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Soil factors determining the change in forests between dry and wet Chacos

Gonzalo Navarro[a], José Antonio Molina[a,*], Silvio Vega[b]

[a] Departamento de Biología Vegetal II, Universidad Complutense de Madrid, 28040-Madrid, Spain
[b] Departamento de Suelos y Ordenación Territorial, Universidad Nacional de Asunción, Paraguay

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ABSTRACT

This work consists of an extensive study of soil properties and floristic composition of the Paraguayan Chacoan forests. The role of the soil factors was determined conditioning the classical landscape differentiation between the dry western Chaco and the wet eastern Chaco. Soil horizon A best explains the previous classification of the forests. It highlights the soil differences between the eastern and western Chaco. CCA ordination including all forest, soil and geographical factors primarily arranged the plant associations along a W-E gradient. A significant relationship was found between the composition of the northern Paraguayan Chaco forest and geographic longitude, drainage and altitude. CCA ordination focusing on alluvial forests and soil features identified clay content as the primary soil factor discriminating forest types; it also underlined the importance of cation exchange and the content of exchange bases in the soil for differentiating dry and wet Chacoan forests.

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Introduction

The Chaco is a flat area extending over 800,000 km^2 mainly in northern Argentina, western Paraguay, and south-eastern Bolivia. The Chaco is one of the few areas in the world where the transition between the tropics and the temperate belt does not occur in the form of a desert, but rather as semi-arid forests and woodlands (Morillo, 1967).

The Chaco climate is characterized by severe drought in the cool season (from May to September) and a rainy warm season. The decreasing temperature gradient from the northern to southern Chaco has caused a separation between the largely frost-free northern Chaco and the southern Chaco which is regularly subjected to frosts, leading to a marked floristic impoverishment (Cabido et al., 1993). Additionally, the increase in rainfall from west to east has led to a differentiation in the plant landscape between the dry Chaco (dry western Chaco) and the wet Chaco (wet eastern Chaco) (Ramella and Spichiger, 1989; Cabrera, 1971; Ragonese, 1970; Morillo and Adámoli, 1968; Hueck, 1966; Castellanos, 1944). However, this climatic differentiation does not in itself account for the change in landscape from the dry Chaco to the wet Chaco on the local level which occurs through forests on poorly drained soils (Navarro et al., 2006). We hypothesize that soil factors such as texture and internal drainage are important in this landscape change.

A large part of the Chacoan forest has been subjected to fires, human exploitation, grazing, logging and ploughing which have affected the structural composition and distribution of the vegetation and its associated fauna as well as causing soil degradation (Bonino, 2006; Abril et al., 2005; Bonino and Araujo, 2005; Cabral et al., 2003; Zak and Cabido, 2002; Gardner et al., 1995; López de Casenave et al., 1995). However, most of the northern Paraguayan Chaco, which includes the Biosphere Reserve of Gran Chaco, is still well conserved (Navarro, 2005a) and thus constitutes a suitable area for determining how soil factors can influence forest distribution on a broad scale. We aimed to relate soil features and floristic composition on the regional scale of the Gran Chaco Biosphere Reserve, and to determine specifically the role of soil factors in the transition between the dry and wet Chaco.

Study area

The area studied here comprises the north of Paraguay, with parallel 21°30′′ as its southern limit. This area includes an extension of about 4,700,000 ha. It is located in the Alto Paraguay and Boquerón Departments, and has the conservation status of “Biosphere Reserve”. According to Navarro (2005b) and Iriondo (1995), the geomorphologic features of the territory are: (1) the old alluvial plain of the Parapetí river; (2) the old western alluvial plain of the Pilcomayo river; (3) Alto Paraguay Eastern Chaco; (4) Chiquitania peripheral mountain ranges transitional to Chaco; (5) Chaco riverine landscape.

According to the four weather stations located in the study area and its surroundings (Fortín Nueva Asunción, Bahía Negra, Mariscal Estigarribia, Base Adrián Jara), the average annual temperature is

* Corresponding author.
E-mail address: jmabril@farm.ucm.es (J.A. Molina).

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quite similar, and varies between 25 and 26.5 °C (Navarro et al., 2006). There is a much greater variability in precipitation (UNA-FIA-CIF-GTZ, 1991; Adámoli, 1985; Esser, 1982; Gorham, 1973). Rainfall values range from 564 to 1103 mm, in an increasing gradient from west to east and from south to north (Navarro et al., 2006). However, this general pattern must be qualified by the intrusion of the mountain ranges located to the northeast of the territory, which orographically favors an increase in the rainfall in this quadrant. The soils of the Chaco plains are developed mainly from fluvial and eolic sediments in the north and from loessic material in the south, and range from sandy to heavy clay (Jakob and Guamán, 1993; Teruggi, 1957). The soils of the studied area have been classified into the following soil types: haplic arenosol, eutric fluvisol, calcaric regosol, eutric cambisol, eutric regosol, calcaric fluvisol, calcic vertisol, vertic cambisol, eutric gleysol, calcic solonetz, haplic fluvisol, eutric leptosol, lithic leptosol and chromic cambisol (Vega, 2005).

