



Variation in woody vegetation among sites with different disturbance histories in the Argentine Chaco

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Abstract

We studied the composition and structure of the woody plant community in a logged/grazed forest, an abandoned road, a burned forest, and a primary forest as a control. The disturbances occurred 10 years prior to the study. The logged/grazed forest was similar in physiognomy to the primary forest, whereas shrubs dominated the abandoned road and burned forest. Using rarefaction techniques, the total species richness (adult, >0.5 cm diameter, and saplings, <0.5 cm diameter) was significantly highest in the logged forest. Basal area and adult plant density were similar in the logged and primary forest, and considerably higher than those of the burned forest and abandoned road, the last two types having more stems per individual. Species composition differed among communities; most notably some pioneer species were absent from the primary forest. For saplings, the abandoned road had the lowest species richness and plant density. Sapling density was highest in the logged forest due to one shrub species that was abundant in disturbed areas. Saplings of one valuable timber species, *Aspidosperma quebracho-blanco*, were abundant on all sites, probably due to the capacity of this species to sprout after root damage. Stem densities in the primary and logged forests were higher than on the abandoned road and in the burned forest except for the smallest diameter class (0.5–1 cm). Logged forest tended to have higher densities, but smaller individuals than the primary forest. Considering the paucity of well-conserved areas in the Argentine Chaco, the management of extended accidental disturbance (i.e. forest fires) should be considered for long-term use and conservation planning.

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1. Introduction

The Chaco is the second most extensive biome in South America, after Amazonia (Hueck, 1978). Semi-deciduous thorny forests, dry thorny forests, open forests, savannas, savannas with palms and grasslands develop on 1,000,000 km² of alluvial plain (Morello

and Adámoli, 1974). The main floristic feature is the dominance of a tree species of the genus *Schinopsis* (Prado, 1993). The area is considered of the highest priority for conservation on a regional scale (Dinerstein et al., 1995). The future status of the Chaco does not appear to be any more promising than that of the Amazon basin (Redford et al., 1990). The Chaco forest of Argentina in particular is facing an accelerated degradation process, with replacement of the original forests by shrubs with low resource-use potential (Saravia Toledo and del Castillo, 1989; Adámoli

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et al., 1990; Red Agroforestral Chaco Argentina, 2000). During the last few decades, the most common land uses have been forestry, extensive cattle raising (with fire use in grassland management), and non-irrigated agriculture (Morello and Saravia Toledo, 1959a,b; Morello and Adámoli, 1974; Red Agroforestral Chaco Argentina, 2000). Other frequent human-related disturbances are accidental forest fires (Adámoli, 1993) and road building, both for extraction of wood products and for petroleum prospecting (Protomastro and Caziani, 1991a,b; Caziani et al., 1997). These disturbances may modify the structure and function of ecosystems (Hobbs and Huenneke, 1992).

Previous studies, in other forests, have shown that selective logging modifies species composition (Fredericksen et al., 1999; Fredericksen and Mostacedo, 2000; Peltzer et al., 2000), changes species diversity and density of regenerating woody plants (Chapman and Chapman, 1997; Magnusson et al., 1999; Peltzer et al., 2000; Pinard et al., 2000), reduces canopy cover (Wilkie et al., 1992), and increases the susceptibility of ecosystems to fire (Uhl and Buschbacher, 1985).

Fire, also, reduces soil seed banks, alters plant growth rates (Uhl et al., 1981; Ashton and Martin, 1996), plant architecture (Ginocchio et al., 1994) and plant species composition (Zedler et al., 1983). Moreover, frequent and more severe fires affect regeneration mechanisms (Hoffmann, 1998), and prolong and increase the complexity of succession patterns (Uhl et al., 1981). On abandoned roads, plant species richness, species composition, density and basal area, are different to those in adjacent forests (Guariguata and Dupuy, 1997; Pinard et al., 2000), as well as sapling species composition (Hill et al., 1995). In the Argentine dry Chaco, regeneration of one of its most valuable tree species, the quebracho blanco (*Aspidosperma quebracho-blanco*), was impaired by traditional management practices that included extensive livestock grazing, logging, and fire (Barchuk and Díaz, 1999).

In this study, we compared the composition, diversity and structure of woody plant communities on sites affected by different disturbances occurring 10 years previously (selective logging with livestock grazing, forest fire, and the opening of a road for petroleum prospecting) as well as primary forest with no prior record of human disturbance, as a control.

2. Methods

2.1. Study site

Copo National Park (114,000 ha, 160 m above sea level) and adjacent areas of this study are situated in northeastern Santiago del Estero Province (25°55'S, 62°05'W; Fig. 1), Argentina. The study site represents the best preserved and most extensive tract of Chaco forest in Argentina. The landscape is flat (nearly horizontal) and homogeneous, with no surface water bodies, and is vegetated by thorny, semi-deciduous forests dominated by quebracho colorado santiagueño (*Schinopsis quebracho-colorado*), quebracho blanco (*A. quebracho-blanco*) and mistol (*Ziziphus mistol*) (“bosques de dos quebrachos”; Prado, 1993). The site lies in the sub-region of the ancient Juramento river basins (Morello and Adámoli, 1974), where the forests grow on inter-fluvial homogeneous soil that occupies above 90% of the total area. Belts of natural grassland occur over the sandy soils of ancient river basins (Ocaranza, 1979). The climate is markedly seasonal, with 80% of the 700 mm average annual rainfall occurring in October–March (spring–summer).

The area was declared a National Park in 2000, with a Provincial Reserve at its western limit. In 1988 (10 years before the present study), a road for oil prospecting (10 m wide) was built in an E–W direction across the present National Park and a forest fire burned 4800 ha of primary forest, apparently burned again in following years. That same year, 1250 ha of primary forests 20 km west of the National Park were selectively logged for *S. quebracho-colorado* and *A. quebracho-blanco* to produce poles and railway sleepers (Fig. 1). Considering the usual forestry use of the region (for poles, railway, charcoal and firewood), the site undergoes low to moderate intensity exploitation.

