Post-fire recovery occurs overwhelmingly by resprouting in the Chaco Serrano forest of Central Argentina

ROMINA C. TORRES,[1,2]* MELISA A. GIORGIS,[2,3] CECILIA TRILLO,[2]
LUIS VOLKMANN,[2] PABLO DEMAIO,[2] JAVIER HEREDIA[2] AND DANIEL RENISON[1,2]
[1]*Centro de Ecología y Recursos Naturales Renovables and IIByT (FCEFyN, Universidad Nacional de Córdoba – CONICET), Vélez Sarsfield 1611, X5016GCA Córdoba, Argentina (Email: romy.ce2008@gmail.com)*, [2]*NGO Ecosistemas Argentinos, and* [3]*Instituto Multidisciplinario de Biología Vegetal, CONICET – UNC, Córdoba, Argentina*

Abstract In fire-prone landscapes, differences in post-fire regeneration by resprouting between species or sites could be far more important in explaining vegetation physiognomy and composition than seed regeneration. This is the first study exploring the relative contribution of tree resprouts and seeds to post-fire crown volume in the Chaco Serrano forest of South America. Additionally, we compare the resprouting response among species and quantify post-fire changes in tree composition among sites. We established 290 permanent plots distributed in three sites affected by wildfires in 2005. For all tree species in all plots we recorded survival of every individual 1 year after the fire; at the plot level, we recorded the above-ground tree volume before and 3 years after the fire. Resprouting from the base was the main resprouting type. Survival varied between species from 73% to 100% for native species and from 7% to 100% for non-natives. Before the fire, crown volume was similar in the three sites, and was completely lost after the fire in 92% of the plots. Three years after the fire, between 8% and 58% of crown volume was recovered. The ratio of crown recovery because of resprouts and seedlings was 1562:1. Tree composition exhibited few changes because of the high post-fire survival of most native species. We conclude that in the semiarid Chaco Serrano ecosystem tree species regenerate mainly by resprouting. This regeneration mode should be taken into account to better understand post-fire successional pathways of these forests, their management and the restoration of burnt forest areas.

Key words: resilience, seedling, South America, sprouting, survival.

INTRODUCTION

It is increasingly recognized that fire plays a key role in vegetation physiognomy and composition. After wildfires, plants may regenerate through resprouting from tissues such as roots, the base of the stem or aerial parts that were not killed by heat, or alternatively, from seeds (Bond *et al.* 2005; Pausas & Keeley 2009). Thus, in fire-prone areas, vegetation physiognomy and tree composition of present-day forests should be explained by both resprouting success ('persistence niche' *sensu* Bond & Midgley 2001) and establishment from seeds ('regeneration niche' *sensu* Grubb 1977). Post-fire resprouts grow faster than seedlings, turnover of populations is reduced, and in extreme cases, the dependence on seeds for population maintenance could become negligible (Bond & Midgley 2001; Pausas *et al.* 2004; Lamont *et al.* 2011).

Persistence by resprouting is presumed to be successful in low productivity sites, where regeneration by seeds is difficult, or in ecosystems with high disturbance rates, like fire-prone areas (Bellingham & Sparrow 2000; Lamont *et al.* 2011). In turn, resprouting may occur from different parts of the plant, depending on bark thickness (Lawes *et al.* 2011; Brando *et al.* 2012), combustibility, bud insulation and bud position in the plant (Knox & Clarke 2011). Thus, resprouting from adventitious buds or from the root collar may be frequent in areas subjected to severe fires or with thin-barked species, whereas resprouting from axillary or terminal buds may be frequent in low-intensity fires or in thick-barked species (Bond & Midgley 2001). Plant height can also affect resprouting type because the tallest individuals might escape from low-intensity fires or keep the highest buds unburnt (Keeley 2006; Vesk 2006; Brando *et al.* 2012). Additionally, bigger plants can have more starch storage than smaller plants, which might increase survival through fires (Bowen & Pate 1993; Canadell & López-Soria 1998; Bond & Midgley 2001; Gurvich *et al.* 2005; Konstantinidis *et al.* 2006).

On the other hand, regeneration by seed after a fire is usually dependent on seed availability at the site, either from dispersal from unburnt vegetation or from the surviving seed bank. In turn, the patterns of

regeneration from seeds present at the site are influenced by patterns of seed predation, moisture, and a suite of environmental filters that influence seedling establishment, all of which have been extensively investigated (Fenner 2000), even in relatively less studied biomes like the South American Chaco (Barchuk & Pilar Díaz 1999; Verzino *et al.* 2004; Barchuk *et al.* 2005; Funes & Venier 2006; Funes *et al.* 2009; Venier *et al.* 2011, 2012; Torres & Renison 2012).

Knowing the proportional contribution of persistence and regeneration niches, and the factors that influence both niches, is important to understand ecosystem dynamics and how to manage and restore burnt forest areas (Keeley *et al.* 2011). Forest areas that depend mostly on resprouting for post-fire regeneration might benefit from strategies that protect resprouts from herbivores, competition from grasses and forbs, and from further fires (Vieira & Scariot 2006; Wang *et al.* 2007; Vallejo *et al.* 2012); in turn, forest sites that mainly depend on seeds might benefit from strategies such as seeding or planting of seedlings at the adequate sites, and modifying sites to favour natural seed regeneration (Ledgard & Davis 2004; Simôes & Marques 2007). However, to date most post-fire restoration efforts have been focused on seeding and planting, often ignoring post-fire growth of resprouts (Moreira *et al.* 2009).