26 forest types have been described in the territory (Navarro et al., 2006), which were initially grouped into 4 groups and 13 subgroups according to their floristic composition and a multiscale of environmental factors (Table 1). The northern Paraguayan Chaco is floristically influenced by the Cerrado, Paraná Basin and Caatinga (Spichiger et al., 2004; Prado, 1993a,b; Prado and Gibbs, 1993). The forest on the sandy soils of the northwest Chaco is the natural potential vegetation of the sandy Médanos and eolic surfaces in the northwest Paraguayan Chaco (forest community types a, b, c; Table 1). The old alluvial plains of the northwest Chaco are covered with xerophytic forests on soils with a greater or lesser degree of drainage (d, e, f, and g) and by xerophytic forests which are poorly drained, at least seasonally (n, o, p, and q). The landscape unit designated the eastern Chaco of Alto Paraguay begins approximately to the east of meridian 59°, and includes forests on poorly drained to flooded soils (m, r, z, x, and y). The Chiquitanian peripheral mountain ranges transitional to the Chaco occupy the contact zone between the far east of the old Parapetí alluvial plain and the undulating flattened ranges of the south-western end of the Brazilian precambric shield. Forests or shrublands have been identified in this region with a predominance of either the Chacoan (h, i, j, k, l, and u) or Chiquitanian element (s, t, v, and w).

The whole study area contains ecosystems in a good state of conservation. However, different types of human disturbance have occurred on pristine vegetation both in the past and in current time (Navarro, 2005a). The most important of these is fire, which particularly affects the Medanos sand forests and the low forests of the transitional Chiquitania to the Chaco. Repeated and regular burning of land for the subsequent introduction of cattle has reduced these woods and chaparrals to marginal enclaves within a plant matrix featuring predominantly grasslands, scrublands and shrublands, forming a fire-generated mosaic of differing stages of substitution and secondary vegetation (Navarro, 2005b). The floodable palm groves and forests in the east of the region have also undergone a process of deforestation (felling, forest fires), and have then been dedicated to agriculture or cattle farming (Cabral et al., 2003). The rest of the area has as yet remained unaffected by human impact, which is limited to the effects of extensive cattle browsing, particularly of cows, in the area around the cattle ranches.

Methods

Data collection and analysis

Vegetation data were based on 56 vegetation samples of 200 m^2 made following the phytosociological methodology (Braun-Blanquet, 1964) along an itinerary of 3500 km in 9 transects, which included the greatest variability of climates, geomorphologies and soils (Navarro et al., 2006; Fig. 1).

36 soil samples were taken, making sure to sample each type of forest at least once and tending to give higher priority to forests with greater spatial representation in the territory. The samples were taken at the center of each vegetation plot. The survey of the soil consisted of semi-detailed observations ("mini-pedons", 60%) and simple observations (sampling pits, 40%). Mini-pedons are small pits with a length, width and depth of 50 cm which are used to describe the soil characteristics according to FAO/UNESCO (1995) and USDA (1996) guidelines; parameters include thickness of horizons, texture to the touch, structure, internal drainage, presence of carbonates, gypsum and/or salts, color (Munsell system), porosity and root content. At the bottom of each ditch the observation was continued with a sampling pit with a depth of between 1.0 and 1.5 m, and the findings were described as above. Up to four horizons could be identified in each pedon. The physical–chemical analysis included the following parameters according to USDA (1996) and ISRIC methods (1987): pH (KCl 1 M, H_2O ′1:1), electrical conductivity, Ca, Mg, K, Na, sum of bases, total cation exchange capacity (CEC), effective cation exchange capacity (ECEC), total cation exchange capacity of clay (CECclay), effective cation exchange capacity of clay (ECECclay), acidity (Al^{3+}), base saturation, organic matter (OM), organic carbon (OC), P (phosphorus), and texture (sand, silt and clay content were expressed based on weight percentage). Moreover, some geographical features such as longitude, latitude and altitude were collected for each locality as a subrogate method for determining the climatic variation of the territory.

Statistical analysis

In order to visualize patterns of soil distribution, different clustering analyses were carried out separately for the three upper horizons (A, B, and C) of 36 soils and 21 soil variables (2 of them semi-quantitative: drainage class and structure) performed with Syntax (Podani, 1993). The minimum sum of squares in these new cluster methods (MSSC) using Euclidean distance as a coefficient of horizon A correlates fairly well with a previous forest classification (Navarro et al., 2006).

Canonical correspondence analysis (CCA) has been widely used to identify which environmental variables are important in the determination of the community composition (ter Braak and Verdonschot, 1995). This method was used to find the relationships between northern Chacoan forest distribution and environmental factors, and specifically between alluvial soils and soil factors. Initially, the analyses consisted of two matrices of 36 samples with 36 plants (the species matrix) and 24 environmental factors (the environmental matrix). We studied 36 common tree species found in the northern Paraguayan Chaco which can be considered as important characteristics of the forest types (Appendix A). Environmental variables were: pH (KCl 1 M, H_2O ′1:1), ΔpH, Ca, Mg, K, Na, CEC, ECEC, sum of bases, bases saturation, OM, CEC-clay, ECECclay, OC, P, sand, silt, clay, drainage, structure, latitude, longitude, altitude. After excluding the Médanos and transitional forest, we focused on alluvial plain forests (Table 1) in 25 samples, 27 species (*Aca emi*, *Amb cea*, *Ana col*, *Asp que*, *Ast uru*, *Ath wei*, *Bul sar*, *Cal mul*, *Coc gua*, *Cop alb*, *Dip flo*, *Geo spi*, *Lon nud*, *Mac mor*, *Pat ame*, *Pip lom*, *Phy rha*, *Pro ela*, *Pro roj*, *Sch bal*, *Sch cor*, *Sch het*, *Sch que*, *Sph tet*, *Tab nod*, *Tri gar*, *Trit sch* – Appendix A; Abbreviations: legends Figs. 3 and 4) and 15 soil variables (pH H_2O ′1:1, Ca, Mg, K, Na, CEC, sum of bases, base saturation, CECclay, ECECclay, OC, P, sand, slime, clay). The computer program used was CANOCO (ter Braak and Smilauer, 1998).