2.2. Study design

The sites studied (primary forest, logged/grazed forest, abandoned road and burned forest) are located in the inter-fluvial lands. We attempted to sample the woody community in these areas with no or very low intensity of livestock grazing. However, in logging areas, it was almost impossible to find sites without livestock.

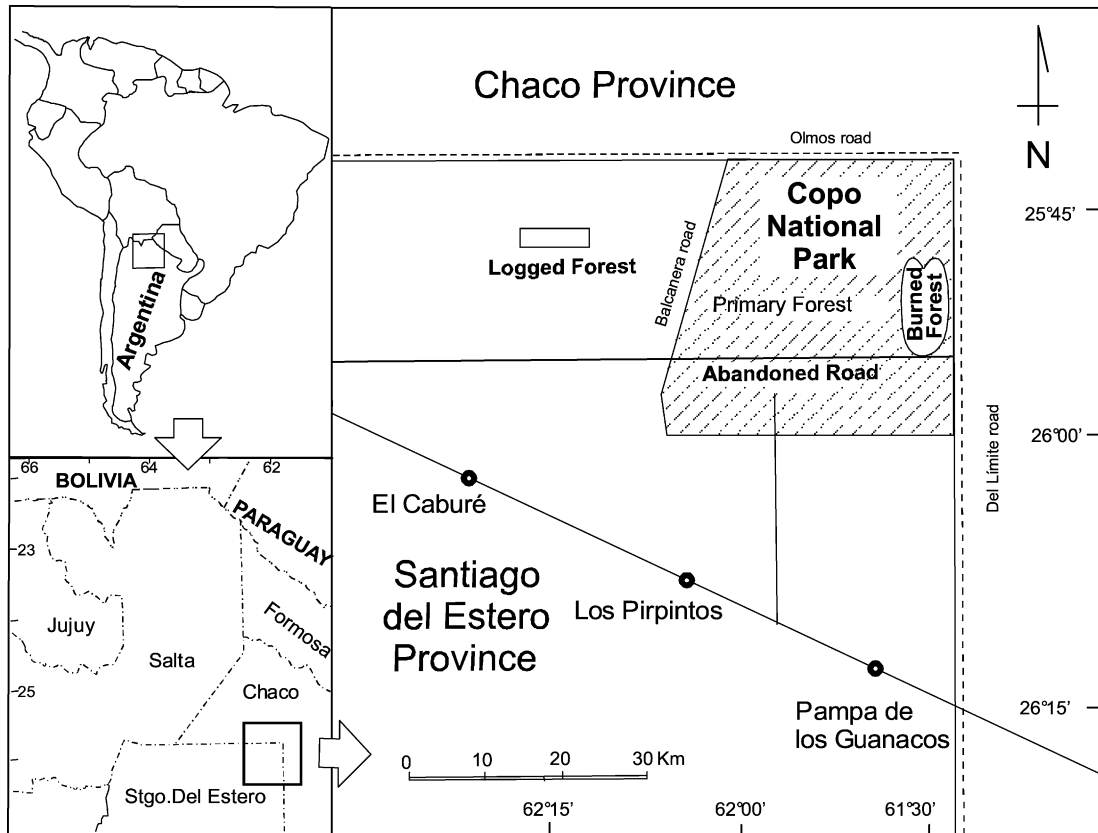


Fig. 1. Map of study site located in Santiago del Estero province, northwestern Argentina. The four sites are indicated: primary forest, logged/grazed forest, abandoned road and burned forest.

Although we compared non-replicable sites, we endeavored to increase sampling representation of each site by avoiding plot concentration in an area. Each site had access by two to four roads, and plots distributed in each area were at least 200 m apart. The direction of the major axis for plot allocation was sorted among eight orientations, except for the abandoned road.

The abandoned road is a straight 10 m wide path, today almost impassable and closed by vegetation growth. Center-edge heterogeneity was evident, and the edge was in turn occasionally affected by debris deposit. We chose to analyze the most homogeneous area represented by a 4 m core strip of the road center, re-colonization of which would affect migration of cattle, hunters, intruders and fires. Thus, we placed the major axis of plots along the E–W direction of the road.

Sample units were 2 m × 100 m plots, 12 in logged/grazed forest, 12 in burned forest, 12 in abandoned road, and 10 in primary forest. Shrubs in the primary and logged/grazed forests were sampled within a 2 m × 50 m subplot, because of their high density. The fieldwork was conducted between December 1997 and May 1999.

2.3. Measurements

The variables were defined for two different size categories:

- (a) *Adult plants*: In each plot, we identified species and measured diameter at breast height (dbh) of all trees, and diameter of every stem >0.5 cm at 20 cm height for shrubs and trees whose stems did not reach breast height. For each plot, we

calculated species richness, density (individuals ha^{-1}), basal area ($\text{m}^2 \text{ha}^{-1}$), and mean number of stems per individual. This variable was also calculated for shrubs alone. Stems per individual were measured as number of stems >0.5 cm diameter, at breast height for trees and at 20 cm height for shrubs. Furthermore, stem density by diameter class (from 0.5 to >40 cm diameter) was calculated for each plot.

- (b) *Saplings*: Individuals <0.5 cm diameter were considered saplings, including individuals originating both from seed and adult plant sprouts. Saplings were identified and counted by plot to estimate density and species richness.

Total species richness was calculated taking into account all the individuals in each plot (adults plus saplings).

2.4. Data analysis

We compared community diversity among sites by species rank-abundance curves (Magurran, 1988), using basal area for adult plants and density for saplings.

Species richness and density of both groups, basal area and number of stems per individual, were compared among sites using one-way ANOVA (Neter et al., 1990) with Tukey 'a posteriori' tests. Differences were considered significant at $P < 0.05$. ANOVA assumptions were satisfied after \log_{10} transformation. All variables were transformed, an operation required by the majority, and enhancing adjustment to the assumptions of the others (adult and sapling species richness). For each diameter class, stem density was analyzed using Kruskal–Wallis test with multiple non-parametric comparisons (Zar, 1999), due to the high heterogeneity of variances even after data transformations.

