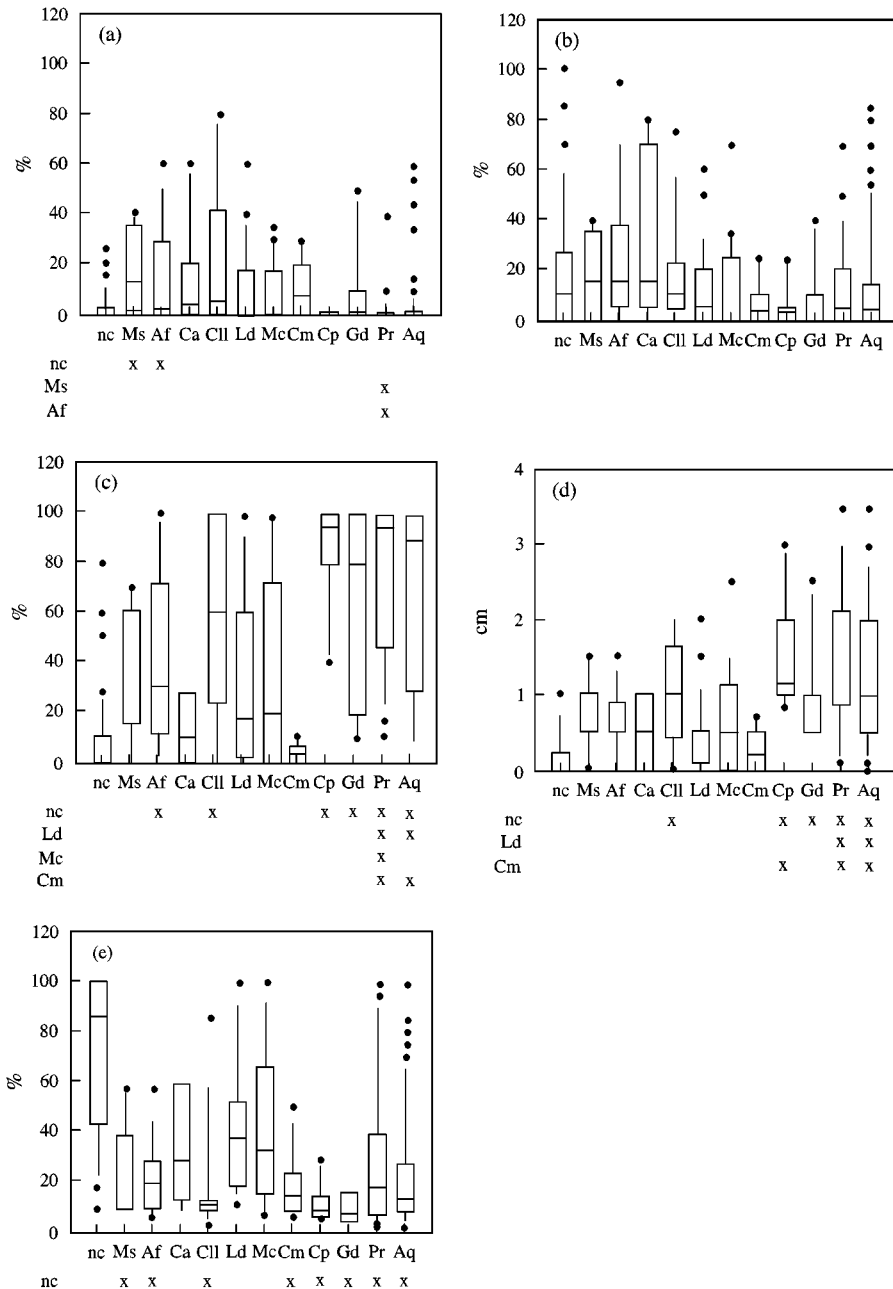
Figure 1. Medians and ranges of five microhabitat variables considering canopy cover type. Variables were measured inside of a 24 cm^2 circle centred on each seedling ($n = 30$ per species). nc = without canopy over the seedlings. The following letters represent canopy cover provided by tree and shrub species: Ms = *Maytenus spinosa*, Af = *Acacia furcatispina*, Ca = *Capparis atamis-quea*, Cll = *Celtis pallida*, Ld = *Larrea divaricata*, Mc = *Mimozyganthus carinatus*, Cm = *Condalia microphylla*, Cp = *Cercidium praecox*, Gd = *Geoffrea decorticans*, Pr = *Prosopis* spp., Aq = *Aspidosperma quebracho-blanco*. Crosses indicate significant differences between medians (Kruskal-Wallis and Dunn test). (a) Thallophytes cover; (b) herb cover; (c) litter cover; (d) litter depth; (e) percent light.
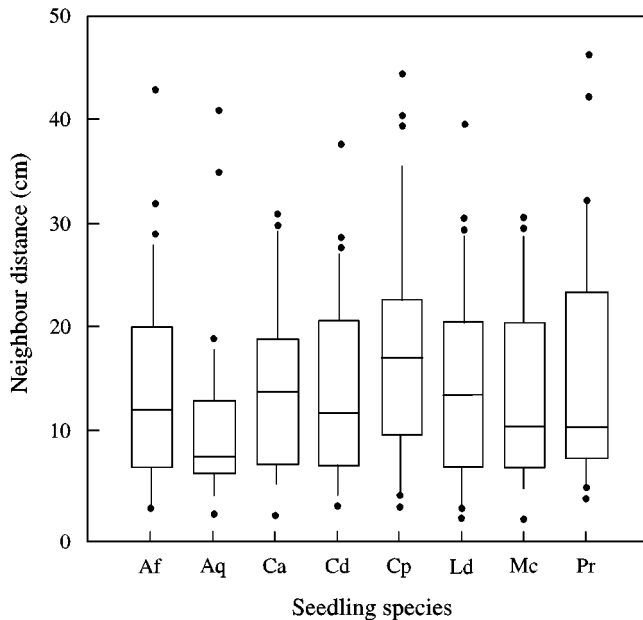
Figure 2. Medians and ranges for distance from each seedling species to the nearest neighbour. The following letters represent species seedlings: Af = *Acacia furcatispina*, Aq = *Aspidosperma quebracho-blanco*, Ca = *Capparis atamisquea*, Cd = *Celtis pallida*, Cp = *Cercidium praecox*, Ld = *Larrea divaricata*, Mc = *Mimozyganthus carinatus*, Pr = *Prosopis* spp. Distance was not significant ($p > 0.05$).