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Table 1
Classification and structure (species richness and forest height) of the forests of the northern Paraguayan Chaco. Grey-colored background indicates endemic forests to the north and central Paraguayan Chaco.

			Forest community type	Species richness (numbers)	Forest height (m)	
					Tree canopy	Emergents
North Western Chacoan Forests		1. Sand forests (Médanos)	*a: Agonandra excelsa-Schinopsis cornuta*	35	10	15
			b: Piptadeniopsis lomentifera-Schinopsis cornuta	43	10	18
			c: Piptadeniopsis lomentifera-Schinopsis aff. *heterophylla*	42	5	17
		2. Xerophytic forests of the old alluvial plains	*d: Bulnesia sarmientoi-Aspidosperma quebracho-blanco*	50	6	16
			e: Acacia emilioana-Schinopsis aff. *heterophylla*	53	7	17
			f: Tabebuia nodosa-Schinopsis quebracho-colorado	51	5	13
			g: Piptadeniopsis lomentifera-Schinopsis quebracho-colorado	48	6	15
		3. Forests on poorly drained soils	*n: Prosopis elata-Tabebuia nodosa*	41	5	9
			o: Prosopis rojasiana-Bulnesia sarmientoi	40	7	15
			p: Prosopis rojasiana-Tabebuia nodosa	47	5	9
			q: Cordia bordasii-Tabebuia nodosa	30	4	7
North Eastern Chacoan Forests		4. Forests on poorly drained soils of the north eastern Chaco	*m: Lonchocarpus nudiflorens-Schinopsis balansae*	56	17	22
			r: Schinopsis balansae-Tabebuia nodosa	44	9	15
		5. Floodable palm forest of the north-eastern Chaco	*z: Triplaris gardneriana-Copernicia alba*	19	12	14
Transitional forests	Forests of the transitional Chaco to the Chiquitanía	6. Forests on sands	*h: Lonchocarpus nudiflorens Schinopsis cornuta*	63	9	16
		7. Hill forests	*i: Pseudobombax heteromorphum-Astronium urundeuva*	28	17	20
		8. Forests on the alluvial plain	*j: Amburana cearensis-Athyana weinmannifolia*	64	17	21
			k: Diplokeleba floribunda-Phyllostylon rhamnoides	44	10	16
			l: Diplokeleba floribunda-Schinopsis quebracho-colorado	55	7	18
		9. Saxicolous shrublands	*u: Caesalpinia marginata-Anadenanthera colubrina*	27	4	6
	Forests and chaparrals of the transitional Chiquitanía to the Chaco	10. Forest on well drained soils	*s: Lonchocarpus lilloi-Acosmium cardenasii*	40	16	18
		11. Hygrophytic forests	*t: Calycophyllum multiflorum-Acosmium cardenasii*	43	17	18
		12. Cerrado Chaparrals	*v: Sphingiphila tetramera-Terminalia argentea*	52	5	11
			w: Pseudobombax tomentosum-Tabebuia selachidentata	25	4	6
Azonal forests		13. Hygrophytic forests of the northern Chaco	*x: Coccoloba guaranitica-Geoffroea spinosa*	30	6	10
			y: Lonchocarpus pluvialis-Ruprechtia exploratricis	17	12	18

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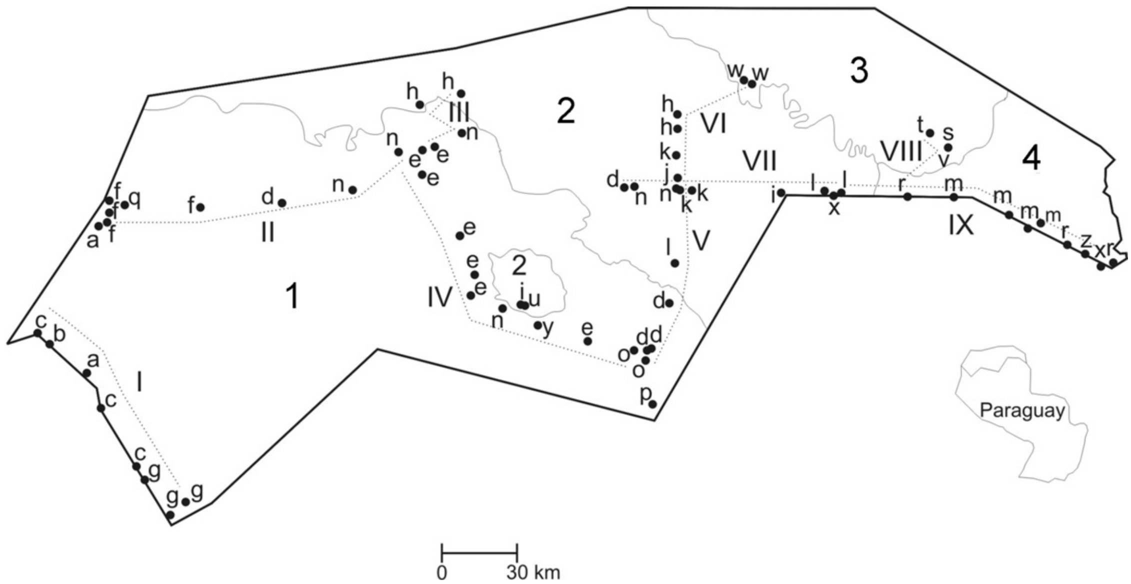

