

Woody population distribution and environmental heterogeneity in a Chaco forest, Argentina

Barberis, Ignacio M.^{1*}; Batista, William B.²; Pire, Eduardo F.¹;
Lewis, Juan Pablo¹ & León, Rolando J.C.²

¹Facultad de Ciencias Agrarias, Universidad Nacional de Rosario, Argentina, C.C. 14, S2125ZAA Zavalla, Argentina;

²Facultad de Agronomía, Universidad de Buenos Aires, Av. San Martín 4453, C1417DSQ Buenos Aires, Argentina;

*Corresponding author; Fax +543414970080; E-mail ibarberi@fcagr.unr.edu.ar

Abstract. In southern humid Chaco forests dominated by *Schinopsis balansae*, woody plants are clumped and species composition varies spatially over short distances. We examined how these spatial patterns are associated with local environmental heterogeneity for three size classes of woody individuals: adults, saplings, and seedlings. Our study was based on the detailed description of two forest plots (3200 m² in total) in which we mapped all individuals of woody species, and delimited patches with different microrelief, soil moisture, and ground cover of terrestrial bromeliads. Our results showed that woody-individual distribution is related to local environmental heterogeneity. For all size classes, density of woody individuals was highest on convex patches. These convex patches were dominated by both tree (*Acacia praecox* and *Achatocarpus praecox*) and shrub species (*Celtis pallida*, *Capparis retusa* and *Grabowskia duplicata*), while level patches were dominated only by tree species (*Schinopsis balansae*, *Prosopis* spp. and *Geoffroea decorticans*). Drier patches contained all the woody species present in the forest, while wetter patches contained only a subset of them. Within convex patches, trees are likely to occur in places with bromeliad colonies and shrubs in patches without bromeliads. The results suggest forest structure is controlled by environmental heterogeneity associated with microrelief and soil moisture.

Keywords: Bromeliad; Forest structure; Humid; Microrelief; *Schinopsis balansae*; Southern humid Chaco; Subtropical.

Nomenclature: Burkart (1969-1987); Digilio (1971-1974); Pérez Moreau (1994).

Abbreviation: MRPP = Multiple Response Permutation Procedure.

Introduction

Vegetation patterns have long been recognized to be associated with environmental heterogeneity (Gleason 1926; Cooper 1926; Whittaker 1967; Austin 1985). In forest stands, microtopography and soil heterogeneity often determine spatial patterns of woody species regen-

eration that result in clumped distributions of trees or tree species (Beatty 1984; Huenneke & Sharitz 1986; Streng et al. 1989; Peterson & Pickett 1990; Itoh 1995; Clark et al. 1998; Svenning 1999). Effects of these factors may be complicated by disturbances related to animal activity and tree falls, which remove the upper layers of the soil and generate fine-scale microtopography (Oriens 1982; Beatty & Stone 1986; Nakashizuka 1989; Pire et al. 1991; Hansell 1993; Carlton & Bazzaz 1998). In addition, within-forest-stand environmental heterogeneity may be related to plant sociability, due to clonal growth, or to limited dispersion, which can reinforce patterns of tree species distribution (Brokaw 1983; Denslow et al. 1991; Wada 1993; Takahashi 1997). As a consequence of these associations, identifying the controls of forest composition and dynamics requires to characterize the correspondence between forest structure and local environmental heterogeneity.

In the southern humid Chaco, stands of the *Schinopsis balansae* forest type (*quebrachal*) have the trees clumped in patches of different species composition (Lewis & Pire 1981; Lewis 1991; Lewis et al. 1997). Two factors have been proposed to account for this spatial pattern: microrelief (Lewis & Pire 1981; Lewis 1991; Barberis et al. 1998), and ground cover heterogeneity (Bordón 1978; Martínez-Crovetto 1980). Sites of these forests are flat in general but they have a conspicuous microrelief (Espino et al. 1983). Because the associated soils have low hydraulic conductivity (Espino et al. 1983), a large proportion of rainfall runs off to local depressions and, as a consequence, the microrelief is associated with a strong spatial pattern of soil moisture and aeration. Ground cover in these forests is also spatially heterogeneous as large gaps have a dense grass cover and shaded areas are often colonized by two prickly bromeliads: *Aechmea distichantha* and *Bromelia serra* (Lewis & Pire 1981). This ground cover heterogeneity is likely to affect the movement patterns of water, litter, and propagules among different patches in these forests. Spatial patterns of propagule arrival, as well as

in soil moisture and aeration regimes, associated with microrelief and ground cover patterns are likely to affect establishment and survival of woody individuals and might determine the clumped pattern characteristic of this forest type.

In this paper we assess the associations between local environmental heterogeneity and distribution patterns of woody individuals, as well as species composition in a stand of the *Schinopsis balansae* forest type. Our analysis addressed the following questions for the adult, sapling, and seedling size-classes:

1. Are woody individuals clumped in patches associated with specific topographic positions, soil moisture, or ground cover characteristics? If so, what are the habitats that support higher plant density?

2. Are there any consistent differences in woody-species composition among forest patches associated with different topographic positions, soil moisture, or ground cover? If so, what are the differences in woody-species composition among habitats?

3. Are there differences in growth form composition (trees or shrubs) among forest patches associated with specific topographic positions, soil moisture, or ground cover characteristics? If so, are these patterns similar for different size classes?

4. Are there differences in the spectrum of dispersal syndromes (bird or small mammal, cattle, wind, or gravity dispersal) of the seedling class among forest patches with different topographic positions, soil moisture, or ground cover?