The factors influencing regeneration by resprouting and by seeds have been studied in several fire-prone shrub and forest communities in Australia, South Africa, North America, the Mediterranean basin and Asia (Pausas 1999; Kruger & Midgley 2001; Vesk & Westoby 2004; Pausas & Verdú 2005; Keeley 2006; Wang *et al.* 2007; Zhu *et al.* 2012). However, few studies have quantified the relative contribution of resprouts and seedlings to woody community recovery after a fire (Hoffmann 1998; Kennard *et al.* 2002; Ganatsas *et al.* 2004; Hooper *et al.* 2004; Otterstrom & Schwartz 2006). Hence, it is still difficult to determine the important factors affecting regeneration niche and persistence at the regional scale. The relative importance of tree species recruitment by seed has not been studied in the Chaco Serrano forest of South America and few studies have been conducted on the variation in post-fire resprouting ability in relation to sites, fire incidence and pre-fire size of individuals. Thus, our aims were to (1) quantify post-fire biomass recovery and compare regeneration mode (either by resprouting or by seedling); (2) compare resprouting type among study sites and species, and determine whether fire incidence and pre-fire tree size could be related to differences in fire response of woody species; (3) quantify the magnitude of fire-induced changes in tree composition.

We expected a reduction in crown volume because of fires and a ratio of post-fire recovery by resprouts to post-fire recovery by seeds of at least 19:1, as reported

for other ecosystems with fire-prone vegetation (e.g. Ganatsas *et al.* 2004). Because resprouting was the predominant post-fire recovery strategy, we expected few changes in floristic composition of the woody communities studied.

METHODS

Study area

The study was conducted in the lower Córdoba Mountains, central Argentina. The vegetation in the study area corresponds to the Chaco Serrano forest (Cabrera 1976). The dominant trees in mature forests are *Schinopsis marginata* Engl. and *Lithraea molleoides* (Vell.) Engl., which are co-dominant with different tree species along the altitudinal, latitudinal and longitudinal gradients (Giorgis *et al.* 2011a). Fires, combined with livestock grazing, urbanization and agriculture, have greatly reduced forest extension and mature forests are almost non-existent (Gavier & Bucher 2004; Zak *et al.* 2004; Renison *et al.* 2011). Additionally, in the last two decades large areas of remnant Chaco Serrano forests have been invaded by several non-native species (Giorgis *et al.* 2011b,c); in some sectors, these species represent more than 90% of the plant cover (Hoyos *et al.* 2010). Mean annual precipitation is about 800 mm, mainly concentrated in the warm season (October to April) and mean annual temperature is about 13.9°C (Capitanelli 1979). Precipitations during the study period were lower than the mean (annual mean of 644 mm between 2004 and 2007; range: from 554 to 727). Fires, which nowadays are mainly ignited by humans, with a return interval of 2–15 years, generally occur at the end of the dry season, from June to October or November, depending on the start of the wet season (Miglietta 1994). Past fire regimes are unknown, but a long history of fire disturbances is presumed because most trees are resprouters (Gurvich *et al.* 2005).

We selected three sites affected by fires that occurred between September and November 2004. There are no records of the fire intensities, but these three fires completely scorched most of the above-ground parts of the plants present in the area and part of the top soil; hence, we assume that the fires were of high intensity, typical of the dry season in years of low precipitation. The three burnt sites differed in vegetation composition, environmental characteristics and land-use history: (1) Río Ceballos (31°9′S; 64°18′W, slope 24%, south aspect, 787 m a.s.l.); this site is located at the foothills of the Sierras Chicas, near the locality of Río Ceballos, which has a population of 19 100 inhabitants. The Río Ceballos site was affected by one fire in 2003, the year before the study fire, and no fires in the previous 13 years. A large portion of the area is surrounded by stands of non-native glossy privet (*Ligustrum lucidum*, Hoyos *et al.* 2010). There were no livestock at this study site before or after the fire; (2) Cuesta Blanca (31°28′S; 64°34′W, slope 17%, south-west aspect, 750 m a.s.l.) is at the foothills of the Sierras Grandes and 0.2 km from the small locality of Cuesta Blanca; the area was burnt by an extensive fire 20 years before our study. Most trees were shrub-like, with some isolated tall trees. The area was used for goat and horse

grazing at very low densities (0.074 goats ha^{-1} and 0.015 horses ha^{-1}, as determined from 34 direct counts from November 2004 to February 2006); and, (3) Uritorco (30°50′S; 64°29′W, slope 17%, east aspect, 1000 m a.s.l.) at the foothills of the Sierras Chicas and 10 km from the town of Capilla del Monte, with 10 400 inhabitants. Selective logging was performed in the area about 60 years before our study, two forest fires affected part of the area 10 and 20 years before the study fire, whereas the remaining area has been unaffected by disturbances for over 60 years, this being the best preserved sector of the study area. The Capilla del Monte site was used for cattle grazing at low densities of about 0.026 cattle ha^{-1} (pers. comm. of the land manager, 2004).

Survival and growth by resprouting

From July to November 2005 (about 1 year after the fires), we established 290 permanent 12.6-m^2 circular plots (90 plots in Río Ceballos, 100 in Cuesta Blanca and 100 in Uritorco) where we recorded live and dead tree individuals >30 cm tall. We identified dead individuals to the species level based on bark and shape of the remaining stems. We considered a species to be of tree growth form when it reached at least 4 m in height and 7 cm of diameter at 1.30 m height (Demaio *et al.* 2002). We estimated pre-fire basal circumference, crown height and width based on the remaining tree stems (following Renison *et al.* 2002). The use of remaining tree stems may underestimate pre-fire tree size; however, in the study region only small branches and twigs are completely burnt, representing an insignificant proportion of the total pre-fire woody biomass (Gurvich *et al.* 2005). We also recorded fire incidence on each tree as the proportion of the crown that was scorched; for surviving individuals, we determined if it resprouted from the base, stem or root, and measured crown height and width (live tissue, usually the resprouts). We revisited plots for two subsequent years and again recorded all the tree individuals >30 cm within the plot, their species, basal circumference, height, and crown width.