Given that the number of sampled individuals can influence the number of recorded species, we compared species richness by rarefaction curves (standardized species richness). This statistical method allows an estimate of the expected species richness from randomized sub-samples of individuals in a collection or census (Gotelli and Graves, 1996). Curves were built by calculating mean species richness value from random samples of increasing abundance, with 1000 iterations for each abundance level, using the EcoSim

program (Gotelli and Entsminger, 2002). The program calculates a 95% confidence interval for every mean species richness value.

To test similarity of species composition among sites, multiresponse permutation procedures (MRPP) were used. This is a non-parametric multivariate technique which, unlike equivalent parametric techniques, does not require multivariate normality or homogeneity of variances (Zimmerman et al., 1985).

3. Results

The logged/grazed forest was similar in physiognomy to the primary forest. Trees dominated the basal area of both the primary and logged/grazed forests, whereas shrubs dominated the basal area of the abandoned road and burned forest (Fig. 2).

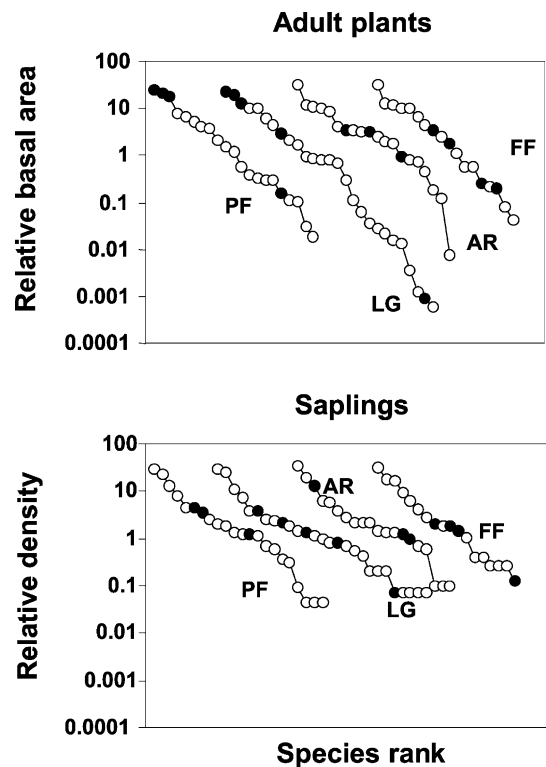


Fig. 2. Species rank-abundance curves for primary forest, and areas disturbed 10 years before sampling, Santiago del Estero, Argentina. Open circles are shrub species and solid circles are tree species. PF, primary forest ($n = 10$); LF, logged/grazed forest ($n = 12$); AR, abandoned road ($n = 12$); BF, burned forest ($n = 12$).

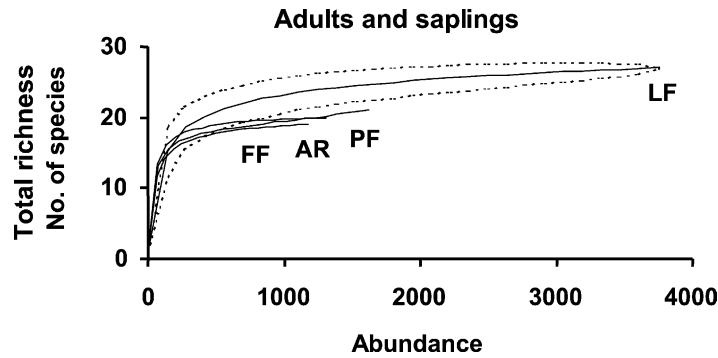


Fig. 3. Rarefaction curves for standardized total species richness. The dotted lines correspond to the 95% confidence interval of estimated richness for logged/grazed forest.

Total standardized species richness was significantly higher in the logged/grazed forest than in the other sites ($P < 0.05$) (Fig. 3).

3.1. Adult plants

Species richness differed among sites (ANOVA: $F_{3,42} = 11.999$, $P < 0.001$), with the burned forest lower than the other sites (Fig. 4A). Standardized species richness was highest in the logged/grazed forest ($P < 0.05$). Density differed among sites

(ANOVA: $F_{3,42} = 58.493$, $P < 0.001$) with the primary and the logged/grazed forests showing similar densities, but these were three times higher than that of the other sites (Fig. 4B). Basal area was considerably different among sites (ANOVA: $F_{3,42} = 303.211$, $P < 0.001$), being similar between primary and logged/grazed forest, which were many times higher than that of the burned forest and abandoned road (Fig. 4C). The number of stems per individual differed among sites (ANOVA: $F_{3,42} = 38.596$, $P < 0.001$). Considering trees and shrubs, the burned forest and

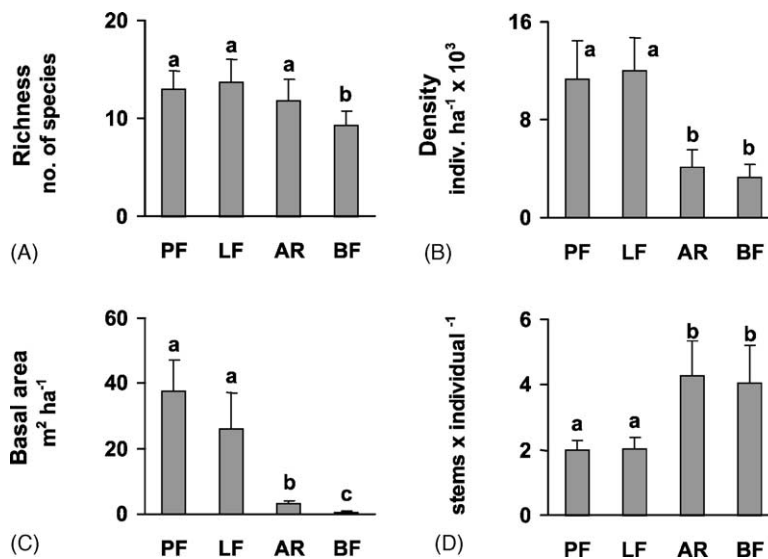


Fig. 4. Adult plants species richness (A), density (B), basal area (C) and number of stems per individual (D) (mean + S.D.) for primary forest, and areas disturbed 10 years before sampling, Santiago del Estero, Argentina. PF, primary forest ($n = 10$); LF, logged/grazed forest ($n = 12$); AR, abandoned road ($n = 12$); BF, burned forest ($n = 12$). Means with the same letter are not significantly different at $P = 0.05$ (Tukey test).