Material and Methods

Study area

The Gran Chaco spreads over N Argentina, E Bolivia, W Paraguay, and small portions of S Brazil (Cabrera 1976; Prado 1993). The vegetation encompasses a mosaic of dry forests, savannas, grasslands, and wetlands arranged along moisture and salinity gradients (Morello & Adámoli 1974; Prado 1993). In Argentina, four phytogeographic districts are recognized: the eastern Chaco characterized by *Schinopsis balansae*, the western Chaco by *Schinopsis lorentzii*, the Sierra Chaco by *Schinopsis marginata*, and the Savannas Chaco by *Elyonurus muticus* and *Spartina argentinensis* (Cabrera 1976). The southernmost portion of the eastern Chaco is the Santa Fe Forest Wedge (Cuña Boscosa Santafesina), which is covered by different forest types arranged along environmental gradients correlated with the elevation gradient, and treeless areas with grasslands or wetlands. At the top of the elevation gradient mixed dense forests or Austro-Brazilian transitional forests are

found; downward *Schinopsis balansae* forests (quebra-chales) occur, which are the most widespread and characteristic forest type of the area; at the bottom, next to wetlands, *Prosopis nigra* var. *ragonesei* forests (algarrobales) or *Copernicia alba* palm groves (Lewis & Pire 1981; Lewis 1991; Lewis et al. 1994). In the *Schinopsis balansae* forests, most woody species are deciduous, with small leaves and frequently with spiny structures (Lewis et al. 1997), and the soil surface has a noticeable microrelief (Barberis et al. 1998).

This study was conducted in a 400-ha stand of the *Schinopsis balansae* forest type (Lewis et al. 1997) located at Las Gamas, near Vera, Santa Fe, Argentina (Estación Experimental Tito Livio Coppa, 29° 28' S, 60° 28' W, 58 m a.s.l.). The climate is humid temperate to warm, with a mean annual temperature of ca. 20 °C, and a mean annual precipitation of ca. 1000 mm. Rainfall is concentrated in the summertime (December-March) and a drought of variable length occurs in winter. The forest is located on a mosaic of soils with low hydraulic conductivity and high sodium content (Espino et al. 1983). During the first half of the 20th century, this stand was heavily lumbered for the tannin industry, and subsequently for fuel extraction and charcoal production. Nowadays, this stand, like most of the Santa Fe Forest Wedge forests, although partially recovered, is not completely mature or at a steady state, and cattle grazing and mild firewood extraction are now main disturbances.

Data

Habitat

We positioned two parallel plots, one 220 m × 10 m and the other 100 m × 10 m, within one of the farthest paddocks of the forest stand from Las Gamas village (Barberis 1998). As one of the plots was planned to be a cattle enclosure (cf. Lewis et al. 1997), their location within the paddock was restricted for cattle management purposes. In March 1989, we classified patches into five habitats: convex patches with bromeliad colonies (Eb), convex patches without bromeliad colonies (E), dry plains (Pd), wet plains (Ph), and depressions (D; Barberis et al. 1998). Patches were mapped following their contour in the field (scale 1:100; Barberis et al. 1998). Microrelief was assessed with an optical level along the centre of each plot. Maximum differences in altitude between convex patches and adjacent depressions were ca. 55 cm (Barberis 1998). Soil moisture was subjectively characterized 6 days after a 21-mm rainfall. Patches where the soil was well drained were classified as dry, while patches where the soil was still soaked or flooded were classified as wet. As these rather crude soil-moisture classes were closely associated with different herbaceous community types (Lewis & Pire 1981) we assumed that they reflected

adequately the heterogeneity of soil-moisture regime. Based on this characterization, convex patches were classified as dry, depressions were classified as wet, and plains were split into dry and wet (Barberis et al. 1998). Patch areas included in our plots ranged between 5 m² and 260 m² (Barberis 1998). In our analyses, we only included the 34 patches that covered over 20 m² in the plots (6 Eb, 6 E, 8 Pd, 7 Ph, and 7 D).

Vegetation

In March 1989, we mapped, identified to the species level, and measured for height all woody individuals in the plots. We classified all individuals as adults, saplings, or seedlings using height as a proxy variable (Lewis et al. 1997). Adults were defined as individuals taller than 0.6 m for shrub species, and taller than 1.6 m for tree species; saplings were defined as individuals between 30 cm and adult height; and seedlings were identified as individuals < 30 cm tall. Species were classified as shrubs or trees depending on whether the individuals branched out at the base or not respectively. *Achatocarpus praecox* and *Capparis retusa*, whose individuals can adopt either form, were classified based on the most frequent growth form in our stand (i.e., *Achatocarpus praecox* as a tree and *Capparis retusa* as a shrub). Within our plots, there were 29 woody species (15 trees, 13 shrubs, and one undetermined), 18 of which had individuals in all three size classes (i.e. adults, saplings, and seedlings), four in two classes, and the other seven in only one class.

Analysis

Association between environmental heterogeneity and spatial distribution of woody individuals

To analyse the spatial association between woody individuals and habitats, we overlaid the woody-individual map onto the habitat-patch map, and counted all woody individuals in every patch larger than 20 m². For each size class (i.e., adults, saplings, and seedlings), density was compared among habitats using generalized linear models (Dobson 1990). In these models, the number of individuals in each patch was treated as a Poisson variable whose expected value was a function of the patch area and the patch habitat. While the patch area functioned as a covariate, hypotheses were tested about differences in the parameters associated with each habitat. To correct for overdispersion of the data, the models were fitted by quasi-maximum likelihood (McCullagh & Nelder 1989), using SAS, Proc GENMOD (Anon. 1996). Within the models, multiple comparisons were performed between pairs of habitats. Confidence levels in these comparisons were adjusted by the Bonferroni method (Neter et al. 1990).