Fig. 1. Study area. Landscape unities, samples and transects. Landscape unities: (1) Western old alluvial plains; (2) transitional Chaco to Cerrado; (3) transitional Cerrado to Chaco; (4) Eastern Chaco. The letter next to the sites (solid circles) corresponds to the forest community types shown in Table 1. Transects and dominant direction: I, Parque Nacional Teniente Enciso Garay-Nueva Concepción, SE-NW; II, Gabino Mendoza-Colonia San Alfredo, W-E; III, Tapacaré-El Puente, NE-SW; IV, Colonia San Alfredo-Madrejón, NW-SE; V, Fortín Teniente Martínez-Agua Dulce, S-N; VI, Adrián Jara-Agua Dulce, N-S; VII, NE Cerro León-Pozo de Buey, W-E; VIII, Estancia Campo Grande-Choroveca/Pozo de Buey, N-S; IX, Pozo de Buey-Bahía Negra, NW-SE.

Results

Forest structure

Forest species richness clearly decreases only in some hygrophytic forest types (*Lonchocarpus pluvialis-Ruprechtia exploratricis* community, *Triplaris gardneriana-Copernicia alba* community) which are adapted to seasonal flooding. The average height of the forest canopy appears to be directly related with the following factors: rainfall, soil drainage, and flooding type – flowing or still waters – (Table 1). The forests in the eastern subhumid Chaco are of greater height than in the western semi-arid Chaco. Moreover, within these forests, those with well- to moderately well-drained soils have the greatest average canopy height; it is considerably lower in the forests on poorly drained clay substrates. Finally, in the group of floodable forests, a higher tree canopy can be observed in forests flooded by flowing waters, as compared to those flooded by stagnant waters. The exception to this regularity is constituted by the chaparrals of the Cerrado in the mountains of the NE, due to the fact that these develop on shallow and/or stony soils.

Soil clustering

Classification of soil horizon A shows three large clusters which can be related with factors such as, for example, granulometric properties, organic matter, Ca and Na (Fig. 2). Cluster relations show a greater similarity between clusters I and II than either of these with cluster III. Cluster I, which includes forests on well-drained soils [Forests of *Schinopsis cornuta* (a, b), forest of *Acosmium cardenasii* (s), and chaparrals of *Terminalia argentea* (v) and of *Tabebuia selachidentata* (w)], has the lowest values for clay ($\mu = 14 \pm 5.74$), organic matter ($\mu = 0.65 \pm 0.42$), Ca ($\mu = 3.20 \pm 2.13$) and Na ($\mu = 0.16 \pm 0.03$). Cluster II, which includes most of the xerophytic forest samples of the old alluvial plain on well- to poorly drained soils [*Aspidosperma quebracho-blanco* forest (d), *Schinopsis heterophylla* forest (e), and transitional forests on alluvial plains such as *Athyana weinmannifolia* forest (j) and *Phyllosthylon rhamnoides* forest (k)], has intermediate values for clay ($\mu = 25.83 \pm 7.71$), organic matter ($\mu = 1.45 \pm 0.70$), Ca ($\mu = 5.96 \pm 1.67$) and Na ($\mu = 0.65 \pm 0.36$). Cluster III, which includes the *Schinopsis balansae* forests of the NE Chaco (m, r) and the floodable palm stands of *Copernicia alba* (z), as well as some samples of the forests of the NW Chaco on poorly drained soils, has the greatest values for clay ($\mu = 39.54 \pm 7.71$), organic matter ($\mu = 2.29 \pm 0.95$), and soluble salts such as Ca ($\mu = 16.48 \pm 6.79$) and Na ($\mu = 2.56 \pm 1.22$). The presence of forests in different clusters reveals different trends within a very broad variability. For example, the *Tabebuia nodosa* forest (n) is distributed between cluster II and III based on the intermediate or greater contents of the above-mentioned elements. All the above results indicate that the greatest difference between soils in the north of the Paraguayan Chaco occurs between the eastern and western Chaco, and then between well-medium drained and poorly drained soils.