was 41% better than a randomly constructed classification matrix. PCA I differentiated between microhabitats with high percentage of light (occupied by seedlings of *C. praecox*, *L. divaricata* and *Prosopis* spp.) and those with higher percentages of herb, moss and litter, and tree or shrub canopy (occupied by seedlings of *C. pallida*, *C. atamisquea* and *M. carinatus*). PCA II differentiated microhabitats with higher herb and thallophyte cover and those with higher litter cover and litter depth, occupied by seedlings of *A. furcatispina* (Table 2 and ordination from discriminant analysis in Fig. 5).

Discussion

Except for herb cover, all microhabitat variables measured varied among patches determined by canopy cover. These patches determine microhabitats with particular organic matter contents and nutrient cycles (Mazzarino *et al.*, 1991*a*,*b*). Soil water dynamics also differ between patches, showing lower differences in percentages of soil water content during the rainy period (5·59 ± 0·65, tree canopy; 4·92 ± 0·74, shrub canopy; 4·26 ± 0·56, open sites, January 1993), than during the dry period (2·48 ± 0·88, tree canopy; 1·73 ± 0·67, shrub canopy; 0·96 ± 0·44, open sites, October 1993) (Páez, unpublished data). The microhabitat differences correlated with abiotic, resource and competitive and/or facilitative conditions in patches where seedlings of different species appear to be non-randomly distributed (Fig. 5).