Relationship between environmental heterogeneity and forest species composition

We tested for consistency of species composition differences among habitats using a Multiple Response Permutation Procedure (MRPP; Biondini et al. 1988). We ran separate tests comparing species composition of the adult, sapling, and seedling components between pairs of habitats. In the tests, each patch corresponded to a multivariate observation containing the densities of each species, and the habitats were the classes compared. Depressions were not included in these analyses because in each patch the number of individuals was too small to adequately characterize the species composition. 1 – Sørensen index of similarity was used as a measure of dissimilarity. Differences between treatments were considered significant at a *P*-level < 0.0083 (Bonferroni's correction: $\alpha = 0.05/6$ comparisons). In addition, 1 – Sørensen index of similarity was used to compare the floristic composition among size classes for each habitat at the forest scale; and the β -diversity index (Whittaker 1967) to assess species-composition variability among patches. Computation of the distances was performed using the PC-ORD software (McCune & Mefford 1997). To test for differences in the proportions of tree and shrub species among habitats we used χ^2 -tests (Sokal & Rohlf 1995). These tests were run for the adult and seedling classes.

Relationship between environmental heterogeneity and dispersal syndrome composition

We used published data (Caziani 1996; Feldman & Feldman 1987), information from N. Montaldo, G. Roitman and M. Cabido, and our field observations to classify woody species by their dispersal syndrome (see App. 1). We distinguished four groups: (1) Birds or small mammals; (2) Cattle; (3) Wind; (4) Gravity. We used χ^2 -tests (Sokal & Rohlf 1995) to examine the association between environmental heterogeneity and dispersal syndrome of the species for the seedling class.

Results

Spatial distribution of woody individuals

For all size classes, the generalized linear models revealed significant differences in the density of woody individuals among patches of different habitats (Adults $F_{4,29} = 29.66$, $P < 0.0001$; saplings $F_{4,29} = 45.54$, $P < 0.0001$; seedlings $F_{4,29} = 7.83$, $P < 0.0002$). For adults, mean density was significantly higher in the convex patches (Eb, E) than in all other patch types, and significantly higher in dry plains (Pd) than in wet plains (Ph) and depressions (D; Fig. 1a). There were no significant

differences in average adult density between convex patches with and without bromeliad-dominated ground cover (Eb, E), or between wet plains (Ph) and depressions (D; Fig. 1a). For saplings, mean density was significantly higher in convex patches (Eb, E) than in patches of other habitats; while there were no significant differences between sapling densities in Eb and E, or among Pd, Ph, and D (Fig. 1b). For seedlings, mean densities were significantly lower in the wet plains (Ph) than in the dry patches (Eb, E, Pd). In depressions (D), mean seedling density was very low but varying among patches; consequently, mean seedling density in the depressions only differed significantly with that on convex patches without bromeliads (Fig. 1c).

Environmental heterogeneity and species composition

The MRPP tests detected significant differences in woody-species composition among habitats more frequently for the adult than for the sapling and seedling components (Table 1). For the adult class, species composition differed significantly between convex (Eb, E) and level (Pd, Ph) patches. No significant species composition differences were found between patches Eb and E or between dry and wet plains. For the sapling class, the MRPP tests showed significant species-composition differences between Eb patches and plains (Pd, Ph) and between convex patches and wet plains (Ph). However, these tests showed no significant differences in species composition between E patches and dry plains (Pd). For the seedling class, significant differences in species composition were found between Eb patches and plains. In contrast, no significant differences were found between convex patches (Table 1). In general, total numbers of woody species were higher in dry (Eb, E, Pd) than in wet patches (Ph); the variability in species composition among individual patches of each habitat, as measured by the β -diversity (Whittaker 1967) was lower in convex patches than in plains (Table 1).

Lists of dominant woody species of each habitat were largely coincident for the adult and sapling size classes but markedly different between these and the seedling class (Fig. 2). In the adult component, convex patches with bromeliad ground cover were dominated by the tree species *Acacia praecox* and *Achatocarpus praecox* and by the shrub *Celtis pallida*; convex patches without bromeliads were dominated by the shrub species *C. pallida*, *Capparis retusa*, and *Grabowskia duplicata*; and plains (Pd and Ph) by the tree species *Acacia praecox*, *Schinopsis balansae*, *Prosopis* spp. and *Geoffroea decorticans* (Table 1). In the sapling class, convex patches were dominated by *A. praecox*, *Achatocarpus praecox*, *C. pallida*, *G. duplicata*, and *Myrcianthes cisplatensis*; while the plains were domi-