Table 1

Mean basal area ($\text{m}^2 \text{ha}^{-1}$) \pm S.D. of adult plants in areas disturbed in 1988 and in the primary forest of the Chaco forests, Santiago del Estero, Argentina

Species	Primary forest ($n = 10$)	Logged forest ($n = 12$)	Abandoned road ($n = 12$)	Burned forest ($n = 12$)
Trees				
<i>A. quebracho-blanco</i>	9.281 \pm 8.891	3.428 \pm 3.891	0.110 \pm 0.058	0.001 \pm 0.002
<i>S. quebracho-colorado</i>	8.196 \pm 8.196	6.137 \pm 8.580	0.030 \pm 0.036	0.020 \pm 0.022
<i>Z. mistol</i>	6.814 \pm 7.483	5.289 \pm 4.358	0.105 \pm 0.283	0.010 \pm 0.012
<i>Caesalpinia paraguariensis</i> ^a	0.060 \pm 0.188	0.0002 \pm 0.001	0.000	0.000
<i>P. nigra</i>	0.000	0.748 \pm 1.197	0.000	0.001 \pm 0.003
Shrubs				
<i>Acacia</i> sp.	0.000	0.001 \pm 0.003	0.000	0.000
<i>A. aroma</i> ^a	0.000	0.000	0.024 \pm 0.033	0.003 \pm 0.010
<i>A. furcatispina</i>	0.464 \pm 1.469	1.204 \pm 1.150	0.0003 \pm 0.001	0.000
<i>Acacia praecox</i>	2.589 \pm 1.994	2.686 \pm 2.827	0.367 \pm 0.438	0.039 \pm 0.057
<i>Achatocarpus praecox</i>	1.551 \pm 0.881	0.420 \pm 0.521	0.006 \pm 0.020	0.025 \pm 0.052
<i>B. praecox</i>	0.000	0.575 \pm 0.958	0.065 \pm 0.194	0.006 \pm 0.022
<i>C. atamisquea</i>	0.806 \pm 0.859	0.243 \pm 0.393	0.000	0.000
<i>C. retusa</i>	2.859 \pm 1.564	2.690 \pm 1.378	1.006 \pm 0.656	0.058 \pm 0.044
<i>C. salicifolia</i>	0.123 \pm 0.313	0.204 \pm 0.444	0.081 \pm 0.124	0.0003 \pm 0.001
<i>C. speciosa</i>	0.109 \pm 0.281	0.218 \pm 0.363	0.109 \pm 0.153	0.015 \pm 0.020
<i>C. tweediana</i>	0.040 \pm 0.077	0.078 \pm 0.185	0.026 \pm 0.048	0.066 \pm 0.073
<i>C. coccinea</i>	0.565 \pm 0.574	0.220 \pm 0.395	0.317 \pm 0.297	0.001 \pm 0.002
<i>C. pallida</i>	1.993 \pm 1.500	1.669 \pm 0.862	0.354 \pm 0.158	0.185 \pm 0.151
<i>C. australe</i>	0.000	0.000	0.105 \pm 0.203	0.000
<i>Jodina rhombifolia</i>	0.219 \pm 0.351	0.0003 \pm 0.001	0.000	0.0005 \pm 0.001
<i>Lycium</i> sp.	0.011 \pm 0.018	0.004 \pm 0.008	0.015 \pm 0.021	0.059 \pm 0.129
<i>Maytenus spinosa</i>	0.113 \pm 0.235	0.006 \pm 0.008	0.058 \pm 0.059	0.000
<i>Mimosa detinens</i>	0.041 \pm 0.072	0.030 \pm 0.045	0.137 \pm 0.203	0.003 \pm 0.008
<i>P. sericantha</i> ^a	0.000	0.009 \pm 0.031	0.000	0.000
<i>Ruprechtia triflora</i> ^a	0.007 \pm 0.023	0.181 \pm 0.394	0.000	0.000
<i>Schinus polygamus</i>	1.396 \pm 1.467	0.0002 \pm 0.001	0.279 \pm 0.344	0.076 \pm 0.086
<i>S. chacoënsis</i> ^a	0.000	0.016 \pm 0.051	0.004 \pm 0.014	0.000
<i>T. nodosa</i> ^a	0.000	0.008 \pm 0.026	0.000	0.000
<i>Ximenia americana</i> ^a	0.150 \pm 0.474	0.004 \pm 0.013	0.000	0.000
Total	37.386 \pm 9.986	26.068 \pm 10.944	3.195 \pm 0.953	0.571 \pm 0.259

^a Unreported species in the previous studies in the same area (Protomastro and Pelotto, unpublished data; López de Casenave et al., 1995).

the abandoned road had significantly more stems per individual than both the primary and logged/grazed forests, which were similar to each other (Fig. 4D).

Using basal area, species composition differed among sites (MRPP: $T = -11.34$, $P < 0.001$) (Table 1). In the primary and logged/grazed forests, species composition did not differ at the proposed 0.05 significance level, but at a very close probability (MRPP: $T = -1.689$, $P = 0.067$). The trees, *A. quebracho-blanco*, *S. quebracho-colorado* and *Z. mistol*, were the dominant species and, with the shrub *Capparis retusa*, represented more than 65% of basal

area in both sites (Table 1). In contrast, the abandoned road and the burned forest, both dominated by shrubby vegetation, differed in species composition (MRPP: $T = -5.156$, $P < 0.001$) (Table 1), with *C. retusa* and *Celtis pallida* representing more than 30% of the basal area, respectively.