Woody species were divided into native and non-native species. We considered non-native species those listed as adventitious, introduced, naturalized or exotic in the catalogue of the Vascular Plants of the Southern Cone (Zuloaga *et al.* 2008). Argentine native species from a phytogeographic region other than Chaco Serrano were also considered as non-native (Giorgis *et al.* 2011c).

Seed regeneration

We recorded the species, number and height of seedlings in a subsample consisting of four fixed 0.25-m^2 quadrats placed within the circular plots once a year in 2005, 2006 and 2007. We subsampled seedlings in this smaller but more intensively searched area to make sure we detected all seedlings.

Data analysis

To quantify biomass recovery by resprouting and seedling regeneration for sampling each year we first estimated an indicator of crown volume of trees and seedlings using the formula $V = 4/3 \star \pi \star r^3$, $r =$ (tree height + tree greatest width + tree width perpendicular to greatest width)/3)/2. For post-fire estimations we considered the live tissue (usually resprouts). For seedlings we considered width as 50% of seedling height. We then analysed changes in crown volume (cubic root transformed) of resprouts of the most abundant species and seedlings among sampling years separately using repeated measures analysis of variance. We modelled time (pre-fire and post-fire years 1, 2 and 3) as the within-subject factor, site as a between-subject factor with three levels (sites) and time $\star$ sites interaction.

To compare resprouting type among sites and species, we carried out a multinomial logistic regression using the data of species that were present in at least eight plots obtained on the first sampling date (2005). The response variables were the categories: dead, stem resprouts, root resprouts, basal resprouts, multiple resprouts (from different parts of the plant) and escape (some unburnt part of the crown). We included fire incidence and pre-fire height as covariables and the native/non-native groups as a categorical variable. We also included the interactions pre-fire height $\star$ site and fire incidence $\star$ site in the model.

To determine the main directions of variation in tree composition, a data matrix of 1024 plots × 21 species was subjected to Detrended Correspondence Analysis (DCA, Legendre & Legendre 1998). We used 1024 plots and 21 species because to run the program we deleted 34 records with zero individuals in at least one of the studied years and three species with represented by a single individual. Thus, each plot was positioned along two main axes that summarized their composition. We analysed the changes in axis values over time using a repeated measures analysis of variance.

RESULTS

Fires killed all the above-ground biomass in 92% of the plots (268 out of 290), whereas the remaining 8% (22 out of 290) had at least one tree with one branch or part of the stem remaining alive. Twelve of these partially burnt plots were located in Uritorco, five in Río Ceballos and five in Cuesta Blanca. In the study plots we recorded 1665 individuals taller than 30 cm, mean 4567 ± 170 individuals ha^{-1}, of which 90% were native and 10% were non-native trees. There were 15 native species, with six species recorded in all three sites, two species recorded at two sites and seven species recorded exclusively in one of the sites (Appendix S1). We also recorded a total of nine non-native tree species in the Río Ceballos and Cuesta Blanca sites, with no non-natives being recorded in Uritorco. Río Ceballos showed the highest density of non-native trees, mainly *Ligustrum lucidum*, which was in 43% of the plots. One year after the fire, survival varied among species, from 73% to 100% for native species and from 7% to 100% for non-natives (Appendix S2).

Resprouts and seedlings

The ratio of estimated above-ground crown volume regenerated by resprouts to that regenerated by seeds was 1562:1 three years after the fire, in 2007 (crown volume of resprouts and seedlings was 2342.9 ± 217.1 and 1.5 ± 0.6 m³ ha⁻¹, respectively; Fig. 1).

The estimated pre-fire crown volume was similar across sites, ranging from 7123.4 ± 930.8 m³ ha⁻¹ in Uritorco to 7871.7 ± 858.3 m³ ha⁻¹ in Cuesta Blanca (Fig. 1a). After the fire, crown volume was gradually restored by resprouting to 32%, 58% and 8% of the pre-fire crown volume, for Uritorco, Río Ceballos, and Cuesta Blanca, respectively, at the end of the study period, in 2007 (Fig. 1a). Biomass recovery was significantly higher in Uritorco and Río Ceballos than in Cuesta Blanca (both Tukey post-hoc tests $P < 0.01$), with no differences between Río Ceballos and Uritorco (Tukey post-hoc test $P = 0.2$; repeated measures ANOVA, site effect F = 12.57, $P < 0.001$).

Basal post-fire resprouting was the main survival mode (71%), followed by resprouting from roots (8%) and stems (0.1%). We recorded two or more resprouting types (e.g. basal and root resprouts) in 2.6% of the cases, and part of the crown was unburnt in 1% of the cases. The resprouting type was related to pre-fire size, site and species (Multinomial logistic regression, $n = 1637$, $\chi^2 = 828.47$, $P < 0.001$, Table 1). The presence of stem resprouts was positively related to pre-fire height, except for Cuesta Blanca, where the opposite pattern was observed (site ⋆ pre-fire height interaction). Two species showed a different
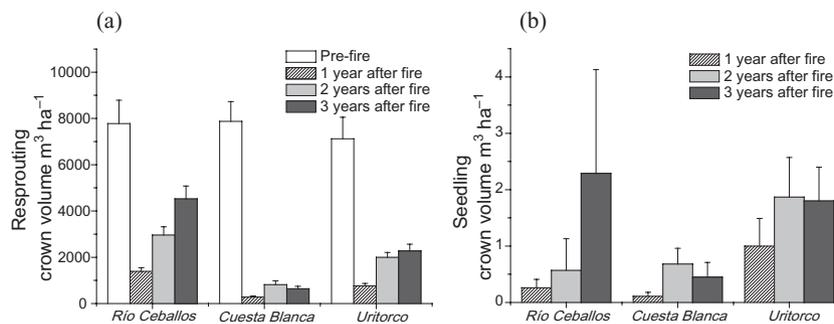
Fig. 1. (a) Mean of pre- and post-fire estimated crown volume of resprouting, and (b) post-fire estimated crown volume of seedlings in the three study sites. Bars show SE.