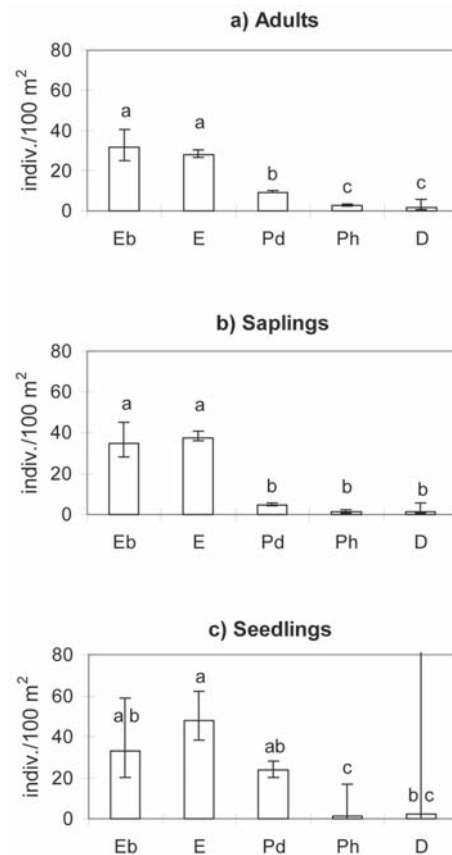


Fig. 1. Mean density and 95% confidence intervals for (a) adults, (b) saplings (c) and seedlings of woody species (individuals/100 m²) in each habitat. Means with the same letters are not significantly different (Bonferroni's method; $P < 0.005$). Eb = convex patches with bromeliads; E = convex patches without bromeliads; Pd = dry plains; Ph = wet plains; D = depressions. For seedlings, the upper limit of the confidence interval in depressions (D) is ca. 165 individuals/100 m².

nated by *C. pallida*, *Geoffroea decorticans*, and *Prosopis* spp. (Table 1). In contrast, in the seedling class, two species with low density of adults and saplings (*M. cisplatensis* and *Aspidosperma quebracho-blanco*) were dominant in all types of habitats (Table 1).

In the seedling class, the proportion of tree species relative to shrub species did not differ significantly among habitats ($\chi^2_3 df = 3.24$; $P = 0.355$; Fig. 3). In contrast, in the adult class, the proportion of trees relative to shrubs differed significantly among habitats ($\chi^2_3 df = 49.76$; $P < 0.001$). As trees and shrubs tended to co-dominate on the convex patches the proportion of trees was significantly lower in convex than in level patches ($\chi^2_1 df = 33.54$; $P < 0.001$; Fig. 3). In convex patches, the proportion of trees was significantly higher on those with a bromeliad dominated ground cover than on those without bromeliads ($\chi^2_1 df = 14.61$; $P < 0.001$).

Table 1. Distribution of adult, sapling, and seedling individuals of woody species among different habitats. Results based on MRPP tests comparing habitats according to their species composition in different patches for adults, saplings, and seedlings of woody species. For each size class, habitats with a different letter are significantly different at a *P*-level of 0.0083 according to MRPP tests. Values show the relative density of individuals of each species in each habitat, and the column total shows total density (individuals/100 m²) of each habitat. Bold values indicate that the species was defined as dominant in this habitat (i.e., relative density higher than 10%). Habitat codes: Eb = convex patches with bromeliads; E = convex patches without bromeliads; Pd = dry plains; Ph = wet plains. ‘Other species’ include in the adult class: *Acacia caven*, *Acanthosyris falcata* and *Tabebuia nodosa*; in the sapling class: *Acacia caven*, *Banara umbraticola*, *Caesalpinia paraguariensis*, *Holmbergia tweedii* and *Senna pendula* var. *paludicola*; in the seedling class: *Banara umbraticola*, *Jodina rhombifolia*, *Sapium haematospermum*, and a non-identified species. Growth form codes: T = trees, S = shrubs.

Habitat	Adults				Saplings				Seedlings			
	Eb	E	Pd	Ph	Eb	E	Pd	Ph	Eb	E	Pd	Ph
MRPP results	a	a	b	b	a	ab	bc	c	a	ab	b	b
T <i>Acacia praecox</i>	28	9	31	4	14	14	8		14	7	6	8
T <i>Achatocarpus praecox</i>	14	9	1		18	15	8		5	2	3	
S <i>Celtis pallida</i>	11	23	3		9	21	18	9	4	6	3	
S <i>Capparis retusa</i>	8	11	1		7	8			7	3	5	
S <i>Grabowskia duplicata</i>		16	1	9	1	20		9			1	8
T <i>Schinopsis balansae</i>	6	3	16	26	5		5	9	7	4	9	25
T <i>Geoffroea decorticans</i>		8	12	30		5	21	18		1	5	17
T <i>Prosopis</i> spp.	2	3	19	22		1	18	36	1		2	
T <i>Myrcianthes cisplatensis</i>	7	3	3		27	4	3		28	42	31	42
T <i>Aspidosperma quebracho-blanco</i>	2	1	3	4	1		5		11	16	12	
S <i>Lycium cuneatum</i>	1				2			9	3	2	14	
S <i>Maytenus vitis-idaea</i>	8	3	3	4	7	4	3		2	1	1	
T <i>Sideroxylon obtusifolium</i>	3	1	3		1				7	2	2	
T <i>Ziziphus mistol</i>	4		1							2	1	
S <i>Schinus fasciculatus</i>	4	1			1		3		1		1	
S <i>Celtis iguanea</i>	2	3					3			1		
S <i>Coccoloba argentinensis</i>	3				2				3	5		
S <i>Erythroxylum microphyllum</i>		3			1	2	3		5	7	5	
S <i>Aloysia gratissima</i>		1			1	2	3					
Other species	1	3	3		3	2		9	1	1	2	
Density (individuals/100 m ²)	31.60	28.16	9.21	2.67	34.76	37.17	4.75	1.28	33.02	48.06	23.77	1.39
Number of species	17	18	15	7	20	14	13	7	16	16	19	5
Number of species per sector	9.17	6.50	3.75	1.86	8.50	5.33	2.63	1.14	9.50	7.00	4.88	1.29
Range of number of spp. per patch	(4-16)	(3-12)	(1-11)	(0-5)	(2-15)	(0-7)	(0-9)	(0-3)	(6-14)	(2-12)	(0-16)	(0-3)
β-diversity	1.85	2.77	4.00	3.77	2.35	2.63	4.95	6.13	1.68	2.29	3.90	3.89

Relationship between environmental heterogeneity and dispersal syndrome composition

In the seedling class, there were significant differences among habitats in the dispersal-syndrome profile of recruited individuals (χ^2_3 d.f. = 18.52; *P* < 0.001) (species dispersal syndromes are given in App. 1). The

proportion of seedlings from species dispersed by gravity was higher, and the proportion of seedlings from species dispersed by cattle was lower in convex than in level patches (Fig. 4). The proportions of seedlings from species dispersed by birds or wind were similar among habitats (Fig. 4).