   Litter amount may determine microhabitat conditions such as organic matter contents, nutrient cycles, water dynamics, daily and seasonal temperatures regimes and light quantity and quality (Facelli & Pickett, 1991*a*,*b*,*c*). Litter cover and depth showed the highest values under tree canopy, intermediate values under shrub canopies, and very
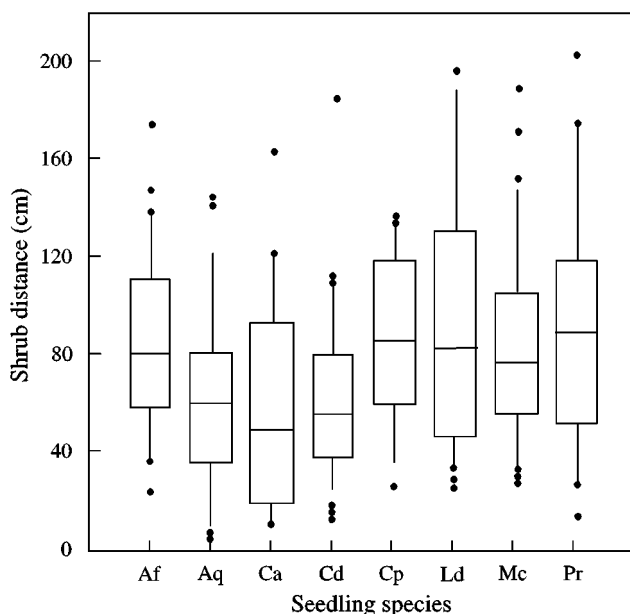
Figure 3. Medians and ranges for distance from each seedling species to the nearest shrub. The following letters represent species seedlings: Af = *Acacia furcatispina*, Aq = *Aspidosperma queb-racho-blanco*, Ca = *Capparis atamisquea*, Cd = *Celtis pallida*, Cp = *Cercidium praecox*, Ld = *Larrea divaricata*, Mc = *Mimozyganthus carinatus*, Pr = *Prosopis* spp. Distance was significant ($p < 0.05$).

low values in patches without canopy cover. In the studied forests, litter quality differed as well, with the highest N content in litter under *Prosopis* spp. and the lowest values under shrubs and the interspaces (Mazzarino *et al.*, 1991*b*). Differences in the amount of accumulated litter in different patches are determined by balance between local litter production and decomposition, and litter displacement (Facelli & Carson, 1991; Facelli & Pickett, 1991*a*; Peterson & Facelli, 1992; Berendse, 1994; Aerts & de Caluwe, 1997). Litter may affect the species regeneration cycle directly, acting on germination and seedling establishment by light interference and production of inhibitory compounds (Facelli, 1994). On the other hand, litter may compensate these negative effects by lowering soil desiccation (Hamrick & Lee, 1987; Facelli & Pickett, 1991*b*). Indirect effects act upon seedling population dynamics throughout seedling mortality, reduction of competence from herbs, and increasing insect herbivory (Sydes & Grime, 1981*a,b*; Facelli & Pickett, 1991*b*; Facelli, 1994).