Table 1. Variables/term included in the multinomial regression model predicting the post-fire resprouting type of woody species in the Chaco Serrano forest

Terms	Stem resprouts Wald	Stem resprouts P	Root resprouts Wald	Root resprouts P	Basal resprouts Wald	Basal resprouts P	Multiple resprouts Wald	Multiple resprouts P	Escape Wald	Escape P
Variables										
Site	0.0	0.9	0.0	0.9	0.0	0.9	0.0	0.9	0.0	0.9
Río Ceballos							**27.1**	**<0.001 (−)**		
Native/non-native species	0.0	0.9	0.2	0.7	0.9	0.3	0.1	0.7	0.0	0.9
Species	**0.2**	**0.6**	0.06	0.8	**0.6**	**0.4**	0.1	0.7	0.0	0.9
Aspque†	**4.0**	**0.05 (+)**								
Ligluc‡			**5.7**	**0.02 (−)**	**8.5**	**0.004 (−)**				
Covariables										
Pre-fire height	**15.3**	**<0.001 (+)**	0.2	0.6	2.2	0.1	0.0	0.9	0.1	0.7
Fire incidence	0.0	0.9	0.0	1	0.0	1	0.0	0.9	0.0	0.9
Interactions										
Pre-fire height*Site	**5.2**	**0.02 (−)**	0.4	0.5	1.5	0.2	0.2	0.7	0.0	0.9
Cuesta Blanca	**5.2**	**0.02 (−)**								
Fire incidence*Site	0.0	0.9	0.0	0.9	0.0	1	0.0	0.9	0.0	0.9

†*Aspidosperma quebracho-blanco*. ‡*Ligustrum lucidum*. The general trend of the relationship is indicated in parentheses when the term was significant. The category 'Dead individuals = 0' was considered as the reference for comparisons with the resprouting types (Frequency of fire-induced mortality = 0.17). Model Fit Statistics Nagelkerke Pseudo R² = 0.47. Full model χ^2 (d.f. = 115) = 828.47, $P < 0.001$. Significant values are indicated in bold.
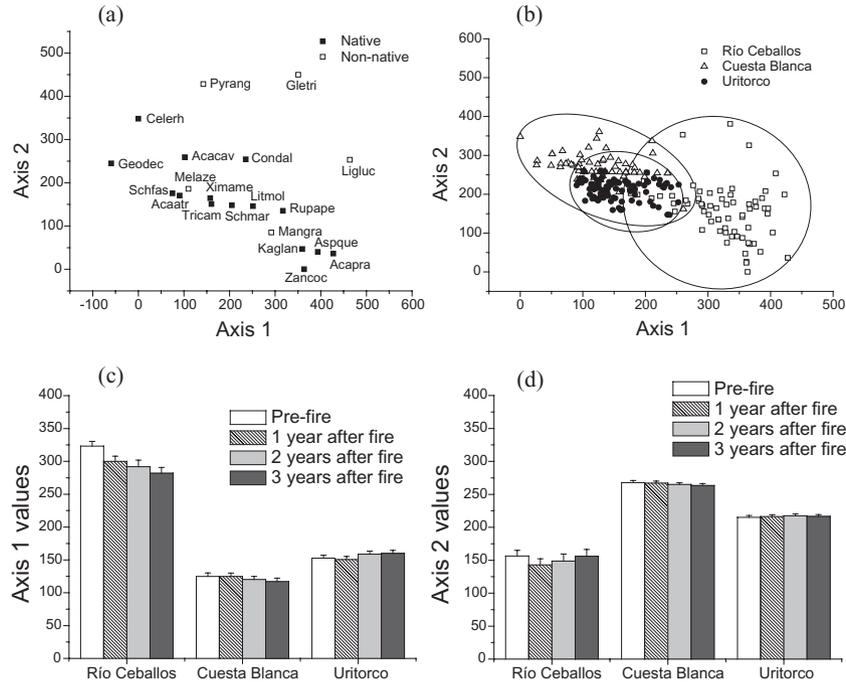
Fig. 2. Detrended Correspondence Analysis (DCA) ordination (Axes 1 and 2) of 1024 plots on the basis of 25 native and non-native tree species. In (a) species and (b) pre-fire plot location on DCA ordination (Axes 1 and 2). In (c) we show values of axis 1 of the DCA ordination, for all study years, and in (d) values for axis 2. Bars show SE. Abbreviations for the names of the native species: *Acacia atramentaria* (Acaatr), *Acacia caven* (Acacav), *Acacia praecox* (Acapra), *Aspidosperma quebracho-blanco* (Aspque), *Celtis erhermbergiana* (Celerh), *Condalia* spp. (Condal), *Geoffroea decorticans* (Geodec), *Kageneckia lanceolata* (Kaglan), *Lithraea molleoides* (Litmol), *Ruprechtia apetala* (Rupape), *Schinopsis marginata* (Schmar), *Schinus fasciculatus* (Schfas), *Trithrinax campestris* (Tricam), *Ximenia Americana* (Ximame), *Zanthoxylum coco* (Zancoc). Non-native especies: *Gleditsia triacanthos* (Gletri), *Ligustrum lucidum* (Ligluc), *Manihot grahamii* (Mangra), *Melia azedarach* (Melaze), *Pyracantha angustifolia* (Pyrang).

post-fire response from the remaining ones: the tall native *Aspidosperma quebracho-blanco* had the highest number of stem resprouts, and the non-native *L. lucidum* presented the lowest survival. Fire incidence, the species type (native or non-native) and the fire incidence ⋆ site interaction had no effect on resprouting type (Table 1).