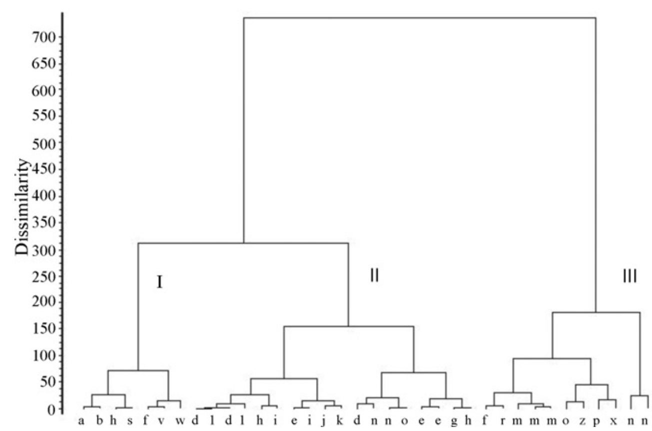

Fig. 2. Clustering analysis of soil horizon A using MSSC and Euclidean distance.

Regional variation across sites and species

The first two canonical axes of the CCA accounted for nearly 30% of the total variation (Table 2), a typical value for strong gradients (ter Braak and Verdonschot, 1995). The eigenvalues for the first two axes were high, indicating that environmental variables

Table 2
Relationships between forest species assemblages and environmental factors.

Canonical axes	Axis 1	Axis 2	Axis 3	Axis 4	Total inertia
Eigenvalues	0.610	0.582	0.479	0.454	5.930
Species–environment correlations	0.960	0.930	0.921	0.938	
Cumulative percentage variance of species data	10.3	20.1	28.2	35.8	
Cumulative percentage variance of species–environment relation	14.8	28.9	40.5	51.6	

are good predictors of species distribution and abundance. Canonical correlations between species axes and environmental axes were all greater than 0.9 and three of these (longitude, drainage and altitude) were significant ($P < 0.01$) in the Monte Carlo test of Canoco. The first major axis in the ordination reflects the east-west gradient (geographical longitude) which can be considered a surrogate form of rainfall variation in the territory. The eastern Chacoan forests, floodable palm forests, hygrophytic forests, transitional forests and chaparrals, and the more poorly drained forests of the old alluvial plain located in eastern areas are arranged to the right of zero (Fig. 3). Characteristic tree species of these forests are: *Schinopsis balansae*, *Copernicia alba*, *Geoffroea spinosa*, *Lonchocarpus lilloi*, *Terminalia argentea*, *Tabebuia selachidentata*, *Bulnesia sarmentoi* and *Tabebuia nodosa*, among others. All the other forests found in the western areas score below zero. Characteristic tree species of these forests are: *Piptadeniopsis lomentifera*, *Schinopsis* aff. *heterophylla*, *Schinopsis quebracho-colorado*, *Schinopsis cornuta*, *Aspidosperma quebracho-blanco*, *Acacia emilioana*, among others. The second axis is related to K content in soils and sand. This gradient appears mainly to represent the drainage capacity of the soil. Values above zero include forests growing on more sandy soils which correspond mostly to more xerophytic communities in areas that rarely or never experience flooding (forests of the Médanos and forests transitional to Chiquitania on sandy soils), although these zones always include patches of soils which are poorly drained or subject to flooding. The ordination scheme also points to the presence of three distinct ecological–biogeographical areas: the old alluvial plain forest of the dry Chaco which covers a range of terrains from eolic sandy areas (Médanos) to floodable heavy clay soils and gilgai microrelief; the transitional forest of NE Chaco floristically influenced by the Chiquitania and the Cerrado; and the eastern Chacoan forest of the wet and swamp Chaco.

The CCA analysis focusing on the influence of the soil features in alluvial plain forest composition also showed high eigenvalues,