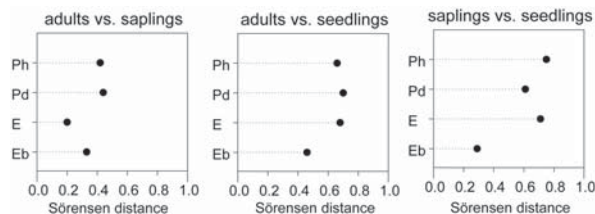


Fig. 2. 1– Sørensen index among different components of the forest (adults vs. saplings, adults vs. seedlings, and saplings vs. seedlings) in each habitat. Habitat codes: Eb = convex patches with bromeliads; E = convex patches without bromeliads; Pd = dry plains; Ph = wet plains.

Discussion

Environmental heterogeneity and spatial distribution of woody individuals

In *Schinopsis balansae* forests of the humid Chaco, patches of closed forest typically alternate with stretches of savanna-type vegetation (Morello & Adámoli 1974; Lewis & Pire 1981; Lewis 1991; Placci 1995; Lewis et al. 1997). In our plots, this pattern was strongly associated with microrelief. Convex patches (Eb, E) supported closed canopy forest with high density of adult trees and

saplings and a ground cover containing prickly bromeliad patches and high density of tree and shrub seedlings. In contrast, level and concave patches (Pd, Ph, D) supported open vegetation with low density of trees and saplings and a dense grassy ground cover. Seedling density was similar to that on convex patches in dry plains (Pd) but substantially lower in the wetter patches (Ph, D).

The association between microtopography and distribution of woody individuals suggests that, in our forest, environmental heterogeneity might strongly influence the regeneration of woody species. In convex patches, high density of adult trees is likely to result in abundant primary seed dispersion (cf. Augspurger & Franson 1988; Schupp et al. 1989). As the closed canopy intercepts the rain and the bromeliad clusters trap seeds and slow down run-off, secondary dispersion away from the convex patches is likely to be reduced. In level patches, in contrast, low tree density possibly results in reduced primary seed dispersion and, because run-off is intense as a result of grazing and trampling reducing soil cover and permeability, many seeds are likely to be washed away into the swamps (Barberis pers. obs.). In addition to these patterns of seed dispersion, differences in seedling and sapling mortality possibly reinforce the spatial pattern of woody individual distribution. In the plains and depressions, mortality is likely to be high as seedlings and saplings of woody species are exposed to rather extreme environmental conditions. In the plains and depressions, moisture of the upper soil layers is strongly seasonal as the sites are frequently flooded in summer and very dry in winter (Espino et al. 1983). As a consequence, woody plants are exposed to root anoxia

in the summer and to water stress and strong competition from grasses during winter droughts (Parodi 1942). These hardships are intensified by cattle trampling compacting the topsoil and damaging seedlings directly. In addition, summer growth of grasses and sedges in the plains and depressions builds up biomass that becomes very flammable after winter drought, and, although fires are not very common (Morello 1970), when they occur, they produce high mortality of woody individuals (Pire pers. obs.). In contrast, in convex patches, topsoil moisture is less fluctuating, grass density is lower, and prickly bromeliad colonies prevent cattle trampling (Bordón 1978) and surface-fire spread (Tortorelli 1947), determining a more favourable habitat for the establishment and survival of trees and shrubs. Our seedling counts are consistent with the notion that patterns of seed arrival, and seedling establishment and survival, account for the patterns of woody individual density in our forest.

Clumped distribution of woody species has also been observed in xerophytic forests of the semi-arid Chaco (Morello & Adámoli 1974), and the *Celtis tala* forest of the Espinal province, a phytogeographic area confined to the Chaco Domain (Parodi 1940). In both areas, as in our study, the forest is located on positive relief with well-drained soils (e.g. silty loam in the semi-arid Chaco and calcareous soils in the coast of the Espinal province).

In this study we did not consider the probable compositional, structural, and functional differences between the edge and the interior of the forest. For example, in an old-growth stand of the semi-arid Chaco, the edge showed a very dense cover of thin stems and higher cover near the ground in the shrub stratum compared to the interior of the forest (López de Casenave et al. 1995). Likewise, sapling density of *Celtis tala* was higher at the edge than in the interior of the forest or the grassland in a 'talar' forest of the Espinal province (Arturi 1997). However, there was no difference in seedling numbers of *Celtis tala* among environments, suggesting that differences in sapling number was not related to seed availability or germination, but to seedling mortality (Arturi 1997). A similar pattern was ob-

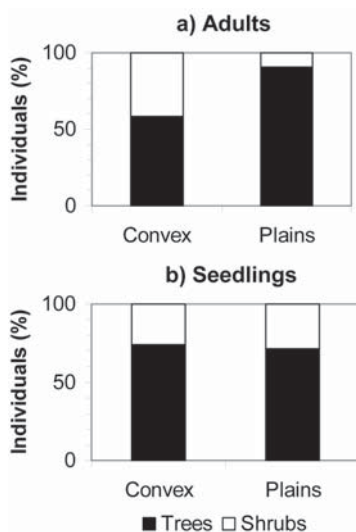


Fig. 3. Distribution of tree and shrub individuals in convex patches and plains for (a) the adult and (b) the seedling classes.

