Effects of vegetation and herbivores on regeneration of two tree species in a seasonally dry forest

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ABSTRACT

Tree establishment in harsh environments such as seasonally dry forests has traditionally been described as facilitated by existing shrubs and trees, which ameliorate harsh abiotic conditions; however, an alternative explanation postulates that facilitation is mediated by reduced herbivore damage, especially under shrubs. We established seeding and planting trials using two tree species (*Ruprechtia apetala* and *Schinopsis lorentzii*) in a full factorial design that included three vegetation types and two herbivore treatments at three sites (234 plots per species). Six months after seeding, seedling counts represented 0.95 and 0.47% of the sown seeds and survival of planted saplings was 81% and 46% for *R. apetala* and *S. lorentzii*, respectively. Average growth was negative due to over winter diebacks for both species. The performance of our target species was influenced by vegetation in a pattern which would suggest either mixed abiotic and herbivore-mediated facilitation or entirely herbivore-mediated facilitation. By contrast, we did not find resulting patterns suggesting a strict abiotic-mediated facilitation by shrubs and trees. We conclude that in dry mountain forests, remnant woody vegetation patches are important for the effective establishment of our study species in grazed sites, whereas effective establishment is feasible outside woody patches, in ungrazed sites.

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1. Introduction

Forest tree species are increasingly dependent on their ability to colonize new areas in order to cope with accelerated climate change and shifting cultivation patterns, which often involve the abandonment of extensive agricultural areas (Grau and Aide, 2008; Jump et al., 2009; Koralewski et al., 2015). However, colonization of seasonally dry new areas has been described as an extremely hazardous process because multiple biotic filters combined with the harsh abiotic conditions imposed by the long dry season prevent early establishment of seedlings and saplings (Vieira and Scariot, 2006). Several researchers have particularly emphasized that establishment may be severely hampered in open areas due to high radiation, water limitation and extreme temperatures; these factors are mitigated in sites where woody patches already exist and where shade reduces seed and seedling desiccation, preventing the harmful effects of drought periods (Aide and Cavelier, 1994; Aide et al., 1995; Vieira and Scariot, 2006). Shaded sites may also have a more stable environment because plant cover ameliorates the effect of winter frost and soil erosion (Lundmark and Hällgren, 1987; Gutiérrez and Squeo, 2004).

The potential facilitative role of plant cover on tree establishment in harsh environments is now widely recognized (review by Gómez-Aparicio, 2009); however, the knowledge necessary for using facilitation to assist forest colonization of open sites in seasonally dry climates is still scarce. Facilitation is often species-specific and dependent on the competitive abilities of the target species (Soliveres et al., 2014). However, the competitive abilities of forest tree species are poorly known in seasonally dry forests. Furthermore, domestic livestock is often the most abundant large herbivore in seasonally dry forests and one of the most widespread economic activities after agriculture (Izquierdo and Grau, 2009). In open sites, livestock can negatively affect tree establishment through trampling and browsing of saplings, whereas this effect may be mitigated under thorny or unpalatable shrubs and trees (del Moral et al., 2010; Papachristou and Platis, 2010).

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To the best of our knowledge, the relative importance of direct facilitation through amelioration of the harsh abiotic conditions and of indirect herbivore-mediated facilitation in seasonally dry forests has only been reported by Tálamo et al. (2015a). In that observational study, the authors found a positive spatial association between saplings of two tree species and thorny vegetation at grazed sites and no association at ungrazed sites. The study of Tálamo et al. (2015a) has important implications for forest colonization of open sites. If, as suggested in that work, facilitation in seasonally dry forests is mainly determined by indirect effects of herbivores and not by the previously postulated amelioration of harsh abiotic conditions (Gómez-Aparicio, 2009), open sites could be colonized by forests species through livestock exclusion. By contrast, this may not be feasible if nurse plants ameliorate harsh abiotic conditions, as proposed by Gómez-Aparicio (2009).

The apparent contradiction between established theory and the finding that facilitation is mainly due to the influence of livestock grazing in a seasonally dry forest may be due to population filters exerting their effects at different plant life stages. Small seedlings may be more vulnerable to microclimatic conditions such as strong radiation and lack of moisture, whereas larger saplings are more likely to be browsed (Fenner and Thompson, 2005; Renison et al., 2015). Thus, in situations in which the limiting stage is sapling survival or growth and not seedling establishment, the purely abiotic influences at the early stages might be almost completely overridden by herbivore effects on saplings, as occurs in analogous situations at treelines (Speed et al., 2010) or in differing topographies (Renison et al., 2015).

Here, we aim at assessing seeding and planting success of two native tree species in three different vegetation patch types in grazed and ungrazed sites in a seasonally dry mountain forest of central Argentina. The selected target species are two native non-thorny endangered tree species often associated with mature forests situated in dry sites and on slopes with high incident radiation. We hypothesized that our target species would be mainly favored by the protection from harsh abiotic conditions provided by woody vegetation at early stages (hereafter abiotic-mediated facilitation), and that this protection would be mainly due to indirect facilitative effects mediated by protection from livestock at later stages (hereafter herbivore-mediated facilitation). We expected that seedling success would be lower in the open herbaceous patches than under shrubs and trees both in grazed and ungrazed sites (under a strict abiotic-mediated facilitation hypothesis, Fig. 1 a). Instead, we expected enhancement of planted sapling survival and growth of target species by shrubs and trees only in grazed sites (under a strict herbivore-mediated facilitation hypothesis, Fig. 1 c) or an enhancement mediated by shrubs and trees under both grazing situations, but higher in grazed sites (under a mixed hypothesis of both abiotic- and herbivore-mediated facilitation, Fig. 1 b).