Seedling regeneration was extremely rare. In the 1160 sampling quadrats covering a total area of 290 m² we recorded seedlings of 14 native species, with 38, 31 and 58 seedlings in the first, second and third years after the fire, respectively. We recorded two species of non-native tree seedlings with a total of five seedlings (Appendix S3). The estimated seedling crown volume was not significantly different among years (Repeated measures ANOVA, within-subject effects, $n = 278$, F = 2.81, $P = 0.1$; Fig. 1b). We found significant differences among sites in estimated seedling crown volume (between-subject effects, $n = 278$, F = 4.39, $P = 0.01$), being higher in Uritorco than in Río Ceballos and Cuesta Blanca ($P = 0.04$ and $P = 0.03$, respectively), without significant differences between Río Ceballos and Cuesta Blanca ($P = 0.9$; repeated measures ANOVA post-hoc tests).

Changes in tree composition

The ordination analysis (DCA) showed two main axes with eigenvalues for axes 1 and 2 of 0.66 and 0.54, respectively. Both native and non-native species were well distributed along the space defined by the ordination (Fig. 2a). Plots in the three study sites (Uritorco, Río Ceballos and Cuesta Blanca) were partially segregated in the space defined by the DCA axes 1 and 2, with Río Ceballos plots at the upper extreme of axis 1 and Cuesta Blanca plots at the lower extreme (Fig. 2b). Along axis 2, the study sites were not clearly separated, with Río Ceballos plots particularly showing more variability than Uritorco and Cuesta Blanca. Plot position along axes 1 and 2 changed significantly during the successive years after the fire in Río Ceballos but not in Cuesta Blanca and Uritorco (Repeated measures ANOVA: axis 1, $n = 255$, F = 13.7, $P < 0.001$; year ⋆ site F = 15. 2, $P < 0.001$; axis 2, $n = 255$, F = 5.1, $P < 0.02$; year ⋆ site F = 7.3, $P = 0.001$), although these changes were relatively small compared with differences in composition among sites (between-subject effect, axis 1, F = 301.1, $P < 0.001$; axis 2, F = 129.1, $P < 0.00$; Fig. 2c,d).

An identical analysis excluding non-natives produced a very similar pattern of results for axis 1 and no significant differences on axis 2 (Repeated measures ANOVA: axis 1, $n = 256$, F = 3.5, $P = 0.06$; year $\star$ site F = 6.5, $P = 0.002$; between-subject effect, $P < 0.001$; axis 2, $n = 256$, F = 0.9, $P = 0.3$; year $\star$ site F = 1.8, $P = 0.2$, between-subject effect, $P = 0.02$).

DISCUSSION

Resprouts and seedlings

The high ratio of biomass regenerated by resprouting to that regenerated by seeds obtained in our study is in accordance with previous studies that have suggested that resprouting species are dominant in fire-prone areas, where seedling establishment is difficult because of water limitations during the dry season (Knox & Clarke 2006; Lamont *et al*. 2011), as occurs in our study area. To the best of our knowledge, this ratio has not been reported for other South American ecosystems and is higher than previously reported ratios (e.g. Ganatsas *et al*. 2004). According to these results, the study of resprouting patterns should contribute to a better understanding of post-fire vegetation succession than the study of regeneration by seed alone (Bond & Midgley 2001).

As a consequence of the overall high post-fire survival (except for one non-native species), the main effect of fire, as measured in this study, was loss of crown volume. Similar findings were reported by Verzino *et al*. (2005) for our study region and by Bran *et al*. (2007) for semiarid environments. The loss of crown volume is known to reduce various ecosystem services, like the provision of windshield and shade, and is known to change the composition of other taxa (i.e. for medicinal plants, Verzino *et al*. 2005; for wood decaying polypores, Robledo & Renison 2010). Furthermore, we found different patterns of crown volume recovery among sites, with Cuesta Blanca presenting the slowest recovery. Cuesta Blanca is the only study site with presence of goats (see study area section). Even at low densities goats might have delayed post-fire resprout growth. In addition, this site is more to the west than Río Ceballos and its lower productivity may be because of a regional gradient of precipitation that decreases from east to west (Capitanelli 1979). On the other hand, the Uritorco site is the driest of the three study sites (west and north of Río Ceballos, with the consequent greater evapotranspiration). However, Uritorco was the best preserved study site, suggesting a synergistic effect between productivity, fire history and livestock density that influences the recovery of biomass, as reported for other ecosystems (Coop *et al*. 2010).

In our study region the end of the fire season coincides with the start of the rainy summer and an increase of temperature and humidity would be expected to be favourable for seedling recruitment. However, the harsh environmental conditions prevailing during the long cold and dry winter season seem to limit forest recovery by seedlings even under water addition treatments (Casillo *et al*. 2012) or in the absence of fires (Torres & Renison 2012). The low regeneration by seeds could not be explained by the lack of seed viability, because Chaco Serrano species have relatively high seed viability (Funes *et al*. 2009; Torres & Renison 2012). We also rule out the complete destruction of reproductive structures and seed bank by fire (Hoffmann 1998), because seedlings were similarly scarce in unburnt areas (Torres & Renison 2012). Seedling regeneration could be restricted to periods of favourable climatic conditions, as occurs in other semiarid and arid forest (Holmgren *et al*. 2006; Squeo *et al*. 2007). Thus, the high post-fire survival by resprouting might assure the long-term persistence of seed sources for seedling recruitment under suitable environment conditions (Enright *et al*. 1998). On the other hand, the surrounding sites could be a key factor determining post-successional regeneration because of provision of seed sources for establishment, as reported for other regions of the world (Pausas 1999; Chazdon 2003; Sibold & Veblen 2006; Kitzberger *et al*. 2007; Coop *et al*. 2010).