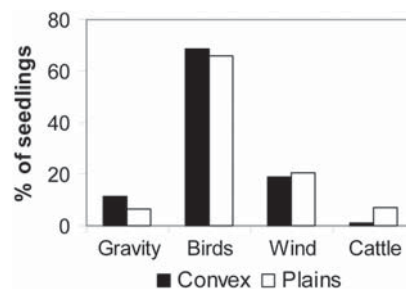


Fig. 4. Distribution of woody seedlings from species with different dispersal syndrome in convex patches and plains.

served in our stand of *Schinopsis balansae* where seedlings of most species grew all over the ground in convex patches, whereas saplings were mainly located at the edge of convex habitats (Barberis 1998).

Environmental heterogeneity and species composition

In our forest, species composition differences are consistently associated with local environmental heterogeneity. While most woody species in the forest occur on convex patches and dry plains, only a subset without exclusive species occurs on wet plains (Ph). On the convex patches, the forest is dominated by both trees and shrubs, whereas in the plains, the forest is dominated by tree species only. This pattern is clear for the adult stratum but less evident for the sapling and even less for the seedling strata suggesting that woody species distribution might reflect spatial patterns both of seed dispersion and/or of growth and survival (cf. Augspurger & Franson 1988; Schupp et al. 1989; Schupp 1995).

Patterns of seed dispersion

Patterns of seed dispersion are likely to differ among patches as a result of the differences in vegetation structure. On the convex patches, seedlings of woody species with multiple dispersal syndromes, and especially those dispersed by birds and small mammals or reptiles, were well represented (see App. 1). On level patches, in contrast, seedlings of species dispersed by birds or small animals were underrepresented (only *Myrcianthes cisplatensis* and *Grabowskia duplicata* were present), and species dispersed by cattle (*Geoffrea decorticans*) or wind (*Schinopsis balansae*) were overrepresented. These data suggest that seed dispersal by cattle and wind predominates on the level patches while dispersal by birds and small animals, or by gravity, predominates on convex patches, essentially as a result of vegetation structure differences (Augspurger & Franson 1988; Schupp et al. 1989). Seedling growth and survival may later change the pattern of sapling distribution. However, this issue is in need of further research in order to find out which one of these processes is relatively more important.

Acknowledgements. We greatly appreciate the logistic support given by Luis Schaumburg and Rodolfo Comuzzi from Las Gamas, Ministerio de Agricultura y Ganadería de Santa Fe. We thank Martín Aguiar, Susana Perelman and Jim Dalling for their useful comments on an earlier version of the manuscript. We are grateful to Marcelo Cabido and Exequiel Ezcurra for improving the quality of this paper. We acknowledge CONICET and Facultad de Ciencias Agrarias, Universidad Nacional de Rosario for financial support.

References

- Anon. 1996. *SAS/STAT® Software: changes and enhancements through release 6.11*. SAS Institute Inc., Cary, NC.
- Arturi, M.F. 1997. Regeneración de *Celtis tala* y su relación con el pastoreo, la cobertura herbácea y arbórea en el NE de la provincia de Buenos Aires, Argentina. *Ecol. Austr.* 7: 3-12.
- Augspurger, C.K. & Franson, S.E. 1988. Input of wind-dispersed seeds into light-gaps and forest sites in a Neotropical forest. *J. Trop. Ecol.* 4: 239-252.
- Austin, M.P. 1985. Continuum concept, ordination methods and niche theory. *Annu. Rev. Ecol. Syst.* 16: 39-61.
- Barberis, I.M. 1998. *Distribución y regeneración de especies leñosas en relación con la heterogeneidad ambiental en un bosque de Schinopsis balansae del sur del Chaco oriental*. M. Sc. Thesis, Universidad de Buenos Aires, AR.
- Barberis, I.M., Pire, E.F. & Lewis, J.P. 1998. Spatial heterogeneity and woody species distribution in a *Schinopsis balansae* (Anacardiaceae) forest of the Southern Chaco, Argentina. *Rev. Biol. Trop.* 46: 515-524.
- Beatty, S.W. 1984. Influence of microtopography and canopy species on spatial patterns of forest understory plants. *Ecology* 65: 1406-1420.
- Beatty, S.W. & Stone, E.L. 1986. The variety of soil microsites created by treefalls. *Can. J. For. Res.* 16: 539-548.
- Biondini, M.E., Mielke, P.W. & Redente, E.F. 1988. Permutation techniques based on euclidean analysis spaces: a new and powerful statistical method for ecological research. *Coenoses* 3: 155-174.
- Bordón, A. 1978. *Las bromeliáceas terrestres*. Report INTA EERA Presidencia. Roque Sáenz Peña, Presidencia Roque Sáenz Peña, AR.
- Brokaw, N.V.L. 1983. Groundlayer dominance and apparent inhibition of tree regeneration by *Aechmea magdalenae* (Bromeliaceae) in a tropical forest. *Trop. Ecol.* 24: 194-200.
- Burkart, A. 1969-1987. *Flora Ilustrada de Entre Ríos (República Argentina)*. Colección Científica del I.N.T.A., Buenos Aires, AR.
- Cabrera, A.L. 1976. Regiones fitogeográficas argentinas. In: *Enciclopedia Argentina de Agricultura y Jardinería*. Vol. II, Issue 1. Editorial Acme, Buenos Aires, AR.
- Carlton, G.C. & Bazzaz, F.A. 1998. Resource congruence and forest regeneration following an experimental hurricane blowdown. *Ecology* 79: 1305-1319.
- Caziani, S.M. 1996. *Interacción plantas-aves dispersoras de semillas en un bosque chaqueño semiárido*. Ph.D. Thesis, Universidad de Buenos Aires, AR.
- Clark, J.S., Macklin, E. & Wood, L. 1998. Stages and spatial scales of recruitment limitation in southern Appalachian forests. *Ecol. Monogr.* 68: 213-235.
- Cooper, W.S. 1926. The fundamentals of vegetation change. *Ecology* 7: 391-413.
- Denslow, J.S., Newell, E. & Ellison, A.M. 1991. The effect of understory palms and cyclanths on the growth and survival of *Inga* species. *Biotropica* 23: 225-234.
- Digilio, A.P.L. 1971-1974. *Notas preliminares para la flora chaqueña (Formosa, Chaco y Santiago del Estero)*. Centro de Investigaciones de Recursos Naturales, I.N.T.A.,