2. Materials and methods

2.1. Study area and species

The study area is located in the south of Valle de Punilla, in the Córdoba Mountains of central Argentina (S 31.48 W 64.54, 700 m a.s.l.). The vegetation corresponds to the Chaco Serrano district (Cabrera, 1976) of the Gran Chaco Region, one of the most extensive seasonally dry forests in the world. Chaco Serrano is an open canopy forest in exposed and disturbed sites but with a dense canopy in ravines. The dominant trees in mature stands are *Schinopsis lorentzii* (Griseb.) Engl. and *Lithraea molleoides* (Vell.) Engl., which are co-dominant with different tree species along the altitudinal, latitudinal and longitudinal gradients (Giorgis et al., 2011). The climate is warm temperate to subtropical, with a mean annual temperature of 13.9 °C and a mean annual precipitation of about 725 mm, concentrated in the warm season, from September to March (Colladon et al., 2010). Heavy forest logging took place during the 19th and 20th centuries, followed by an intensification of the traditional livestock production system (Baxendale and Buzai, 2009). By the late 20th century, the remnant forests of the Gran Chaco were being lost at an annual rate of 2.2%, mainly due to the expansion of the agricultural frontier (Zak et al., 2004). Most of the remaining Chaco forests persist in the drier flatlands or in mountain areas where agriculture is not feasible due to pronounced slopes; however, they are being rapidly replaced by non-native tree plantations, urbanizations and invasion of non-native species (Hoyos et al., 2010), with only less than 12% of the native forests still remaining in the mountains of central Argentina (Zak et al., 2004). In addition, the lack of vegetation cover caused by fires and overgrazing produces high rates of soil loss in the most susceptible areas (Renison et al., 2010; Cingolani et al., 2013).

The vegetation in the experimental area is an open forest mainly composed of fire-tolerant pioneer woody species with multiple basal stems resulting from post-fire resprouting. The area has been affected by fires and livestock grazing at least since the 1950s, and is fairly representative of the present state of Chaco Serrano in the Córdoba Mountains where open shrublands are the most abundant vegetation type (Giorgis et al., 2011). Mean annual temperature of the study years (2007–2010 period) was 16.5 °C and mean annual precipitation was 623.25, concentrated in the warm season according to data recorded 3 km away from the study site (Fig. 2; Renison R., unpublished data). We selected two species present in mature stands of Chaco Serrano forest: *Ruprechtia apetala* Weddell,
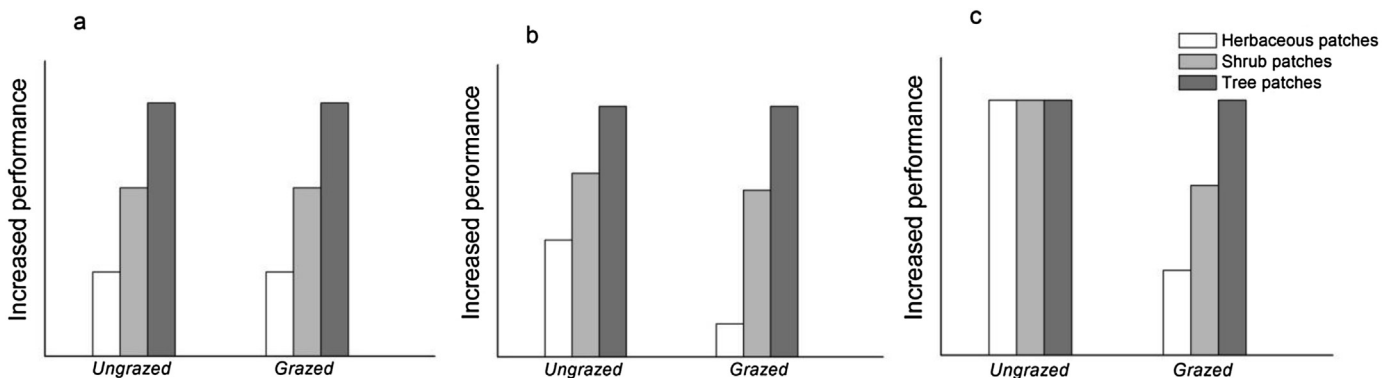

Fig. 1. Predicted pattern of results under (a) a strict abiotic facilitation hypothesis (b) a mixed hypothesis of both abiotic- and herbivore-mediated facilitation, and (c) a strict herbivore-mediated facilitation hypothesis.
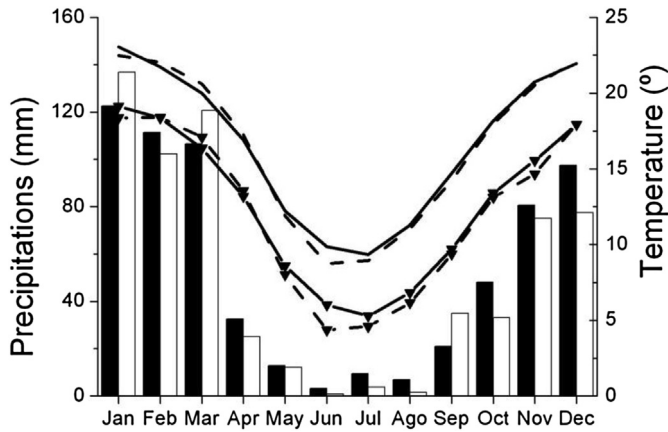
Fig. 2. Climate diagram for the study area. Columns show mean precipitations for the 2003–2013 period (black columns) and for the study period (2007–2010, white columns). The two upper lines show mean temperature for the 2003–2013 period (continuous line) and for the study period (2007–2010, dashed line). The two lower lines (solid triangles) show mean minimum temperature for the 2003–2013 period (continuous line) and for the study period (2007–2010, dashed line).

a numerically common but seldom dominant species, and *S. lorentzii* (Griseb.) Engler, which often dominates the canopy of mature stands.