Species composition also differed among sites with density as a measure of abundance (MRPP: $T = -10.708$, $P < 0.001$). Comparing sites with similar physiognomy, the primary and logged/grazed forests had different species composition (MRPP: $T = -2.449$, $P = 0.018$); the dominant species (more

Table 2

Mean density (individuals ha⁻¹) ±S.D. of adult plants in areas disturbed in 1988 and in the primary forest of the Chaco forests, Santiago del Estero, Argentina

Species	Primary forest (n = 10)	Logged forest (n = 12)	Abandoned road (n = 12)	Burned forest (n = 12)
Trees				
<i>A. quebracho-blanco</i>	500.0 ± 154.6	450.0 ± 430.1	529.2 ± 244.4	45.8 ± 39.6
<i>S. quebracho-colorado</i>	155.0 ± 59.9	250.0 ± 254.9	50.0 ± 47.7	66.7 ± 86.2
<i>Z. mistol</i>	405.0 ± 275.3	166.7 ± 124.9	41.7 ± 59.7	58.3 ± 76.4
<i>C. paraguariensis</i>	5.0 ± 15.8	8.3 ± 28.9	0.0	0.0
<i>P. nigra</i>	0.0	100.0 ± 147.7	0.0	8.3 ± 19.5
Shrubs				
<i>Acacia</i> sp.	0.0	25.0 ± 86.6	0.0	0.0
<i>A. aroma</i>	0.0	0.0	29.2 ± 33.4	8.3 ± 19.5
<i>A. furcatispina</i>	5.0 ± 15.8	466.7 ± 260.5	4.2 ± 14.4	0.0
<i>Acacia praecox</i>	910.0 ± 613.6	1366.7 ± 1129.3	250.0 ± 215.3	212.5 ± 237.5
<i>Achatocarpus praecox</i>	1520.0 ± 1226.4	916.7 ± 763.8	4.2 ± 14.4	91.7 ± 200.9
<i>B. praecox</i>	0.0	216.7 ± 298.0	54.2 ± 137.3	4.2 ± 14.4
<i>C. atamisquea</i>	500.0 ± 371.2	316.7 ± 340.7	0.0	0.0
<i>C. retusa</i>	2580.0 ± 1362.0	3566.7 ± 1172.7	1462.5 ± 905.6	600.0 ± 319.1
<i>C. salicifolia</i>	140.0 ± 183.8	83.3 ± 164.2	87.5 ± 104.7	8.3 ± 19.5
<i>C. speciosa</i>	80.0 ± 187.4	116.7 ± 185.0	87.5 ± 113.1	58.3 ± 66.9
<i>C. tweediana</i>	210.0 ± 440.1	175.0 ± 362.1	62.5 ± 106.9	304.2 ± 331.3
<i>C. coccinea</i>	230.0 ± 141.8	133.3 ± 98.5	233.3 ± 148.2	33.3 ± 38.9
<i>C. pallida</i>	3300.0 ± 1522.4	3100.0 ± 897.5	787.5 ± 403.5	1062.5 ± 578.5
<i>C. australe</i>	0.0	0.0	25.0 ± 39.9	0.0
<i>J. rhombifolia</i>	35.0 ± 53.0	8.3 ± 28.9	0.0	12.5 ± 31.1
<i>Lycium</i> sp.	70.0 ± 94.9	50.0 ± 100.0	54.2 ± 68.9	529.2 ± 1029.7
<i>M. spinosa</i>	180.0 ± 193.2	66.7 ± 65.1	116.7 ± 68.5	0.0
<i>M. detinens</i>	130.0 ± 226.3	100.0 ± 185.9	154.2 ± 216.8	12.5 ± 31.1
<i>P. sericantha</i>	0.0	25.0 ± 86.6	0.0	0.0
<i>R. triflora</i>	10.0 ± 31.6	275.0 ± 718.7	0.0	0.0
<i>S. polygamus</i>	280.0 ± 257.3	8.3 ± 28.9	87.5 ± 90.7	133.3 ± 103.0
<i>S. chacoënsis</i>	0.0	25.0 ± 45.2	4.2 ± 14.4	0.0
<i>T. nodosa</i>	0.0	8.3 ± 28.9	0.0	0.0
<i>X. americana</i>	5.0 ± 15.8	8.3 ± 28.9	0.0	0.0
Total	11250.0 ± 3274.3	12037.5 ± 2901.3	4125.0 ± 1431.2	3250.0 ± 1128.3

than 70% of total density), were the same for both sites (*C. pallida*, *C. retusa*, *Achatocarpus praecox* and *Acacia praecox*) but differed in order of importance. Species composition of the abandoned road differed from that of the burned forest (MRPP: $T = -4.391$, $P = 0.0023$) (Table 2), with a similar basal area pattern for the dominant species.

3.2. Saplings

Species richness and density differed among sites (ANOVA: $F_{3,42} = 16.057$, $P < 0.001$ and $F_{3,42} = 48.54$, $P < 0.001$, respectively). The abandoned road

had significantly lower richness than all other sites (Fig. 5A). However, standardized species richness of the logged/grazed forest tended to be lower than that of the other sites. The logged/grazed forest had the highest density, mainly due to *Acacia praecox* saplings (Fig. 5B).