Changes in tree composition

We identified few changes in tree composition; this result was expected because of the high survival of all native species recorded in our study (more than 70%). Furthermore, these changes were relatively small compared with differences in composition among sites. Similar results were reported in Chaco Serrano forest by Verzino *et al*. (2005). The pre-fire differences in floristic composition are not likely to be because of differences in fire history of sites because previous studies on floristic composition and structure of Chaco Serrano forest show that differences in floristic composition are mainly because of variations in temperature and precipitation along altitudinal, latitudinal and longitudinal gradients; and second, to fire and livestock (Giorgis *et al*. 2011a). However, our results only reflect tree changes induced by one fire. Because fires are highly recurrent in Córdoba Mountains, species with reduced resprouting capacity may have become locally extinct (e.g. Lloret & Vilà 2003), and therefore might not have been detected in our study. In the communities with recurrent fires and a dominant resprouting strategy, changes in the dominant species have been detected only over long periods (Díaz-Delgado *et al*. 2002). Some authors

have highlighted that the resilience of communities to fire can vary spatially and temporally; hence, management strategies should be carefully planned, taking into account this variability (Rodrigo *et al.* 2004).

Implications for conservation

Given the dominance of post-fire tree resprouting (persistence niche) over regeneration by seeds (regeneration niche) in Chaco Serrano forests, we suggest that the restoration of burnt areas should mostly consider protection of resprouts from post-fire disturbances, including further fires, urban sprawl, browsing by domestic herbivores and competition by non-native species. All types of regeneration contribute to post-fire recovery and even though the Chaco woody community shows great ability to persist after fire, seedling establishment should also be enhanced, especially in extremely degraded areas where tree resprouting is not vigorous or trees have completely disappeared because of high fire recurrence. In a visit to the study area 5 years after the study fires, all plots from Cuesta Blanca were again burnt by a wildfire, 20 of the plots of Río Ceballos were urbanized and only Uritorco remained undisturbed. The Chaco Serrano forest is clearly under high human pressure (Zak & Cabido 2002; Gavier & Bucher 2004) and further studies focusing on resprouting and seedling establishment in relation to fire frequency and their interactions with other disturbances are needed to fully understand post-fire forest recovery.

ACKNOWLEDGEMENTS

REFERENCES

Barchuk A. H. & Pilar Díaz M. P. (1999) Regeneration and structure of *Aspidosperma quebracho-blanco* Schl. in the Arid Chaco (Córdoba, Argentina). *For. Ecol. Manage.* 118, 31–6.

Barchuk A. H., Valiente-Banuet A. & Pilar Díaz M. P. (2005) Effects of shrubs and seasonal variability of rainfall on the establishment of *Aspidosperma quebracho-blanco* in two edaphically contrasting environments. *Aust. Ecol.* 30, 695–705.

Bellingham P. J. & Sparrow A. D. (2000) Resprouting as a Life History Strategy in Woody Plant Communities. *Oikos* 89, 409–16.

Bond W. J. & Midgley J. J. (2001) Ecology of sprouting in woody plants: the persistence niche. *Trends Ecol. Evol.* 16, 45–51.

Bond W. J., Woodward F. I. & Midgley G. F. (2005) The global distribution of ecosystems in a world without fire. *New Phytol.* 165, 525–38.

Bowen B. J. & Pate J. S. (1993) The significance of root starch in post-fire shoot recovery of the resprouter *Stirlingia latifolia* R. Br. (Proteaceae). *Ann. Bot.* 72, 7–16.

Bran D. E., Cecchi G. A., Gaitán J. J., Ayesa J. A. & López C. R. (2007) Efecto de la severidad de quemado sobre la regeneración de la vegetación en el Monte Austral. *Ecología Austral* 17, 123–31.

Brando P. M., Nepstad D. C., Balch J. K. *et al.* (2012) Fire-induced tree mortality in a neotropical forest: the roles of bark traits, tree size, wood density and fire behavior. *Global Change Biol.* 18, 630–41.

Cabrera A. (1976) Regiones fitogeográficas argentinas. In: *Enciclop. Arg. Agric. y Jardinería*, 2 edn, pp. 1–85.5. Editorial ACME S.A.C.I., Buenos Aires.

Canadell J. & López-Soria L. (1998) Lignotuber reserves support regrowth following clipping of two Mediterranean shrubs. *Funct. Ecol.* 12, 31–8.

Capitanelli J. (1979) Clima. In: *Geografía Física de la Provincia de Córdoba* (eds J. Vazquez, R. Miatello & M. Roque) pp. 45–138. Editorial Boldt, Buenos Aires.

Casillo J., Kunst C. & Semmartin M. (2012) Effects of fire and water availability on the emergence and recruitment of grasses, forbs and woody species in a semiarid Chaco savanna. *Aust. Ecol.* 37, 452–9.

Chazdon R. L. (2003) Tropical forest recovery: legacies of human impact and natural disturbances. *Perspect. Plant Ecol. Evol. Syst.* 6, 51–71.

Coop J. D., Massatti R. T. & Schoettle A. W. (2010) Subalpine vegetation pattern three decades after stand-replacing fire: effects of landscape context and topography on plant community composition, tree regeneration, and diversity. *J. Veg. Sci.* 21, 472–87.

Demaio P., Karlin U. O. & Medina M. (2002) *Árboles nativos del centro de Argentina*. Editorial L.O.L.A., Buenos Aires.

Díaz-Delgado R., Lloret F., Pons X. & Terradas J. (2002) Satellite evidence of decreasing resilience in Mediterranean plant communities alters recurrent wildfires. *Ecology* 83, 2293–303.

Enright N. J., Marsula R., Lamont B. B. & Wissel C. (1998) The ecological significance of canopy seed storage in fire-prone environments: a model for non-sprouting shrubs. *J. Ecol.* 86, 960–73.

Fenner M. (2000) *Seeds: The Ecology of Regeneration in Plant Communities*. CABI Publishing, Wallingford.

Funes G., Díaz S. & Venier P. (2009) La temperatura como principal determinante de la germinación en especies del Chaco seco de Argentina. *Ecol. Austral* 19, 129–38.