R. apetala (Anacardiaceae) is a deciduous tree, of about 4 m in height, fairly abundant in the Córdoba Mountains and in the transition with adjacent lower forests. *R. apetala* has been characterized as "lower risk/near threatened" by IUCN due to habitat degradation by cattle, sheep and goat overgrazing (IUCN, 2013). *S. lorentzii* (Anacardiaceae) is a deciduous tree, of about 20 m in height, present in the boreal part of the Córdoba Mountains, where it is dominant or co-dominant with *L. molleoides*. The species has been characterized as "vulnerable" by IUCN (with its old name: *Schinopsis haenkeana* IUCN, 2013) due to habitat degradation, particularly in the province of Córdoba.

2.2. Field seeding and planting experimental setup

We seeded *R. apetala* and *S. lorentzii* at the start of the rainy season in November 2008 (late spring) in different woody vegetation patches: (1) herbaceous patches, consisting of patches containing only herbaceous vegetation lower than 0.4 m and located in the areas between shrub and tree patches; (2) shrub patches, consisting of islands of one or more woody plants up to 2 m tall with a herbaceous understory partially protected from browsing by the low shrub canopy height; and (3) tree patches, consisting of islands of one or more woody plants over 2 m tall with its accompanying herbaceous understory; cover in these tree patches is usually more sparse and accessible to browsers than in the shrub patches. Tree patches included pioneer woody species that usually dominate disturbed areas, such as *Acacia caven*, *Geoffroea decorticans*, *Condalia buxifolia*, *Schinus fasciculatus* and *Celtis ehrenbergiana*. Shrub patches in most cases included the same species as the tree patches, but individuals were of lower height and had multiple basal stems. In addition, shrub patches also included species such as *Lippia turbinate* and *Aloysia gratissima*. In the three different vegetation patch types, we distributed seeding plots (0.5 × 0.5 m) at three sites at least 500 m apart. One half of each site was protected from livestock with an enclosure of 1.5–2 ha. In each treatment we seeded 13 plots per species with 60 seeds each (468 plots in total: 2 species × 3 vegetation patch types × 2 herbivore treatments × 3 sites × 13 plots; Fig. 3 a and b). The seeds for the experiment were collected from 70 trees of each species from January to October 2008 and stored in paper bags at room temperature and humidity until seeding.

We counted the number of seedlings 6 months after seeding; we marked seedlings and monitored seedling survival and growth until 22 months after seeding. We also recorded the presence of seedlings in an adjacent randomly selected control quadrat. In the laboratory, we characterized the germination rate of a sample of 4200 seeds per species. We placed 20 seeds on filter paper 5 cm in diameter for *R. apetala* and 10 cm in diameter for *S. lorentzii* (20 seeds × 210 dishes × 2 species). We used bigger dishes for *S. lorentzii* because their seeds were two to three times larger than *R. apetala* seeds. We kept dishes in a germination chamber at 25 °C during the 12 h light period and at 15 °C during the 12 h dark cycle. Germinated seeds were counted once a week until no more new germinations were recorded and the dishes were re-moistened with distilled water as necessary.

R. apetala and *S. lorentzii* saplings were planted in the field using the same design as that of the field seeding experiment described above. Saplings were acquired from local producers (El 44 Natural Reserve nursery and Facultad de Ciencias Agropecuarias forest nursery, National University of Córdoba). *R. apetala* saplings were 3
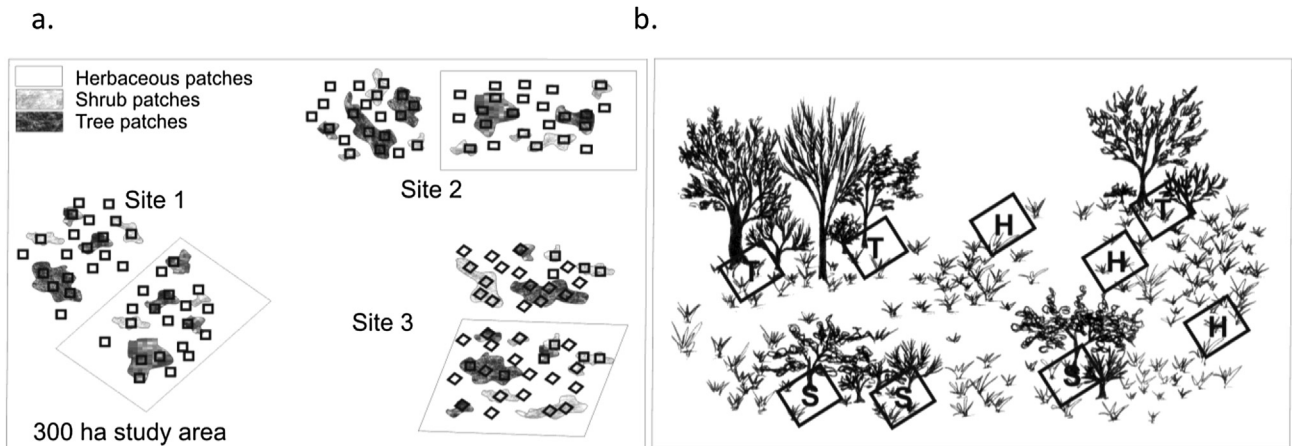