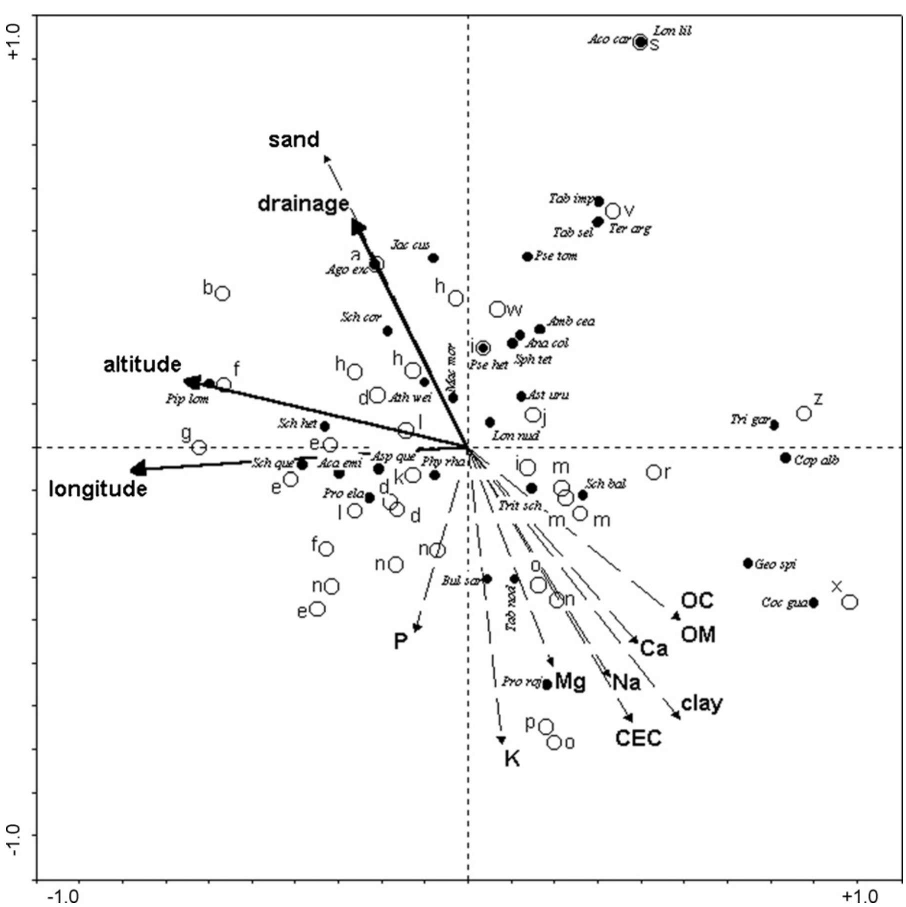

Fig. 3. CCA triplot of forest types, 36 characteristic tree species, and 24 environmental factors. Quantitative environmental variables are indicated by arrows. The abbreviations of the environmental variables are shown in the 'Methods' section. Species (solid circles) are weighted averages of site scores. The species names are abbreviated to the part in italics as follows: *Aca*cia *emi*lioana, *Aco*smium *car*denasii, *Ago*nandra *ex*celsa, *Amb*urana *cea*rensis, *Ana*denanthera *col*ubrina, *Asp*idosperma *que*bracho-blanco, *Ast*ronium *uru*ndeuva, *Ath*yana *wei*nmannifolia, *Bul*nesia *sar*mentoi, *Coc*coloba *gua*ranitica, *Cop*ernicia *alb*a, *Geo*ffroea *spi*nosa, *Jac*aranda *cus*pidifolia, *Lon*chocarpus *lil*loi, *Lon*chocarpus *nud*iflorens, *Mac*lura tinctorea subsp. *mor*a, *Phy*llostylon *rha*mnoides, *Pip*tadeniopsis *lom*entifera, *Pro*sopis *ela*ta, *Pro*sopis *roj*asiana, *Pse*udobombax *het*eromorphum, *Pse*udobombax *tom*entosum, *Sch*inopsis *bal*ansae, *Sch*inopsis *cor*nuta, *Sch*inopsis *het*erophylla, *Sch*inopsis *que*bracho-colorado, *Sph*ingiphila *tet*ramera, *Tab*ebuia *imp*etiginosa, *Tab*ebuia *nod*osa, *Tab*ebuia *sel*achidentata, *Ter*minalia *arg*entea, *Tri*plaris *gar*dneriana, *Tri*thrinax *sch*izophylla.

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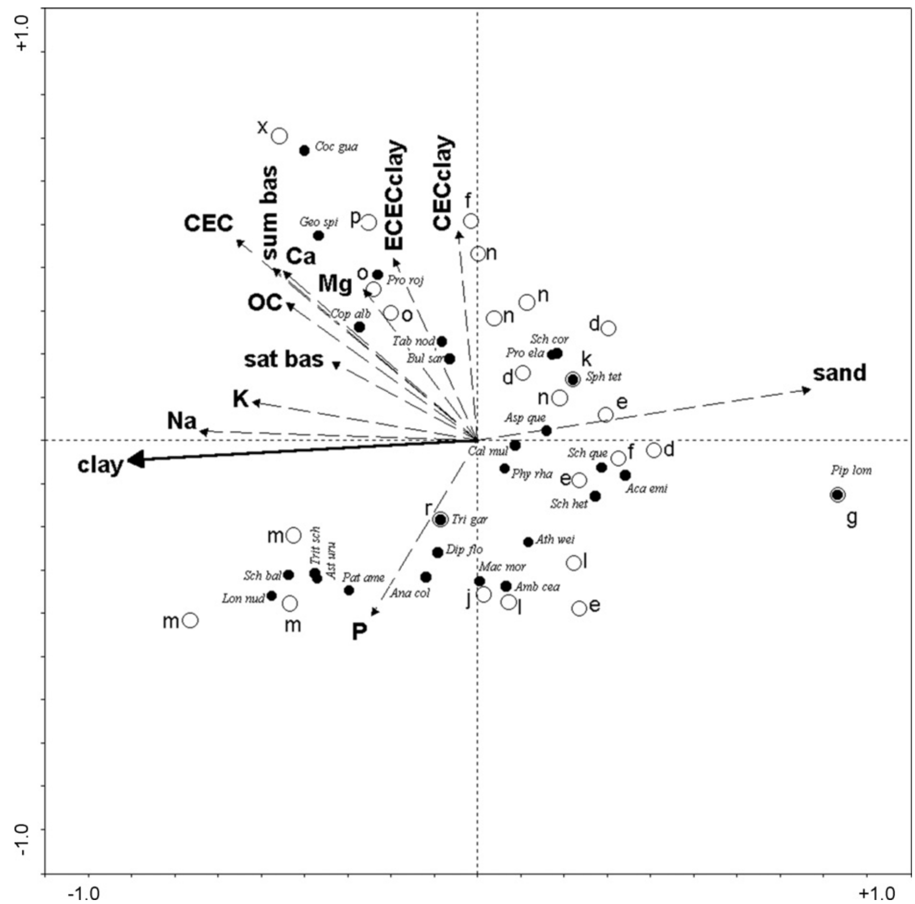