- Castelar, AR.
- Dobson, A. 1990. *An introduction to generalized linear models*. Chapman & Hall, London, UK.
- Espino, L.M., Seveso, M.A. & Sabatier, M.A. 1983. *Mapa de suelos de provincia de Santa Fe*. Tomo II. MAGSF and INTA EERA Rafaela, Rafaela, AR.
- Feldman, I. & Feldman, S.R. 1987. Brush problems in Argentina's rangelands: I. Chañar (*Geoffroea decorticans*) in northwestern Santa Fe province. *Rangelands* 9: 251-254.
- Gleason, H.A. 1926. The individualistic concept of the plant association. *Bull. Torrey Bot. Club* 53: 7-26.
- Hansell, M.H. 1993. The ecological impact of animal nests and burrows. *Funct. Ecol.* 7: 5-12.
- Huenneke, L.F. & Sharitz, R.R. 1986. Microsite abundance and distribution of woody seedlings in a South Carolina cypress-tupelo swamp. *Am. Midl. Nat.* 115: 328-335.
- Itoh, A. 1995. Effects of forest floor environment on germination and seedling establishment of two Bornean rainforest emergent species. *J. Trop. Ecol.* 11: 517-527.
- Lewis, J.P. 1991. Three levels of floristical variation in the forests of Chaco, Argentina. *J. Veg. Sci.* 2: 125-130.
- Lewis, J.P. & Pire, E.F. 1981. *Reseña sobre la vegetación del Chaco santafesino*. I.N.T.A., Serie Fitogeográfica 18. Buenos Aires, AR.
- Lewis, J.P., Pire, E.F. & Vesprini, J.L. 1994. The mixed dense forest of the Southern Chaco. Contribution to the study of flora and vegetation of the Chaco VIII. *Candollea* 49: 159-168.
- Lewis, J.P., Pire, E.F. & Barberis, I.M. 1997. Structure, physiology and species composition of a *Schinopsis balansae* (Anacardiaceae) forest in the Southern Chaco, Argentina. *Rev. Biol. Trop.* 45: 1013-1020c.
- López de Casenave, J., Pelotto, J.P. & Protomastro, J. 1995. Edge-interior differences in vegetation structure and composition in a Chaco semi-arid forest, Argentina. *For. Ecol. Manage.* 72: 61-69.
- Martínez-Crovetto, R. 1980. Estudios fitosociológicos en el sotobosque de los quebrachales del noroeste de Corrientes (República Argentina). *Bol. Soc. Arg. Bot.* 19: 315-329.
- McCullagh, P. & Nelder, J.A. 1989. *Generalized linear models*. Chapman & Hall, London, UK.
- McCune, B. & Mefford, M.F. 1997. *PC-ORD. Multivariate analysis of ecological data*. Version 3.04. M.J.M. Software Design, Gleneden Beach, OR.
- Morello, J. 1970. Modelo de relaciones entre pastizales y leñosas colonizadoras en el Chaco argentino. *IDIA* 276: 31-52.
- Morello, J. & Adámoli, J. 1974. *Las grandes unidades de vegetación y ambiente del Chaco argentino. Segunda parte: Vegetación y ambiente de la provincia del Chaco*. I.N.T.A., Serie fitogeográfica 13. Buenos Aires, AR.
- Nakashizuka, T. 1989. Role of uprooting in composition and dynamics of an old-growth forest in Japan. *Ecology* 70: 1273-1278.
- Neter, J., Wasserman, W. & Kutner, M.H. 1990. *Applied linear statistical models*. Richard D. Irwin, IL.
- Orians, G.H. 1982. The influence of tree-falls in tropical forests in tree species richness. *Trop. Ecol.* 23: 255-279.
- Parodi, L.R. 1940. La distribución geográfica de los talares en la provincia de Buenos Aires. *Darwiniana* 4: 33-56.
- Parodi, L.R. 1942. ¿Por qué no existen bosques naturales en la llanura bonariense si los árboles crecen en ella cuando se los cultiva? *Rev. Cent. Est. Agron.* 30: 387-390.
- Pérez Moreau, R. 1994. *Flora chaqueña (Formosa, Chaco y Santiago del Estero)*. Centro de Investigaciones de Recursos Naturales, I.N.T.A., Castelar, AR.
- Peterson, C.J. & Pickett, S.T.A. 1990. Microsite and elevational influences on early forest regeneration after catastrophic windthrow. *J. Veg. Sci.* 1: 657-662.
- Pire, E.F., Torres, P.S., Romagnoli, O.D. & Lewis, J.P. 1991. The significance of ant-hills in depressed areas of the Great Chaco. *Rev. Biol. Trop.* 39: 71-76.
- Placci, L.G. 1995. *Estructura y comportamiento fenológico en relación a un gradiente hídrico en bosques del este de Formosa*. Ph.D. Thesis, Universidad Nacional de La Plata, AR.
- Prado, D.E. 1993. What is the Gran Chaco vegetation in South America? I. A review. Contribution to the study of flora and vegetation of the Chaco V. *Candollea* 48: 145-172.
- Schupp, E.W. 1995. Seed-seedling conflicts, habitat choice, and patterns of plant recruitment. *Am. J. Bot.* 82: 399-409.
- Schupp, E.W., Howe, H.F., Augspurger, C.K. & Levey, D.J. 1989. Arrival and survival in tropical tree-fall gaps. *Ecology* 70: 562-564.
- Sokal, R.R. & Rohlf, F.J. 1995. *Biometry*. 3rd. ed. W.H. Freeman & Company, New York, NY.
- Streng, D.R., Glitzenstein, J.S. & Harcombe, P.A. 1989. Woody seedling dynamics in an east Texas floodplain forest. *Ecol. Monogr.* 59: 177-204.
- Svenning, J.C. 1999. Microhabitat specialization in a species-rich palm community in Amazonian Ecuador. *J. Ecol.* 87: 55-65.
- Takahashi, K. 1997. Regeneration and coexistence of two subalpine conifer species in relation to dwarf bamboo in the understorey. *J. Veg. Sci.* 8: 529-536.
- Tortorelli, L.A. 1947. *Los incendios de bosques en la Argentina*. Ministerio de Agricultura de la Nación, Dirección Forestal, Buenos Aires, AR.
- Wada, N. 1993. Dwarf bamboos affect the regeneration of zoochorous trees by providing habitats to acorn-feeding rodents. *Oecologia* 94: 403-407.
- Whittaker, R.H. 1967. Gradient analysis of vegetation. *Biol. Rev.* 42: 207-264.