Fig. 3. a) Diagram showing the three study sites within the 300-ha study area and the spatial distribution of vegetation patches and plots (small squares). Small squares inside large squares indicate plots in ungrazed sites; small squares outside large squares indicate plots in grazed sites. b) Diagram showing the vertical structure of vegetation patch types. Squares enclosing letters represent plots in herbaceous (H), shrub (S) and tree (T) patches.

years old and averaged 32.58 ± 0.92 cm in height, whereas *S. lorentzii* saplings were 2 years old and 19.40 ± 0.30 cm in height. Saplings were planted in December 2007. We recorded survival and height of saplings 3 years after planting. We also recorded the proportion of browsed buds and the presence of dieback in the stem once a year during 3 years.

To characterize the pairs of plots where seeding and planting was performed we recorded: (1) local slope inclination, (2) slope aspect with a clinometer and compass (DP 6, RECTA SA, Finland) and (3) solar radiation as visually evaluated in the field as the trajectory (°) of the sun where it projects directly on the ground at the plot (e.g. i.e., in a flat plateau with no obstacles, the value would be 180, with the shade of mountain ridges, rocky outcrops and tree canopies reducing the value).

2.3. Statistical analyses

We compared the species in terms of success of seeding and planting and analyzed differences in performance among treatments for each species separately using Generalized Lineal Mixed Models (GLMM). We considered as response variables: 1) number of seedlings, estimated by counting seedlings 6 months after seeding (assuming a Poisson distribution); 2) planted sapling survival and presence of dieback (assuming a binomial distribution); and 3) planted sapling growth and proportion of browsed stems (assuming a normal distribution). To compare the effect of treatments on each species we included herbivore treatment (two levels: grazed and ungrazed) and vegetation patch type (three levels: herbaceous, shrubs and trees) as fixed factors; and the site as random factor (three levels corresponding to the three enclosures and their respective controls). We included the herbivore treatment × vegetation patch type interaction in the model. We used LSD Fisher post-hoc test for comparisons. To compare species we included as factors: species, herbivore treatment, vegetation patch type and site. We also included the following interactions: species × herbivore treatment, species × vegetation patch type, and species × herbivore treatment × vegetation patch type.

For a better interpretation of results, we analyzed differences in topographic characteristics among vegetation patch types using Kruskal–Wallis test and LSD Fisher post-hoc test. To compare slope aspect we calculated the relative North-South and East-West component of the aspect through cosine and sine transformations, respectively. We used Infostat 2013 statistical package for all analyses (Di Rienzo et al., 2013).

3. Results

3.1. Seeding and planting success of each species

Seedling counts of *R. apetala* 6 months after seeding were twice as high as those of *S. lorentzii*, with counts representing 0.95% and 0.47% of the sown seeds, respectively (of a total of 14,040 seeds of each species; GLMM, n = 468 seeding plots, χ^2 = 23.0, $P < 0.001$). We recorded no seedlings of either species in the adjacent randomly placed quadrats. In the laboratory test, germination percentage was also higher for *R. apetala* (83.68%) than for *S. lorentzii* (13.86%), of a total of 4200 seeds per species (GLMM, n = 140, χ^2 = 880.0, $P < 0.001$). Seedling survival during the period from 6 to 22 months after seeding was 3.75% and 4.55% of the originally recorded seedlings of *R. apetala* and *S. lorentzii*, respectively. The final height of surviving seedlings was 3.60 ± 0.48 cm (n = 5) and 4.17 ± 0.44 cm (n = 3) for *R. apetala* and *S. lorentzii*, respectively. For *R. apetala* we recorded a new set of 17 seedlings 22 months after seeding, but we did not record new seedlings for *S. lorentzii* (Fig. 4 a).

Similarly to results regarding seedling counts, planted sapling survival for *R. apetala* three years after planting was almost twice as high as those of *S. lorentzii*, with survivals of 81% and 46%, respectively (GLMM n = 468, χ^2 = 69.2, $P < 0.001$; Fig. 4 b). Final sapling height was also higher for *R. apetala* than for *S. lorentzii*, but for both species, this variable was lower than the height at plantation date. In addition, we recorded dieback and livestock browsing in all study years (Fig. 4 c and d).

3.2. The role of vegetation patch type and herbivores

Seedling counts for *R. apetala* were similar between vegetation patch types in ungrazed sites, and three times lower in herbaceous than in shrub and tree patches in grazed sites (Fig. 5 a, Table 1 with vegetation patch type × herbivore interaction of $P = 0.08$ but significant LSD Fisher post-hoc test at $P < 0.05$). By contrast, seedling counts for *S. lorentzii* showed a declining pattern from herbaceous to shrub and tree patches in ungrazed sites, and lower counts in herbaceous patches than in shrub and tree patches in grazed sites (Fig. 5 b, vegetation patch type × herbivore treatment interaction, $P < 0.001$, Table 1; LSD Fisher pos-hoc test).