In this study, percentages of incident light differed greatly between patches with canopy cover and open patches. Seedlings of the species studied were found in a wide range of light availability. Seedlings of colonizers of disturbed habitats, such as *C. praecox*, *L. divaricata* and *Prosopis* spp. (Morello, 1970; Morello & Saravia Toledo, 1959), established in open, highly irradiated sites. However, light availability might not be a limiting factor for *L. divaricata* (Ezcurra *et al.*, 1991), nor for some *Prosopis* species. Seedlings of *P. glandulosa* reach saturation of photosynthetic activity at 10% of maximum light (Bush & Van Auken, 1987). At the other end of the light availability gradient were seedlings of *A. quebracho-blanco*, *A. furcatispina*, *C. pallida*, *M. carinatus* and *C. atamisquea*. Although information on seedling light requirements for all these species is not available, it is kown that *Celtis pallida* and some *Acacia* species require low irradiated microhabitats (Bush & Van Auken, 1986; O'Connor, 1995; Francopizana *et al.*, 1996).
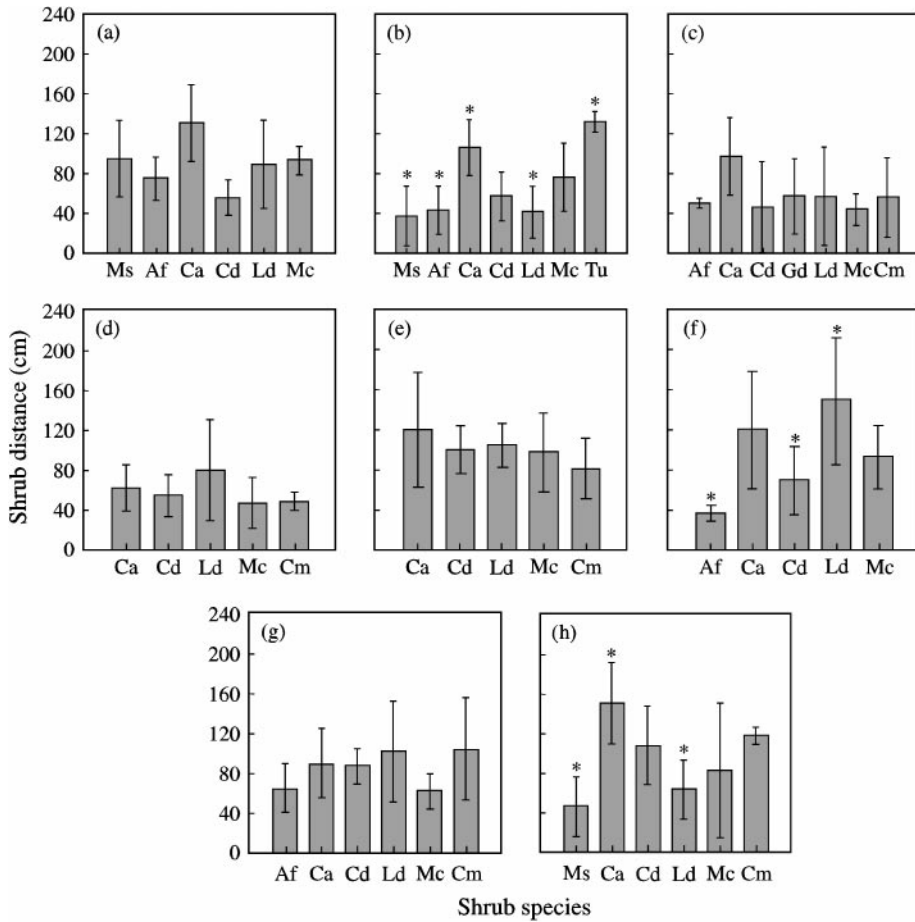
Figure 4. Means and standard deviations for distance from each seedling species to the nearest shrub considering shrub species. The following letters represent nearest shrub species: Ms = *Maytenus spinosa*, Af = *Acacia furcatispina*, Ca = *Capparis atamisquea*, Cd = *Celtis pallida*, Ld = *Larrea divaricata*, Mc = *Mimozyganthus carinatus*, Cm = *Condalia microphylla*, Cp = *Cercidium praecox*, Gd = *Geoffrea decorticans*, Pr = *Prosopis* spp., Aq = *Aspidosperma quebracho-blanco*, Tu = *Trichomaria usillo*. Asterisks indicate significant differences between means (ANOVA followed by Fisher's independence test). (a) *A. furcatispina*; (b) *A. quebracho-blanco*; (c) *C. atamisquea*; (d) *C. pallida*; (e) *C. praecox*; (f) *L. divaricata*; (g) *M. carinatus*; (h) *Prosopis* spp.