Species composition also varied significantly among sites (MRPP: $T = -13.418$, $P < 0.001$). Comparing stands of similar physiognomy, species composition differed between logged/grazed and primary forests (MRPP: $T = -7.808$, $P = 0.001$). In the primary forest, four species represented more than 80% of all sapling density, *C. pallida*, *Acacia praecox*,

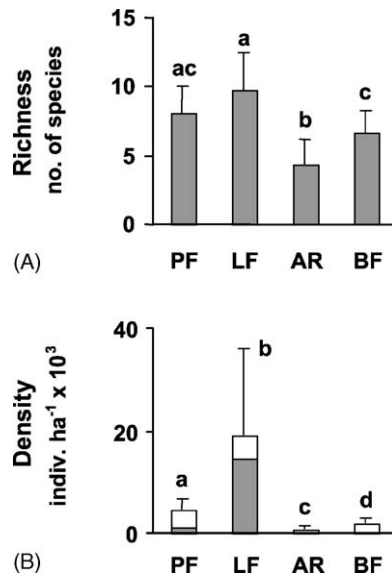


Fig. 5. Sapling species richness (A) and density (B) (mean + S.D.) for primary forest, and areas disturbed 10 years before sampling, Santiago del Estero, Argentina. PF, primary forest ($n = 10$); LF, logged/grazed forest ($n = 12$); AR, abandoned road ($n = 12$); BF, burned forest ($n = 12$). In the density graph, gray area of the bars represents *Acacia praecox* density. Means with the same letter are not significantly different at $P = 0.05$ (Tukey test).

Achatocarpus praecox and *C. retusa*. In the logged/grazed forest, 76% of saplings were *Acacia praecox*, which reduced the species assemblage evenness (Figs. 2 and 5B); followed in importance by *C. pallida*. The species composition of the burned forest was different from that of the abandoned road (MRPP: $T = -6.126$, $P < 0.001$); however, the three dominant species were similar (*C. retusa*, *A. quebracho-blanco* and *C. pallida*). Among tree species, *A. quebracho-blanco* had the highest sampling density, and was similar in all sites (Table 3).

3.3. Diameter class distributions

The abandoned road and the burned forest had higher densities of smaller stems (0.5–1 cm) than the other sites, with only the density in the burned forest significantly higher than that of the primary forest (Kruskal–Wallis test: $H_c = 8.43$, $n = 46$, $P = 0.038$). In the other diameter classes, stem densities in the primary and logged/grazed forests were always higher than in the abandoned road and burned

forest. The logged/grazed forest showed a tendency to higher densities of stems for the smallest classes (0.5–1 and 1–2.5 cm) and lower for the largest classes (10–20, 20–40 and >40 cm) than the primary forest (Fig. 6), although not statistically significant. Maximum stem diameters were 68.7 cm in the primary forest, 73.2 cm in the secondary forest, 13 cm in the abandoned road, and 2.5 cm in the burned forest.

4. Discussion

Our results show that the actual state of vegetation differs significantly among the four sites, each with a different history of disturbance. Sampling represented extensive disturbed areas, but studies designed at a larger scale, including site replication, would be necessary to objectively associate the present conditions of vegetation structure and composition to disturbance. However, the finding of true replicates for fire events of such magnitude, roads built up and abandoned and plots that had been selectively logged in the same time period, allowing coincidental periods of recovery, appears to be practically impossible. Taking into account the homogeneity of the study area with regard to soil conditions, topography and vegetation composition, the differences observed are probably an effect of the disturbances.

The loss of forest physiognomy has been previously related to misuse of natural resources in the Chaco forest (Morello and Saravia Toledo, 1959a), and appears to be one of the most conspicuous and apparently irreversible changes caused by intense disturbance regimes. In our study, the intensively disturbed sites (abandoned road and burned forest) resulted in a shrub–grassland physiognomy. In 10 years, the abandoned road and the burned forest had recovered 9 and 1.5%, respectively, of basal area compared to the primary forest, suggesting that the recovery process evolves slowly. Old prospecting roads (abandoned several decades ago) are visible in recent satellite images of the study area (LANDSAT TM) due to long-term structural alteration (personal observation; Thren and Zerda, 1994). In Malaysian forests, roads abandoned 15 years after logging were still visible as corridors and patches of smaller trees (Pinard et al., 1996). The burned area in this study was mainly colonized by annual herbs, which in turn provide

Table 3

Sapling mean density (individuals ha⁻¹) ± S.D. in areas disturbed in 1988 and in the primary forest of the Chaco forests, Santiago del Estero, Argentina

Species	Primary forest (n = 10)	Logged forest (n = 12)	Abandoned road (n = 12)	Burned forest (n = 12)
Trees				
<i>A. quebracho-blanco</i>	160.0 ± 171.3	225.0 ± 148.5	108.3 ± 94.9	258.3 ± 179.4
<i>S. quebracho-colorado</i>	20.0 ± 42.2	25.0 ± 45.2	16.7 ± 32.6	4.2 ± 14.4
<i>Z. mistol</i>	30.0 ± 48.3	33.3 ± 65.1	4.2 ± 14.4	25.0 ± 50.0
<i>C. paraguariensis</i>	0.0	75.0 ± 142.2	0.0	0.0
<i>P. nigra</i>	0.0	0.0	0.0	0.0
Shrubs				
<i>Acacia</i> sp.	0.0	8.3 ± 28.9	0.0	0.0
<i>A. aroma</i>	0.0	0.0	0.0	4.2 ± 14.4
<i>A. furcatispina</i>	0.0	158.3 ± 242.9	0.0	0.0
<i>Acacia praecox</i>	1150.0 ± 1195.6	14558.3 ± 16325.9	16.7 ± 32.6	83.3 ± 242.5
<i>Achatocarpus praecox</i>	520.0 ± 282.1	658.3 ± 862.8	0.0	0.0
<i>B. praecox</i>	0.0	33.3 ± 88.8	4.2 ± 14.4	0.0
<i>C. atamisquea</i>	50.0 ± 97.2	50.0 ± 79.8	0.0	0.0
<i>C. retusa</i>	470.0 ± 302.0	783.3 ± 674.0	158.3 ± 203.2	670.8 ± 420.7
<i>C. salicifolia</i>	10.0 ± 31.6	8.3 ± 28.9	4.2 ± 14.4	37.5 ± 74.2
<i>C. speciosa</i>	40.0 ± 84.3	66.7 ± 172.3	4.2 ± 14.4	37.5 ± 71.1
<i>C. tweediana</i>	70.0 ± 188.9	16.7 ± 57.7	4.2 ± 14.4	50.0 ± 92.9
<i>C. coccinea</i>	190.0 ± 172.9	266.7 ± 218.8	4.2 ± 14.4	41.7 ± 51.5
<i>C. pallida</i>	1490.0 ± 1613.4	1391.7 ± 766.9	75.0 ± 54.4	229.2 ± 172.5
<i>C. australe</i>	0.0	0.0	0.0	0.0
<i>J. rhombifolia</i>	20.0 ± 42.2	16.7 ± 38.9	0.0	12.5 ± 22.6
<i>Lycium</i> sp.	40.0 ± 69.9	25.0 ± 62.2	8.3 ± 19.5	104.2 ± 233.0
<i>M. spinosa</i>	120.0 ± 198.9	325.0 ± 313.7	62.5 ± 60.8	62.5 ± 64.4
<i>M. detinens</i>	10.0 ± 31.6	141.7 ± 242.9	8.3 ± 19.5	4.2 ± 14.4
<i>P. sericantha</i>	0.0	0.0	0.0	0.0
<i>R. triflora</i>	0.0	150.0 ± 350.3	0.0	0.0
<i>S. polygamus</i>	40.0 ± 51.6	0.0	0.0	8.33 ± 19.46
<i>S. chacoënsis</i>	0.0	0.0	0.0	0.0
<i>T. nodosa</i>	0.0	0.0	0.0	0.0
<i>X. americana</i>	0.0	0.0	0.0	0.0
Total	4430.0 ± 1931.1	19016.7 ± 16595.2	479.2 ± 362.7	1633.3 ± 776.4