Three years after planting, sapling survival of *R. apetala* was 20% lower in herbaceous and shrub patches than in tree patches in ungrazed sites, whereas survival was similarly high and did not differ among vegetation patch types in grazed sites (Fig. 5 c, vegetation patch type × herbivore treatment interaction, $P = 0.04$, Table 1; LSD Fisher pos-hoc test). By contrast, sapling survival of *S. lorentzii* increased with an increase in vegetation cover in ungrazed sites, with a greater increase in grazed sites (Fig. 5, Table 1 with patch type × herbivore interaction of $P = 0.08$ but significant LSD Fisher post-hoc test at $P < 0.05$).

For both species, overall sapling growth was higher in ungrazed than grazed sites (*R. apetala*: $P < 0.001$; *S. lorentzii*: $P = 0.001$, Table 1; Fig. 5 e and f). For *R. apetala*, sapling growth increased with increasing vegetation cover ($P < 0.001$), whereas for *S. lorentzii*, sapling growth did not differ among vegetation patch types ($P = 0.8$).

Dieback affected about 60% of the saplings, with no significant differences between herbivore treatments (*R. apetala*: GLMM, n = 188, χ^2 = 0.2, $P = 0.7$; *S. lorentzii*: GLMM, n = 105, χ^2 = 0.0, $P = 0.9$). Dieback differed among vegetation patch types for *R. apetala* saplings, being higher in herbaceous and shrub patches than in tree patches ($P = 0.03$), whereas for *S. lorentzii*, no effect of vegetation patch type was found ($P = 0.6$). Saplings with dieback sprouted from the base or stem in the next growing seasons, thereby recovering part of their initial height.

As expected, for both species the proportion of browsed stems was higher in grazed than ungrazed sites (Fig. 6 a and b; *R. apetala*: GLMM, n = 188, F = 156.5, $P < 0.001$; *S. lorentzii*: GLMM, n = 104, F = 70.2, $P < 0.001$). For *R. apetala* saplings in grazed sites, the proportion of browsed stems was higher in herbaceous and tree patches than in shrub patches, whereas in ungrazed sites, there was no difference among vegetation patch types (herbivore treatment × vegetation patch type interaction, $P < 0.001$). For *S. lorentzii* saplings the proportion of browsed stems did not differ among vegetation patch types ($P = 0.4$).

3.3. Vegetation patch type characteristics

Patch types differed mainly in sun incidence, which was high in herbaceous patches (136.44° ± 2.12), intermediate in shrub patches (112.13° ± 2.31) and low in tree patches (81.14° ± 1.22; Kruskal–Wallis test, n = 468, H = 119.5, $P < 0.001$). No differences were detected for slope inclination or relative North-South and East-West components of slope aspect (all P values > 0.05).
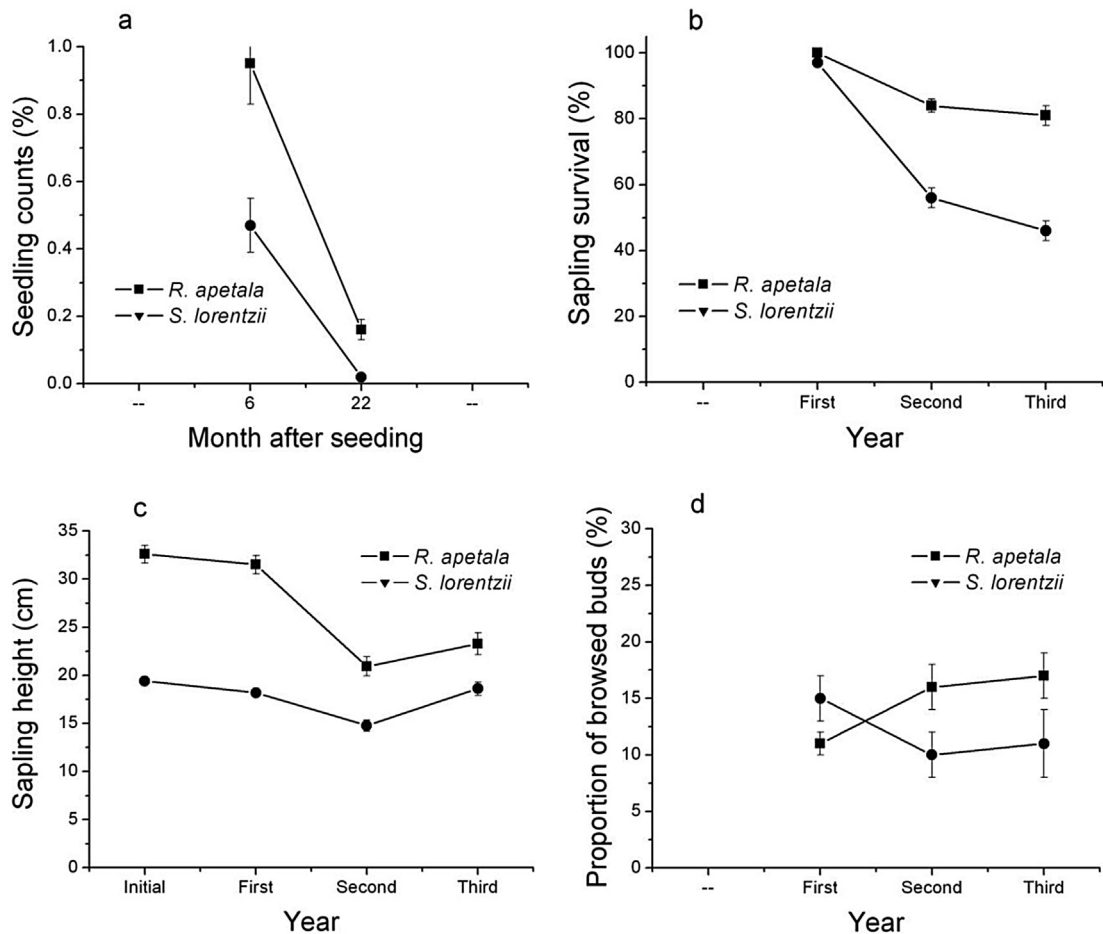
Fig. 4. Mean seedling counts recorded 6 and 22 months after seeding, expressed as a proportion of seedlings emerged from the sown seeds (a), mean annual sapling survival (b), height (c) and (d) proportion of browsed buds for *R. apetala* and *S. lorentzii*. Seedlings at 22 month included survivors and new emerged individuals. Bars show SE.