Fig. 4. CCA triplot of forest types, 27 species and 15 soil variables. The species names not included in Fig. 3 are abbreviated to the part in italics as follows *Cal*ycophyllum *mul*tiflorum, *Dip*lokeleba *flo*ribunda, *Pat*agonula *ame*ricana.

thus highlighting the value of soil variables as good predictors of species distribution and abundance (Table 3). The CCA analysis clearly showed that the main discriminating factor in the soil (the factor which best correlated with axis I) is its clay content (Fig. 4). Clay is also a statistically significant soil parameter ($P < 0.01$) in the Monte Carlo test. This factor leaves a significant group of xerophytic western forests towards the right of the graph which develops on well- to moderately well-drained soils and with silt–loam to sandy textures. They are centered on the following species: *Piptadeniopsis lomentifera*, *Acacia emilioana*, *Schinopsis quebracho-colorado*, *Schinopsis* aff. *heterophylla*. The other groups of forests which flourish on poorly drained or floodable soils with clay or silt textures are split into two sub-groups, corresponding approximately to the forests of the eastern Chaco in the lower left quadrant, and some forests of the western Chaco in the upper left quadrant of the diagram. The soils of the forests in the eastern Chaco, characterized by *Schinopsis balansae*, *Lonchocarpus nudiflorens* and *Astronium urundeuva*, among others, have lower CEC values and higher values of silt and P. The soils of the forest of the western Chaco characterized by *Tabebuia nodosa* and *Bulnesia sarmentoi*, among others, show higher values of CEC, Mg and Ca. The upper half of the diagram also shows two patterns of forest on the old alluvial plains: one centered on *Prosopis rojasiana*, a characteristic species of the Pilcomayo old alluvial plain, and another centered on *Prosopis elata*, a characteristic species of the Parapetí old alluvial plain. The edaphic differentiation between Pilcomayo and Parapetí forests on poorly drained soils is based on content of soluble cations such as Na or K and content of sand. The cation exchange capacity of clay is the soil factor which is most highly correlated with axis 2. The forests on clayey soils of the western Chaco show higher cation exchange capacity values than those of the eastern Chaco. The poorly drained hygrophytic *Coccoloba guaranitica-Geoffroea spinosa* forest correlates with the highest values for both Mg and Ca. It is also noteworthy that the palm forest of *Triplaris gardneriana-Copernicia alba* is associated to high or very high levels of Mg (and secondarily of Ca) in horizon B (not shown in the diagram).

Table 3
Relationships between alluvial–plain forest-species assemblages and soil factors.

Canonical axes	Axis 1	Axis 2	Axis 3	Axis 4	Total inertia
Eigenvalues	0.562	0.475	0.408	0.341	3.856
Species–environment correlations	0.970	0.879	0.932	0.950	
Cumulative percentage variance of species data	14.6	26.9	37.5	46.3	
Cumulative percentage variance of species–environment relation	21.1	38.9	54.2	67.0	
Sum of all unconstrained eigenvalues					3.856
Sum of all canonical eigenvalues					2.666

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Discussion

A gradient of increasing floristic richness towards the north has been documented in the south-eastern Chaco, which is related to a geographic temperature gradient (Lewis, 1991). In the northern Paraguayan Chaco region where the most important gradient is the longitudinal increase in rainfall (Navarro et al., 2006), it has not been possible to identify geographic patterns of species richness on a zonal scale. An unexpected result is the relatively high species richness of forests on sandy soils. We explain this fact as the result of the reiterative and regular action of fire on these forests. This leads to a lower density of the tree canopy and to the appearance of a mosaic of biotopes, which produces an increase in species of seral or pioneer stages (Navarro et al., 2002).

Forest structure can be related firstly with the W-E rainfall gradient and secondly with the drainage capacity of the soils. Very similar structural generalizations have been made for the Chacoan forests adjacent to southeast Bolivia (Navarro, 2002, 1997). Hygrophytic forests and those on poorly drained soils are subjected to regular flooding during the wet season (about four months from January to April), although the pattern of seasonal flooding differs: from deep flooding, to shallow flooding, or simple soil saturation (Navarro, 2002). We hypothesize that these flooding differences cause different root oxygenation conditions and can explain the tendency to lower heights in forests on poorly drained soils, as well as why hygrophytic forests subjected to flowing waters (more oxygenated) are higher than hygrophytic forests subjected to still waters.