abundant burning material during dry seasons (winter), similar to what occurs in the Bolivian forests (Fredericksen, 2000). This may have facilitated the subsequent fire outbreaks (local information, personal communication), delaying invasion of woody species with respect to herbaceous vegetation. Adámoli (1993), Morello and Saravia Toledo (1959a), and Adámoli et al. (1990) consider fire and over-grazing to be determinant factors of the woody/weedy biomass ratio in the Chaco forests. In California shrublands, frequent grassland fires virtually eliminate some shrub species, considerably delaying the re-invasion of shrubs and increasing the probability of recurrent

fires (Zedler et al., 1983). If the recurrent fire regime remains in place, a change in species composition can be expected, favoring species with vegetative reproduction (Adámoli, 1993; Hoffmann, 1998). Our field observations showed that *A. quebracho-blanco*, *Acacia praecox*, *C. retusa*, *C. tweediana*, *C. pallida*, *S. quebracho-colorado*, *Capparis atamisquea* and *Castela coccinea* can sprout after damage; and the first six species dominated the burned forest both as adults and saplings (Tables 2 and 3).

Selective logging may modify species composition, promoting installation and increasing density of shade intolerant species (Fredericksen and Mostacedo, 2000;

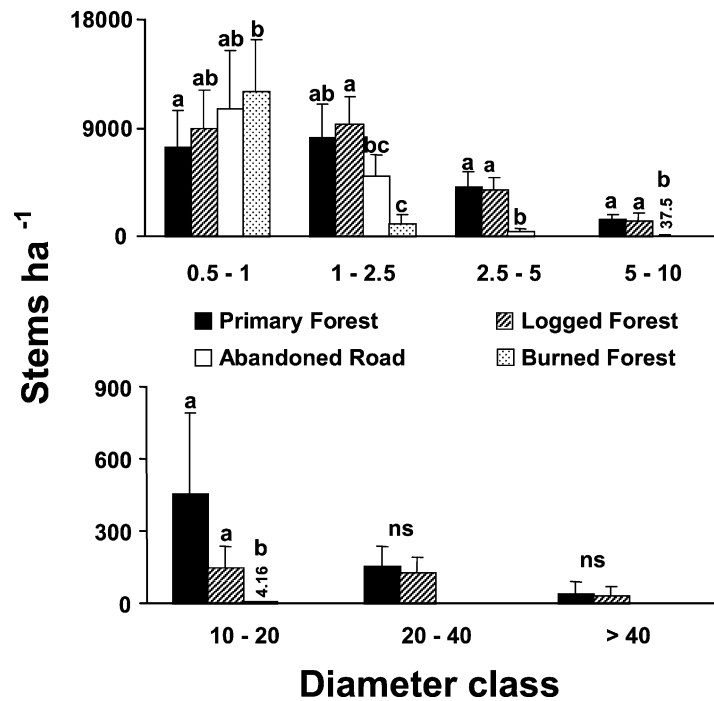


Fig. 6. Stem density (mean + S.D.) by diameter class from 0.5 to >40 cm diameter for primary forest, and areas disturbed 10 years before sampling, Santiago del Estero, Argentina. PF, primary forest ($n = 10$); LF, logged/grazed forest ($n = 12$); AR, abandoned road ($n = 12$); BF, burned forest ($n = 12$). Within each diameter class, sites with the same letter are not significantly different at $P = 0.05$ (non-parametric multiple comparison for Kruskal–Wallis test; Zar, 1999).

Peltzer et al., 2000). In our study, the greater species richness in the logged/grazed forest was due to the addition of species such as *Prosopis nigra*, *Senna chacoënsis* (associated to degraded and saline sites; Morello and Saravia Toledo, 1959a; Sarmiento, 1963), *Prosopis sericantha* (halophytic; Adámoli et al., 1972), *Bougainvillea praecox* and *Tabebuia nodosa*. However, we cannot deny the possibility of this variability being partially related to other differences among sites. The species richness in the abandoned road and burned forest was similar to that of the primary forest, although some species replacement took place. Pioneer species, found in the abandoned road and burned forest, were absent from the primary forest (*P. nigra*, *Acacia aroma*, *Acacia furcatispina*, *B. praecox*, *Cercidium australe*, *S. chacoënsis*). These species often occur in open and disturbed areas, and *P. nigra* and *A. aroma* are dispersed by cattle (Morello and Saravia Toledo, 1959a; Sarmiento, 1963). A different species composition in roads, with a prevalence

of pioneer species at roadsides, was also observed in Malaysian forests (Pinard et al., 2000).