4. Discussion

4.1. Seeding and planting success of each species

The seeding trial highlights previously unreported natural history traits of our study species, such as new *R. apetala* seedling emergence after six months, suggesting that this species forms seed banks, and confirming the fast loss of viability for *S. lorentzii*, as previously reported for the genus (Alzugaray et al., 2005; Prado de Oliveira and Oliveira, 2008). The low seedling success and the relatively higher sapling survival are within the range reported for harsh site conditions, such as in lowland Chaco forests (Barchuk and Díaz, 2005), recently vegetated erosion gullies (Landi and Renison, 2010), as well as for high-altitude treeline taxa (Körner, 2012; Renison et al., 2015). Growth was affected by overwinter dieback in a high proportion of saplings, which caused a negative net change in their height during the first three years. Although dryness may be an important cause of partial or complete plant mortality in seasonally dry forests (Gerhardt, 1996; Mc Laren and Mc Donald, 2003), frosts also produces dieback (Verzino et al., 2003, 2004; Barberis et al., 2011). Temperature and precipitation values in the study area during the study years were similar to values recorded during the 2003–2013 period, as shown in Fig. 2. Further research is necessary to elucidate the relative contribution of frost and desiccation to dieback. Personal observations of the planted trial and of other plantations suggest that dieback becomes less important and positive growths are achieved at year four or five; accordingly, we also advocate further research to improve the growth of planted saplings during the first years, because such long time intervals for positive growth will locally deter the use of these species in gardening and forest restoration projects.

4.2. The role of vegetation patch type and herbivores

Our main results show that, depending on the species and the response variable, there is mixed abiotic- and herbivore-mediated facilitation or entirely herbivore-mediated facilitation. We also found an unpredicted result that suggests that herbivores decreased performance throughout all vegetation types. We did not find results suggesting purely abiotic-mediated facilitation (Table 2, elaborated comparing predictions in Fig. 1 with results in Fig. 4).