Distance to the nearest herb was not related to seedling distribution. There was no evidence of competition between shrub seedlings and herb in the Chaparral (Moreno & Oechel, 1992), although herb plants may reduce shrub seedling growth and/or survival in that habitat (Schultz *et al.*, 1955; Kummerow *et al.*, 1985; Thomas & Davis, 1989).

On the other hand, distance to the nearest shrub was a relevant factor determining seedling microhabitat of different species. *Aspidosperma quebracho-blanco*, *C. atamisquea* and *C. pallida* established close to shrub stems, although seedlings of *A. quebracho-blanco* established far from *C. atamisquea* and *T. usillo* shrubs. *Cercidium praecox*, *L. divaricata* and *Prosopis* spp. established preferentially far from shrubs. *Larrea divaricata* seedlings were distant to adults of the same species. Seedlings of *L. tridentata* close to mature shrubs of the same species experienced the highest mortality rates in Mojave Desert (Sheps, 1973), although there is no conclusive evidence of this

Table 2. *Principal component analysis of the correlation matrix of eight variables representing the microhabitat surrounding established seedlings of dominant tree and shrubs in dry Chaco forest*

Variables	Factor		
	I	II	III
Moss cover	0·25	−0·38	0·66
Herb cover	0·23	−0·49	0·27
Litter cover	0·61	0·46	0·48
Litter thickness	0·06	0·19	−0·07
Nearest neighbour	−0·04	0·05	0·29
Nearest shrub	−0·53	0·15	0·66
Light	−0·17	−0·07	−0·41
Canopy type	0·37	−0·43	−0·19
% Total variance	72·20	19·70	6·20

relationship being caused by allelopathic effects (Barbour *et al.*, 1977). As for *A. quebracho-blanco*, seedlings of *Prosopis* spp. established distant from *C. atamisquea* shrubs. Strong allelopathic effects on desert plants have been found in aqueous extracts of *Capparis decidua* (Gautam & Bishnoi, 1990).

Seedlings of the different dominant species establish in different patches representing a broad range of microhabitat conditions. Bare, arid microsites far from tree and shrub canopies and with high percentages of incident light are occupied by *Cercidium praecox*, *Larrea divaricata* and *Prosopis* spp. seedlings. These species colonize open patches in the forest, taking advantage of the low competition environment, establishing during the brief favourable period before the dry season. On the contrary, seedlings of *C. pallida*, *C. atamisquea*, *M. carinatus* and *A. furcatispina* tend to establish in closed, canopied microsites, with lower incident light and better moisture and nutrient conditions. In particular, presence of *A. furcatispina* seedlings is closely related to litter accumulation. Establishment of *A. quebracho-blanco* seedlings is more difficult to relate to particular variables. Seedling survival in this species may be related to avoidance of insect predation and fungal attacks in moderately open microsites (S. Páez, unpublished). Although light quantity and quality, that may be modified by canopy cover and type (Schmitt & Wulff, 1993), are important factors for seedling establishment in mesic habitats, tolerance to drought and nutrient scarcity, and avoidance to herbivory may be more important in semi-arid habitats.