The classical differentiation recognized by numerous authors between the major floristic groups in the Chaco, namely dry western Chaco and wet eastern Chaco, is consistent and in agreement with our findings for the floristic composition and structure of forests and soils features of the northern Paraguayan Chaco. *Schinopsis quebracho-colorado* is the most common tree in the Chacoan xeromorphic forests (Spichiger et al., 1991). In contrast, *Schinopsis balansae* is a tree which is characteristic of the wet Chaco, although this should more properly be called "floodable Chaco", as these are primarily forests and palm forests which are seasonally flooded or poorly drained. In the northern Paraguayan Chaco, the constant occurrence of *Schinopsis balansae* in the forests of the alluvial plain, approximately to the east of the 59th meridian, together with several of its associated species which are absent towards the west such as *Trithrinax schizophylla*, *Adelia spinosa*, *Fagara pterota*, *Patagonula americana*, *Machaonia brasiliensis*, among others, clearly mark this contact between the western and eastern Chaco. Other trees such as *Tabebuia nodosa*, *Geoffrea decorticans*, *Prosopis alba* and *Prosopis nigra* which have been considered as characteristic species of the wet Chaco (Spichiger et al., 2004) are here considered azonal hygrophytic species as they are present throughout the whole Chaco, both dry and wet (Antezana et al., 2000; Páez and Marco, 2000).

The transition from Western to Eastern Chaco occurs simultaneously with an increase in precipitation, and an increase in hygrophytic forests due to water accumulation in soils. The eastern Chaco is a large distal alluvial fan where many channels are lost or absorbed into the plains, creating extended moist areas or poorly drained soils (Iriondo, 1995). According to our results, there is a general W-E gradient of greater increase in clay, organic matter and soluble cations. The characteristic trees of the forests in both Chacos (*Schinopsis quebracho-colorado* and *Schinopsis balansae*) show a different tolerance to salinity during germination, which may help to explain their distribution. *Schinopsis balansae* is able to germinate in higher salt conditions than *Schinopsis quebracho-colorado* (Meloni et al., 2008; Carnevale et al., 2004). According to our results, soil factors could also explain forest distribution on poorly drained soils in the different alluvial plains of the Pilcomayo and Parapetí, characterized respectively by *Prosopis rojasiana* and *Prosopis elata*. However, we explain their distribution as a mainly biogeographical factor: the alluvial fans of the Parapetí and Pilcomayo are different centers of origin and diversity of Chacoan flora (Navarro, 2002). Our results showing high values of Mg in the lower horizon under floodable palm forests of *Copernicia alba* agree with the observation of $MgSO_4$ crystals in the horizon below 21 cm under semialtura island with *Copernicia alba* in Beni, Bolivia (Langstroth, 1999). Further investigation is required to determine its ecological meaning.

The dominant presence of poorly drained or floodable clay soils in the eastern Chaco is not in itself enough to explain the change from western to eastern forests, as these types of substrates also appear, although in a more localized manner, in the western Chaco (Ramella and Spichiger, 1989). However, major differences in the cation exchange capacity of the types of clays in soils are generally recognized (Fitzpatrick, 1987). We found that the forests on clayey soils of the western Chaco show higher cation exchange capacity values than those of the eastern Chaco. One possible explanation for this fact may lie in the greater proportion of clays with a high exchange capacity (smectites, montmorillonites) in the western forests on clay soils. Conversely, there are a lower proportion of these types of clays and a greater proportion of clays with a low or moderate exchange capacity (illites, caolinites) in the eastern forests on clay soils. The cation exchange capacity of the different types of clays is therefore a key factor in explaining the transition of western to eastern Chaco throughout the alluvial forests.

Appendix A.

Woody species which have been considered as characteristic taxa of the northern Paraguayan Chaco forests in the CCA analyses.

Acacia emilioana Fortunato & Ciald.
Acosmium cardenasii H.S.Irwin & Arroyo
Agonandra excelsa Griseb.
Amburana cearensis (Allemão) A.C.Sm.
Anadenanthera colubrina (Vell.) Brenan
Aspidosperma quebracho-blanco Schlecht.
Astronium urundeuva (Fr. & All.) Engl.
Athyana weinmannifolia (Griseb.) Radlk.
Bulnesia sarmientoi Lorentz ex Griseb.
Calycophyllum multiflorum Griseb. (Castelo)
Coccoloba guaranitica Hassler
Copernicia alba Morong.
Diplokeleba floribunda N.E.Br.
Geoffroea spinosa Jacq.
Jacaranda cuspidifolia Mart.
Lonchocarpus lilloi (Hassler)Burkart
Lonchocarpus nudiflorens Burkart
Maclura tinctorea subsp. *mora* (Griseb.) Vazq.Avila
Patagonula americana L.
Phyllostylon rhamnoides (J.Poiss.) Taub.
Piptadeniopsis lomentifera Burkart
Prosopis elata (Burkart) Burkart
Prosopis rojasiana Burkart
Pseudobombax heteromorphum (Kuntze) A.Robyns
Pseudobombax tomentosum (Mart. & Zucc.) A.Robyns
Schinopsis aff. *heterophylla* Ragonese & J. Castillo ex DC
Schinopsis balansae Engl.
Schinopsis cornuta Loes.
Schinopsis quebracho-colorado (Schltdl.) F.A.Barkley & T. Mey
Sphingiphila tetramera A. Gentry
Tabebuia impetiginosa (Mart. ex DC.) Standl.
Tabebuia nodosa (Griseb.) Griseb.
Tabebuia selachidentata A.H.Gentry
Terminalia argentea Mart.
Triplaris gardneriana Wedd.
Trithrinax schizophylla Drude

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