Contrarily to our expectations, seedling counts pattern in relation to vegetation patch type and herbivores was in accordance with a hypothesis of herbivore-mediated facilitation for both study species. We found no support to our hypothesis of abiotic-mediated facilitation occurring at early regeneration stages, since in ungrazed sites there was no relationship between seedling counts and vegetation patch type for *R. apetala*; we also found an opposite pattern to the expected by facilitation for *S. lorentzii*. As this was a field experiment, we were not able to control for every confounding variable and, therefore, abiotic-mediated facilitation cannot be discarded. For example, in a steppe-woodland ecotone in Patagonia, Chaneton et al. (2010) report how herbivory by tenebrionid beetles seeking refuge under nurse shrubs prevented tree
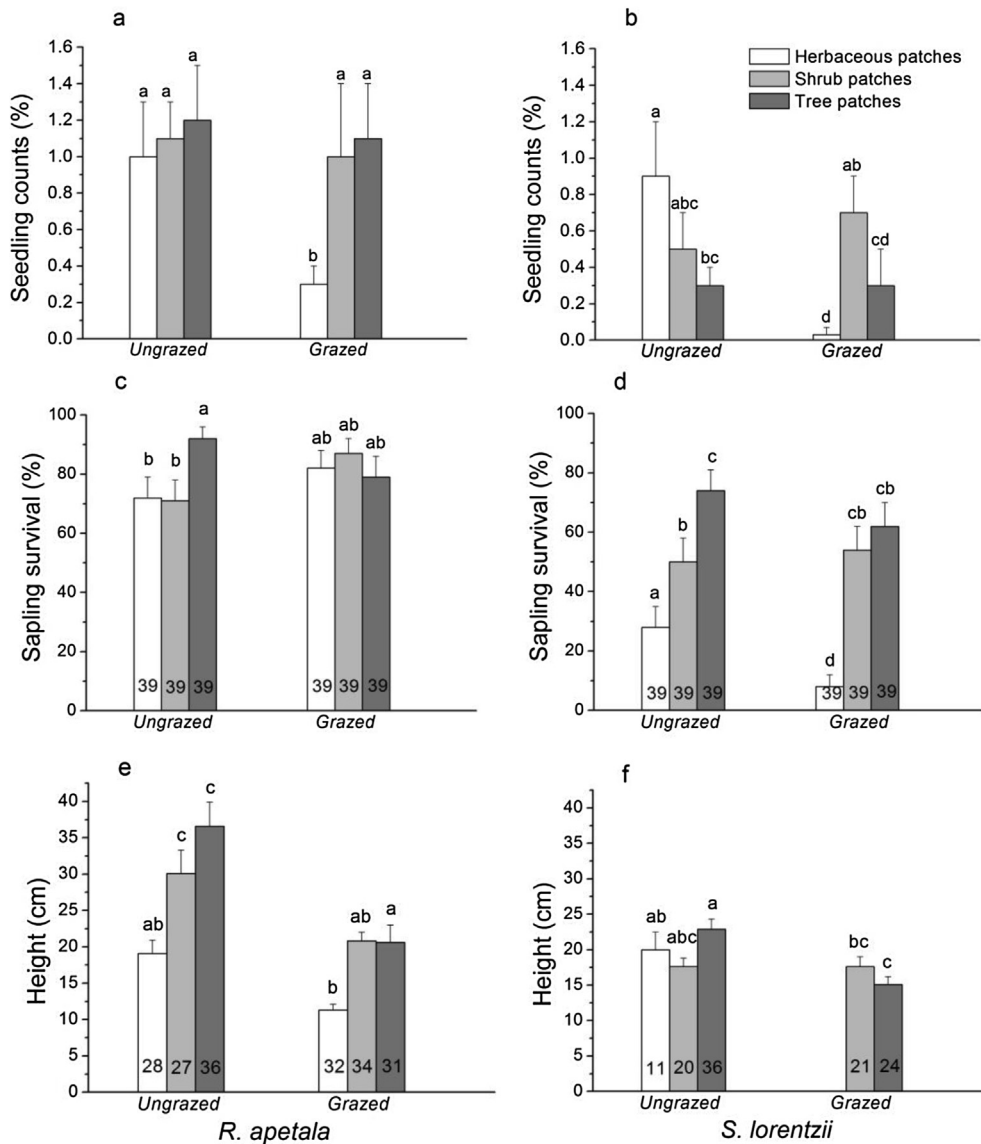
Fig. 5. Performance of *R. apetala* (left panels) and *S. lorentzii* (right panels) measured as seedling counts, expressed as a proportion of seedlings developed from the sown seeds (Mean ± SE) (a and b), planted sapling survival (c and d) and height (f and e) in three vegetation patch types (see legend in figure b), in grazed and ungrazed sites. Seedling counts were evaluated 6 months after seeding, and survival and height, 3 years after planting. We plotted sapling final height which followed a similar pattern to growth but did not have negative values, which makes the interpretation of the figure less straightforward. Bars represent SE. Numbers inside columns correspond to number of plots of each treatment. Different letters show differences at a significance level of P ≤ 0.05 (LSD Fisher post-hoc test).

Table 1
GLMM for *R. apetala* and *S. lorentzii* seedling counts, sapling survival and growth. Significant *P*-values are in bold (P ≤ 0.05).

|	*Ruprechtia apetala*		*Schinopsis lorentzii*	
	Wald χ^2	P	Wald χ^2	P
Seedling counts	N = 234		N = 234	
Herbivore treatment	2.7	0.10	3.9	**0.05**
Vegetation patch type	6.8	**0.03**	4.1	0.13
Vegetation patch type × herbivore treatment	5.0	0.08	21.1	**<0.001**
Sapling survival	N = 234		N = 234	
Herbivore treatment	0.7	0.4	2.3	**0.1**
Vegetation patch type	2.3	0.3	45.7	**<0.001**
Vegetation patch type × herbivore treatment	6.2	**0.04**	5.0	0.08
	F	P	F	P
Sapling growth	N = 188		N = 105	
Herbivore treatment	26.7	**<0.001**	13.6	**<0.001**
Vegetation patch type	10.6	**<0.001**	0.3	0.8
Vegetation patch type × herbivore treatment	1.4	0.2	3.3	0.07
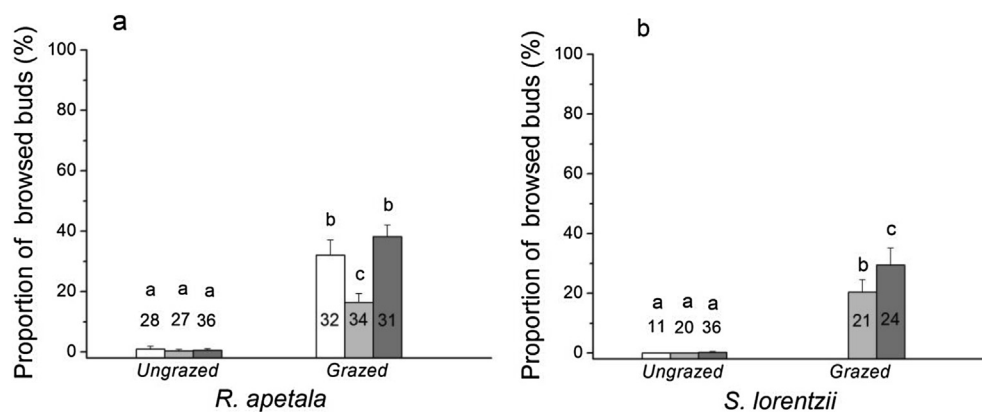
Fig. 6. Proportion of browsed buds three years after plantation for the species *R. apetala* (left panel) and *S. lorentzii* (right panel) in three vegetation patch types (see legend in figure b), in grazed and ungrazed sites. Bars represent SE. Numbers inside columns correspond to number of plots of each treatment. Different letters show differences at a significance level of P ≤ 0.05 (LSD Fisher post-hoc test).