At least for some of the studied species, facilitation could be a relevant mechanism in the establishment of their seedlings. The most commonly reported mechanisms of facilitation in arid environments include cooler temperatures and increased soil nutrients beneath the nurse plant canopy, which favour establishment of other plant species (Franco & Nobel, 1989; Valiente-Banuet & Ezcurra, 1991; Vetaas, 1992; Gutiérrez *et al.*, 1993; Francopiziana *et al.*, 1996; Pugnaire *et al.*, 1996*a,b*; Moro *et al.*, 1997). From this study, it is clear that conditions for facilitation processes are met in dry Chaco forest. Dominant trees and shrubs like *Prosopis* spp., *A. quebracho-blanco*, *G. decorticans*, *C. praecox*, *A. furcatispina*, *C. pallida*, and perhaps *M. spinosa* might be important nurse species in this ecosystem. Relationships between nurse and nursed plants might be similar to those occuring in other arid environments, such as North American deserts. During conversion of upland grasslands to woodland in southern Texas, *Prosopis glandulosa* appears to facilitate establishment of other woody plants, including *Celtis pallida* (Fulbright *et al.*, 1995; Francopiziana *et al.*, 1996).

Finally, it should be noted that since seedlings were not randomly assigned to different patches in this study, these results may be interpreted as correlational
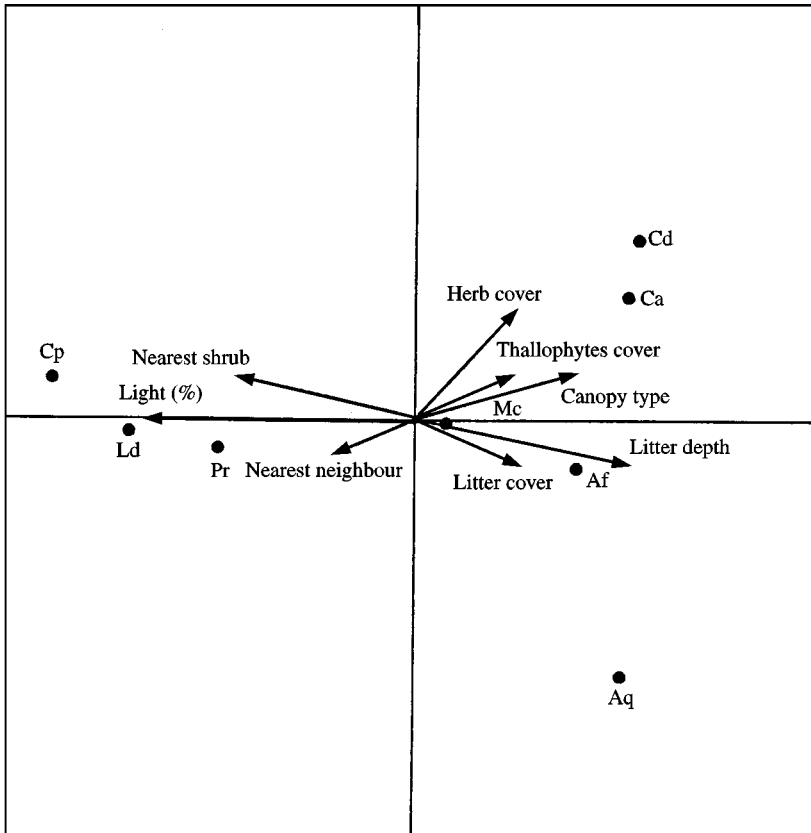
Figure 5. Ordination diagram of microhabitat variables (shown in bold) and centroids of seedling species (dots) using canonical discriminant analysis. The following letters represent species seedlings: Af = *Acacia furcatispina*, Aq = *Aspidosperma quebracho-blanco*, Ca = *Capparis atamisquea*, Cd = *Celtis pallida*, Cp = *Cercidium praecox*, Ld = *Larrea divaricata*, Mc = *Mimozyganthus carinatus*, Pr = *Prosopis* spp.

rather than causal, although the analysis of the occupied sites provides a useful description of the seedling habitat. Differential seed dispersal and seedling survival in different patches may be responsible in part for the observed patterns. However, seedling establishment for most of the species studied is not probably limited by a differential seed distribution, since only *G. decorticans* and *C. praecox* showed adult frequencies less than 50% on 30 points censused in the habitat studied (Páez, unpublished data). Detailed results concerning seed dispersal and long-term seedling survival will be presented elsewhere.

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