Funes G. & Venier P. (2006) Dormancy and seed germination in three Acacia (Fabaceae) species from central Argentina. *Seed Sci. Res.* 16, 77–82.

Ganatsas P. P., Zagas T. D., Tsakaldimi M. N. & Tsitsoni T. K. (2004) Postfire regeneration dynamics in a Mediterranean type ecosystem in Sithonia, northern Greece: ten years after the fire. Proc. 10th MEDECOS conference, 25 April–1 May 2004, Rhodes, Greece.

Gavier G. I. & Bucher E. H. (2004) *Deforestación de las Sierras Chicas de Córdoba (Argentina) en el período 1970–1997.* Academia Nacional de Ciencias, Córdoba. *Miscelánea* N°101.

Giorgis M. A., Cabido M. & Cingolani A. M. (2011a) *Caracterización florística y estructural del Bosque Chaqueño Serrano.* Editorial Académica Española, Córdoba.

Giorgis M. A., Cingolani A. M., Chiarini F. *et al.* (2011b) Composición florística del Bosque Chaqueño Serrano de la Provincia de Córdoba, Argentina. *Kurtziana* **36,** 9–46.

Giorgis M. A., Tecco P. A., Cingolani A. M., Renison D., Marcora P. & Paiaro V. (2011c) Factors associated with alien species distribution in a newly invaded system of Central Argentina. *Biol. Invasions* **13,** 1423–34.

Grubb P. J. (1977) The maintenance of species richness in plant communities: the importance of the regeneration niche. *Biol. Rev.* **52,** 107–45.

Gurvich D. E., Enrico L. & Cingolani A. M. (2005) Linking plant functional traits with post-fire sprouting vigour in woody species in central Argentina. *Aust. Ecol.* **30,** 789–96.

Hoffmann W. A. (1998) Post-burn reproduction of woody plants in a neotropical savanna: the relative importance of sexual and vegetative reproduction. *J. Appl. Ecol.* **35,** 422–33.

Holmgren M., López B. C., Gutiérrez J. R. & Squeo F. A. (2006) Herbivory and plant growth rate determine the success of El Niño Southern Oscillation-driven tree establishment in semiarid South America. *Global Change Biol.* **12,** 2263–71.

Hooper E. R., Legendre P. & Condit R. (2004) Factors affecting community composition of forest regeneration in deforested, abandoned land in Panama. *Ecology* **85,** 3313–26.

Hoyos L. E., Gavier-Pizarro G. I., Kuemmerle T., Bucher E. H., Radeloff V. C. & Tecco P. A. (2010) Invasion of glossy privet (*Ligustrum lucidum*) and native forest loss in the Sierras Chicas of Córdoba, Argentina. *Biol. Invasions* **12,** 3261–75.

Keeley J. E. (2006) Fire severity and plant age in postfire resprouting of woody plants in sage scrub and Chaparral. *Madroño* **53,** 373–9.

Keeley J. E., Pausas J. G., Rundel P. W., Bond W. J. & Bradstock R. A. (2011) Fire as an evolutionary pressure shaping plant traits. *Trends Plant Sci.* **16,** 406–11.

Kennard D. K., Gould K., Putz F. E., Fredericksen T. S. & Morales F. (2002) Effect of disturbance intensity on regeneration mechanisms in a tropical dry forest. *For. Ecol. Manage.* **162,** 197–208.

Kitzberger T., Brown P. M., Heyerdhal E. K., Swetnam T. W. & Veblen T. T. (2007) Contingent Pacific–Atlantic Ocean influence on multicentury wildfire synchrony over western North America. *Proc Natl Acad Sci USA* **104,** 543–8.

Knox K. J. E. & Clarke P. J. (2006) Fire season and intensity affect shrub recruitment in temperate sclerophyllous woodlands. *Oecologia* **149,** 730–9.

Knox K. J. E. & Clarke P. J. (2011) Fire severity and nutrient availability do not constrain resprouting in forest shrubs. *Plant Ecol.* **212,** 1967–78.

Konstantinidis P., Tsiourlis G. & Xofis P. (2006) Effect of fire season, aspect and pre-fire plant size on the growth of *Arbutus unedo* L. (strawberry tree) resprouts. *For. Ecol. Manage.* **225,** 359–67.

Kruger L. M. & Midgley J. J. (2001) The influence of resprouting forest canopy species on richness in Southern Cape forests, South Africa. *Global Ecol. Biogeogr.* **10,** 567–72.

Lamont B. B., Enright N. J. & He T. (2011) Fitness and evolution of resprouters in relation to fire. *Plant Ecol.* **212,** 1945–57.

Lawes M. J., Richards A., Dathe J. & Midgley J. J. (2011) Bark thickness determines fire resistance of selected tree species from fire-prone tropical savanna in north Australia. *Plant Ecol.* **212,** 2057–69.

Ledgard N. & Davis M. (2004) Restoration of mountain beech (*Nothofagus solandri* var. *cliffortioides*) forest after fire. *NZ J. Ecol.* **28,** 125–35.

Legendre P. L. & Legendre L. L. (1998) *Numerical Ecology,* Second English Edition. Elsevier, Amsterdam.

Lloret F. & Vilà M. (2003) Diversity patterns of plant functional types in relation to fire regime and previous land use in Mediterranean woodlands. *J. Veg. Sci.* **14,** 387–98.

Miglietta S. (1994) *Patrón de ocurrencia de incendios y su efecto sobre la vegetación en el Bosque Serrano de Córdoba* (MSc Thesis). Universidad Nacional de Córdoba, Córdoba.

Moreira F., Catry F., Lopes T., Bugalho M. N. & Rego F. (2009) Comparing survival and size of resprouts and planted trees for post-fire forest restoration in central Portugal. *Ecol. Eng.* **35,** 870–3.

Otterstrom S. M. & Schwartz M. W. (2006) Responses to fire in selected Tropical Dry Forest trees. *Biotropica* **38,** 592–8.