recruitment, thus altering facilitation due to amelioration of abiotic conditions, which might seem competition from nurse plants. Similar scenarios could be occurring in our field trial, which need to be explored in future research. Beyond all possible explanations, our experiments show that early establishment in the herbaceous matrix could be greatly enhanced by livestock removal, thereby avoiding livestock trampling, soil compaction or a reduction in protective herbaceous cover due to livestock grazing (also suggested in Torres et al., 2008). Further research is necessary to support these patterns, since low and variable seedling survival was recorded in our study after 6 months, making it difficult to generalize and predict safe microsites, a scenario also shown in other seeding field studies (e.g. Günter et al., 2009; Quero et al., 2011).

Sapling survival presented a pattern in relation to vegetation patch type and herbivores which would suggest no facilitation in *R. apetala* (or facilitation by trees to a small extent if we consider the small but significant difference between shrubs and trees in ungrazed sites). By contrast, in *S. lorentzii* results were in accordance with a mixed hypothesis of both abiotic- and herbivore-mediated facilitation. Survival was high under all treatments for *R. apetala* despite the presence of livestock browsing saplings in all study years. This result is in agreement with studies that show that resprouting after a disturbance is an important persistence trait in Chaco species (Barchuk et al., 2006; Torres et al., 2014). On the other hand, woody vegetation favoured sapling survival in *S. lorentzii*, especially at grazed sites, suggesting that both abiotic- and herbivore-mediated facilitation prevails. Moreover, for *S. lorentzii* we found opposite patterns of apparent competition at the seedling

Table 2
Main response variables for *R. apetala* and *S. lorentzii* in relation with predictions under (a) strict abiotic facilitation hypothesis, (b) mixed hypothesis of both abiotic- and herbivore-mediated facilitation, (c) strict herbivore-mediated facilitation hypothesis.

Response variable	(a) Abiotic	(b) Mixed	(c) Herbivore
Ruprechtia apetala			
Seedling counts	No	No	Yes
Sapling survival	No	No	No
Sapling growth	No	No[a]	No[a]
Schinopsis lorentzii			
Seedling counts	No	No	Yes
Sapling survival	No	Yes	No
Sapling growth	No	—	—

[a] Results reveal an unexpected reduction of growth due to herbivory in almost all vegetation types; hence, herbivores did not increase facilitation.

stage and of apparent facilitation in sapling survival in relation to vegetation types; these contrasting results may make interpretation of results difficult. However, evidence for herbivore-mediated facilitation was detected in the results of both stages, in agreement with Tálamo et al. (2015a), who reported positive spatial associations between *S. lorentzii* and thorny shrubs in a grazed site and no associations in an ungrazed site in Chaco forest.

Sapling growth was reduced by herbivores in almost all vegetation types. In grazed sites we did not find an increase in sapling growth under woody vegetation for *R. apetala* and we could not evaluate this parameter for *S. lorentzii* due to the high mortality in the herbaceous patches at grazed sites (we had no measurements for growth). Our results for *R. apetala* were not predicted by any of our hypothesis, which we attribute to the fact that at the end of the dry season there was scarce green fodder and livestock browsed early sprouting saplings at almost every position where we could plant them, including under thick thorny shrubs, although at lower frequency than in the herb and tree patches (see Fig. 5). Browsing probably affected *R. apetala* growth; however, it did not affect seedling survival due to the species resprouting ability. Livestock probably did not also affect seedling counts through browsing due to the short height of seedlings.

In our study area, shrubs and trees seemed to enhance seedling and sapling establishment as compared to herbaceous vegetation alone under some scenarios and was always partly mediated by livestock, whereas shrubs and trees had negative or no effects under other scenarios. Therefore, our results support the hypothesis that shrubs and trees facilitate the recovery of seasonally dry forests by protecting regeneration from livestock presence (Tálamo et al., 2015a, 2015b), which might include trampling, soil compaction, reduction of herbaceous vegetation and to a lesser extent reduction in browsing. The positive effect of woody vegetation has been mentioned mainly for late-successional tree species of dry forests (Castro et al., 2002; Gómez-Aparicio et al., 2004; Griscom and Ashton, 2011; Salazar et al., 2012); however, few studies have been conducted to determine if this facilitation could be mediated by herbivores (Bertness and Callaway, 1994; Brooker et al., 2008).

We conclude that mixed abiotic- and herbivore-mediated facilitation or purely herbivore-mediated facilitation may be widespread in the Chaco Serrano region and other similar seasonally dry forests where livestock grazing is widespread. This phenomenon has been also mentioned by Graff et al. (2007) for herbaceous plants. Thus, livestock exclusion would permit proper regeneration of our study species in the herbaceous matrix surrounding shrub and tree patches, whereas presence of livestock

reduces regeneration, although to a lesser extent under shrubs.

Our results suggest that in environments with harsh abiotic conditions herbivore pressure would be as important as abiotic limitations to determine positive interactions among woody species. Our findings contribute to the understanding of the factors underlying plant facilitation and their role in response to future environmental changes. This information is important for facilitating dominant tree colonization in seasonally dry forests that partially maintain their woody vegetation after extensive land uses.

Acknowledgments

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