Notwithstanding self-thinning mechanisms, the higher number of stems per individual in the abandoned road and in the burned forest could affect the physiognomy of the regenerated community. In Chilean shrublands, Ginocchio et al. (1994) observed plant architecture changes in response to fire. Some shrub species developed more and longer buds. Fire and cutting could directly affect the form of growth by activating secondary buds (Morello and Saravia Toledo, 1959a), or indirectly affect it by relaxing intra-individual competition. In the same study area, both natural forest–grassland edges and logged/grazed forests are characterized by higher small-stem densities (<2.5 cm diameter) and by the presence of species associated with open areas (López de Casenave et al., 1995; Protomastro and Pelotto, unpublished data). Our conclusions are similar, since the logged/grazed forest showed a tendency towards a higher density of small

stems in comparison to the primary forest (Fig. 6), and species common in natural forest–grassland edges areas were absent in the primary forest (e.g. *Prosopis* sp., *A. furcatispina*).

The high density of saplings in the logged/grazed forest far exceeds that of the primary forest. This higher density was explained by one species only, *Acacia praecox*. This species tends to expand and increase in density in disturbed areas (Morello and Saravia Toledo, 1959a; Sarmiento, 1963; Protomastro, 1988), as well as in natural forest–grassland border areas (López de Casenave et al., 1995). However, *Acacia praecox* saplings were not abundant in more disturbed and open sites, probably because they are sensitive to frost exposure (Protomastro, 1988). Kuusipalo et al. (1998) also found a markedly high density of saplings in logged forests in comparison to a control, whereas Chapman and Chapman (1997) found no differences in sapling density between the logged and control forests 25 years after disturbance. Considering only tree species, sapling density of *A. quebracho-blanco* was higher and similar in all sites, probably explained by its ability to sprout after root damage (Barchuk and Díaz, 1999).

The lower sapling density and species richness found on the abandoned road could be related to a low recruitment rate, due to: (a) soil compaction caused by use of heavy machinery (Pinard et al., 1996; Guariguata and Dupuy, 1997); (b) greater surface erosion leading to topsoil removal (personal observation); (c) microclimatic conditions generated by road building (high soil temperatures and solar radiation, low moisture and nutrient content), limiting the establishment and survival of saplings (Pinard et al., 1996); and (d) grazing and trampling by livestock, exerting a negative pressure on some already established species (Sarmiento, 1963; Adámoli et al., 1972; Pinard et al., 1996; Barchuk et al., 1998), increasing compaction (Abril et al., 1993; Grulke, 1994; Abensperg-Traun et al., 1996; Martín et al., 1998), which would reduce infiltration (Smith et al., 1996; Abril and Bucher, 1999), increasing soil exposure (Bullock and Pakeman, 1977; Grulke, 1994) and modifying contributions to the soil and nutrient cycle (Abril et al., 1993).

In addition to the changes in species composition and structure, the potential for indirect impact appears to be high. Selective logging could indirectly lead to

other disturbances: (a) opening and transit of roads for logging, and forest fragmentation (Thren and Zerda, 1994); and (b) introduction of livestock (Morello and Saravia Toledo, 1959b).

The use of heavy machinery on extraction roads causes soil compaction, possibly compromising species recruitment (Pinard et al., 1996; Guariguata and Dupuy, 1997; Whitman et al., 1998). Despite the smaller surface they affect directly (i.e. 0.02% in the Copo National Park), roads are corridors for occurrence and propagation of other disturbances, such as illegal logging, furtive hunting, human colonization, fire from human ignition sources, and invasion of exotic species (Uhl and Buschbacher, 1985; Wilkie et al., 1992; Guariguata and Dupuy, 1997; Fredericksen, 2000; Putz et al., 2000; Putz et al., 2001). In the study area and close vicinity, the network of oil prospecting roads has simplified the illegal extraction of natural products, the settlement of livestock grazing posts (Protomastro and Caziani, 1991a,b), invasion of exotics (i.e. the fodder spp. *Panicum maximum* var. *Gatoon panic*; Derlindati, personal communication), movement of livestock and fire transmission (personal observation); and some of these petroleum prospecting roads have been transformed into permanent roads (i.e. del Límite Road, Balcanera Road and Olmos Road; Fig. 1).

Logged forests are generally richer in species than the primary forest (Putz et al., 2000). Besides species richness, other variables such as physiognomy, plant growth form and species identity (with variable vulnerability and value for wildlife, Pinard et al., 1999) should also be considered as indicators of the community status. Structural variables at community and landscape scales should be used, too, as indicators of biodiversity for sustainable forest management (Lindenmayer et al., 2000). In our case, the most intensely disturbed sites had species richness levels similar to that of the primary forest, but differed in physiognomy, composition and structure. Although basal area was statistically similar in primary and logged forests, there are differences in the distribution of the variable among shrubs and trees. Shrubs represented 34% of total basal area in primary forest and 44% in logged/grazed forest. Unpublished data on the vertical structure show significant differences in stem and leaf densities at 0–2 m (higher values in logged forest) and above 10 m (higher values in primary forest) (Derlindati and Caziani, unpublished data).

At landscape level, the studied disturbances created patches of different succession stages, physiognomy and species composition, increasing the beta and gamma diversity of the system, but altering large areas of the plant community of highest conservation value: *S. quebracho-colorado* and *A. quebracho-blanco* forest (Prado, 1993).

In view of the paucity of well-conserved areas in the semiarid Argentine Chaco forest (Redford et al., 1990), the management of extended accidental disturbances (i.e. forest fires), and the cost/benefit ratio of different land uses in this region should be taken into account for long-term use and conservation planning.

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