Pausas J. G. (1999) Response of plant functional types to changes in the fire regime in Mediterranean ecosystems: a simulation approach. *J. Veg. Sci.* **10,** 717–22.

Pausas J. G., Bradstock R. A., Keith D. A., Keeley J. E. & the GCTE (Global Change of Terrestrial Ecosystems) Fire Network (2004) Plant functional traits in relation to fire in crown-fire ecosystems. *Ecology* **85,** 1085–100.

Pausas J. G. & Keeley J. E. (2009) A burning story: the role of fire in the history of life. *BioScience* **59,** 593–601.

Pausas J. G. & Verdú M. (2005) Plant persistence traits in fire-prone ecosystems of the Mediterranean basin: a phylogenetic approach. *Oikos* **109,** 196–202.

Renison D., Cingolani A. M. & Suarez S. (2002) Efectos del fuego sobre un bosquecillo de *Polylepis australis* (Rosaceae) en las montañas de Córdoba, Argentina. *Rev. Chil. Hist. Nat.* **75,** 719–27.

Renison D., Hensen I. & Suarez R. (2011) Landscape structural complexity of high-mountain *Polylepis australis* forests: a new aspect of restoration goals. *Restoration Ecol.* **19,** 390–8.

Robledo G. L. & Renison D. (2010) Wood-decaying polypores in the mountains of central Argentina in relation to *Polylepis* forest structure and altitude. *Fungal Ecol.* **3,** 178–84.

Rodrigo A., Retana J. & Picó F. X. (2004) Direct regeneration is not the only response of Mediterranean forest to large fires. *Ecology* **85,** 716–29.

Sibold J. S. & Veblen T. T. (2006) Relationships of subalpine forest fires in the Colorado Front Range with interannual and multidecadal-scale climatic variation. *J. Biogeogr.* **33,** 833–42.

Simões C. G. & Marques M. C. M. (2007) The role of sprouts in the restoration of Atlantic rainforest in southern Brazil. *Restoration Ecol.* **15,** 53–9.

Squeo F. A., Holmgren M., Jiménez M., Albán L., Reyes J. & Gutiérrez J. R. (2007) Tree establishment along an ENSO experimental gradient in the Atacama desert. *J. Veg. Sci.* **18,** 195–202.

Torres R. C. & Renison D. (2012) *Regeneración y respuesta a disturbios en el Bosque Chaqueño Serrano. Recuperación natural y asistida de tres especies arbóreas (Córdoba, Argentina).* Editorial Académica Española, Saarbrücken.

Vallejo V. R., Arianoutsou M. & Moreira F. (2012) Fire ecology and post-fire restoration approaches in southern European forest types. In: *Post-Fire Management and Restoration of Southern European Forests, Managing Forest Ecosystems* (eds F. Moreira, M. Arianoutsou, P. Corona & J. De las Heras) pp. 93–119. Springer Science+Business Media B.V., Dordrecht.

Venier P., Carrizo García C., Cabido M. & Funes G. (2012) Survival and germination of three hard-seeded Acacia species after simulated cattle ingestion: the importance of the seed coat structure. *S. Afr. J. Bot.* **79,** 19–24.

Venier P., Funes G. & Carrizo García C. (2011) Physical dormancy and histological features of seeds of five Acacia species (Fabaceae) from xerophytic forests in central Argentina. *Flora* **207,** 39–46.

Verzino G., Joseau J., Díaz M. P. & Dorado M. (2004) Comportamiento inicial de especies nativas del Chaco Occidental en plantaciones en zonas de pastizales de altura de las Sierras de Córdoba, Argentina. *Bosque* **25,** 53–67.

Verzino G., Joseau J., Dorado M., Gellert E., Rodríquez Reartes S. & Nóbile R. (2005) Impacto de los incendios sobre la diversidad vegetal, sierras de Córdoba, Argentina. *Ecol. Aplicada* **4,** 25–34.

Vesk P. A. (2006) Plant size and resprouting ability: trading tolerance and avoidance of damage? *J. Ecol.* **94,** 1027–34.

Vesk P. A. & Westoby M. (2004) Sprouting ability across diverse disturbances and vegetation types worldwide. *J. Ecol.* **92,** 310–20.

Vieira D. L. M. & Scariot A. (2006) Principles of natural regeneration of tropical dry forests for restoration. *Restoration Ecol.* **14,** 11–20.

Wang X., Kent M. & Fang X. (2007) Evergreen broad-leaved forest in Eastern China: its ecology and conservation and the importance of resprouting in forest restoration. *For. Ecol. Manage.* **245,** 76–87.

Zak M. R. & Cabido M. (2002) Spatial patterns of the Chaco vegetation of central Argentina: integration of remote sensing and phytosociology. *Appl. Veg. Sci.* **5,** 213–26.

Zak M. R., Cabido M. & Hodgson J. G. (2004) Do subtropical seasonal forests in the Gran Chaco, Argentina, have a future? *Biol. Conserv.* **120,** 589–98.

Zhu W. Z., Xiang J. S., Wange S. G. & Li M. H. (2012) Resprouting ability and mobile carbohydrate reserves in an oak shrubland decline with increasing elevation on the eastern edge of the Qinghai–Tibet Plateau. *For. Ecol. Manage.* **278,** 118–26.

Zuloaga F. O., Morrone O. & Belgrano M. J., eds (2008) Catálogo de las plantas vasculares del Cono Sur: Argentina, Sur de Brasil, Chile, Paraguay y Uruguay. Monographs in systematic botany from the Missouri Botanical Garden. Volumen 2. Dicotyledoneae: Acanthaceae-Fabaceae. Editor Missouri Botanical Garden Press, Saint Louis.

SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Tree density of each species at each site before the fire.
Appendix S2. Survival of common native and non-native species 1 year after fire.
Appendix S3. Number of seedlings per species 3 years after fire.