Received 5 August 2001;

Revision received 15 January 2002;

Final version received 5 April 2002;

Accepted 5 April 2002.

Coordinating Editor: E. Ezcurra.

For App. I, see JVS/AVS Electronic Archives;
www.opuluspress.se/pub/archives/index.htm

App. 1. Tree and shrub species present in a *Schinopsis balansae* forest of the Southern Humid Chaco arranged according to their main dispersal modes. A non-identified species was not considered. We used published data (Caziani 1996; Feldman & Feldman 1987), personal communications by N. Montaldo, G. Roitman, and M. Cabido, and our field observations to classify the woody species by dispersal syndrome.

Growth form	Dispersal mode	Species	Family	Fruit
Trees	Birds and small mammals	<i>Acanthosyris falcata</i>	<i>Santalaceae</i>	Drupe
		<i>Achatocarpus praecox</i>	<i>Achatocarpaceae</i>	Drupe
		<i>Jodina rhombifolia</i>	<i>Santalaceae</i>	Capsule with white arillate seeds
		<i>Myrcianthes cisplatensis</i>	<i>Myrtaceae</i>	Berry
		<i>Sapium haematospermum</i>	<i>Euphorbiaceae</i>	Capsule with white arillate seeds
		<i>Sideroxylon obtusifolium</i>	<i>Sapotaceae</i>	Berry
		<i>Ziziphus mistol</i>	<i>Rhamnaceae</i>	Drupe
	Cattle	<i>Acacia caven</i>	<i>Fabaceae (Mimosoideae)</i>	Indehiscent legume
		<i>Caesalpinia paraguariensis</i>	<i>Fabaceae (Caesalpinioideae)</i>	Indehiscent legume
		<i>Geoffroea decorticans</i>	<i>Fabaceae (Papilionoideae)</i>	Drupe
		<i>Prosopis</i> spp.	<i>Fabaceae (Mimosoideae)</i>	Fleshy legume
	Gravity Wind	<i>Acacia praecox</i>	<i>Fabaceae (Mimosoideae)</i>	Legume
		<i>Aspidosperma quebracho-blanco</i>	<i>Apocynaceae</i>	Capsule with winged seeds
<i>Schinopsis balansae</i>		<i>Anacardiaceae</i>	Samara	
<i>Tabebuia nodosa</i>		<i>Bignoniaceae</i>	Capsule with winged seeds	
Shrubs	Birds and small mammals	<i>Banara umbraticola</i>	<i>Flacourtiaceae</i>	Berry
		<i>Capparis retusa</i>	<i>Capparidaceae</i>	Capsule with silique form
		<i>Celtis iguanea</i>	<i>Ulmaceae</i>	Drupe
		<i>Celtis pallida</i>	<i>Ulmaceae</i>	Drupe
		<i>Coccoloba argentinensis</i>	<i>Polygonaceae</i>	Achene with fleshy calyx
		<i>Erythroxylum microphyllum</i>	<i>Erythroxilaceae</i>	Drupe
		<i>Grabowskia duplicata</i>	<i>Solanaceae</i>	Drupe
		<i>Holmbergia tweedii</i>	<i>Chenopodiaceae</i>	Berry
		<i>Lycium cuneatum</i>	<i>Solanaceae</i>	Berry
		<i>Maytenus vitis-idaea</i>	<i>Celastraceae</i>	Capsule with red arillate seeds
		<i>Schinus fasciculatus</i>	<i>Anacardiaceae</i>	Drupe
	Gravity	<i>Aloysia gratissima</i>	<i>Verbenaceae</i>	Schizocarp
		<i>Senna pendula</i> var. <i>paludicola</i>	<i>Fabaceae (Caesalpinioideae)</i>	Drupe