

Influence of conspecific and heterospecific adults on riparian tree species establishment during encroachment of a humid palm savanna

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Received: 9 July 2010 / Accepted: 22 February 2011 / Published online: 8 March 2011
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Abstract Woody plant encroachment of savanna ecosystems has been related to altered disturbance regimes, mainly fire suppression and herbivore exclusion. In contrast, neighbourhood interactions among resident and colonising woody species have received little attention, despite their likely influence on the pattern and rate of tree establishment. We examined how resident palm trees (*Butia yatay*) and established adults of two riparian forest tree species (*Allophylus edulis* and *Sebastiania commersoniana*) influenced seed arrival and seedling performance of the latter two species in a humid savanna of east-central Argentina. Seed traps and seedlings of both riparian species were placed in herbaceous openings, and beneath palm, conspecific and heterospecific adult trees in two unburned savanna patches, and were monitored for 2 years. Only seeds of the bird-dispersed *Allophylus* arrived in palm microsites, yet survival of *Allophylus* seedlings near adult palms was limited by animal damage through trampling and burrowing, a non-trophic mechanism of apparent competition. Seeds of both riparian species dispersed into

conspecific microsites, although adult trees selectively reduced growth of conspecific seedlings, a pattern consistent with the “escape hypothesis”. Further, survival of *Sebastiania* increased in the moister *Allophylus* microsites, suggesting a one-way facilitative interaction between woody colonisers. Our results indicate that dispersal facilitation by resident savanna trees may be critical to riparian species invasion after fire suppression. Distance-dependent effects of conspecific and heterospecific adult trees could contribute to shape the subsequent dynamics of woody seedling establishment. Overall, we show that indirect interactions can play a prominent role in savanna encroachment by non-resident woody species.

Keywords Apparent competition · Escape hypothesis · Facilitation · Forest expansion · Invasion

Introduction

Woody plant encroachment in grasslands and savannas may occur whenever factors limiting woody populations are removed by natural causes or human intervention (Scholes and Archer 1997; House et al. 2003; Sankaran et al. 2004; Bond 2008). In humid savannas, tree abundance is limited chiefly by fire and grazing (Sankaran et al. 2005; Bond 2008), and therefore lignification processes are often triggered by fire suppression and/or grazing exclusion (e.g. Swaine et al. 1992; Russell-Smith et al. 2003). Woody encroachment may involve not only resident savanna tree species but also non-resident species that colonise from nearby patches (Knight et al. 1994; Russell-Smith et al. 2003). Tree colonisation dynamics depend on patterns of seed arrival and subsequent seedling establishment in an environmental mosaic created by adult trees embedded in

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the herbaceous matrix. Established trees of both resident and colonising species may be important in promoting or inhibiting establishment of non-resident woody species (Horn 1974; Yarranton and Morrison 1974; Connell and Slatyer 1977; Archer et al. 1988; Verdú and García-Fayos 1996; Milton et al. 2007). Such neighbourhood-scale interactions provide the mechanisms whereby large-scale factors drive vegetation dynamics (Pickett and McDonnell 1989). Yet, adult-to-seed and -seedling interactions have been rarely investigated in the context of ongoing shifts in woody cover of savanna ecosystems (House et al. 2003).

Adult trees may exert a wide range of direct (mediated by abiotic factors) or indirect (mediated by biotic factors) influences on dispersal and establishment of woody colonisers. Effects of adult trees can be studied by dividing the colonisation process into two stages. First, an early stage, in which seed sources are external and establishment may be influenced by resident savanna trees as well as by herbaceous species. Second, an advanced stage, in which seed sources are mostly local and seedling establishment may also be influenced by previously established adults of the colonising species themselves. Thus, the frequency of different pairwise adult-to-seed and -seedling influences would depend on the stage of woody encroachment, the dispersal modes of woody colonisers, and their relative colonisation success. For example, during the early stage, resident trees are expected to interact more frequently with bird-dispersed colonisers (Archer et al. 1988; Verdú and García-Fayos 1996; Milton et al. 2007). Moreover, the pattern and rate of woody species encroachment is likely to be affected by the nature (direct or indirect) and overall balance of positive and negative adult-seedling interactions acting simultaneously (Chaneton et al. 2010).

Resident savanna trees may induce a variety of distance-dependent effects on newly arrived, colonising seedlings. Established woody plants often create adequate microsites for tree seedling establishment, either through amelioration of abiotic stress or through indirect facilitation mediated by suppression of herbaceous competitors (Scholes and Archer 1997; Brooker et al. 2008). This microsite facilitation coupled with dispersal facilitation may drive a “nucleation” process, whereby woody colonisers tend to clump around the nucleus formed by a nurse tree (Yarranton and Morrison 1974; Verdú and García-Fayos 1996; Milton et al. 2007). Alternatively, adult trees could inhibit establishment of heterospecific seedlings through direct competition, for example by reducing light and soil resource availability (Coomes and Grubb 2000). Further, established trees may attract generalist consumers, which may prevent establishment of colonising species by preying upon their seed or seedlings (i.e. apparent competition; Connell 1990; Chaneton and Bonsall 2000; Orrock et al. 2010). Physical damage produced by animal micro-

disturbances (trampling, nesting, scrapping, burrowing) can be another source of seedling mortality beneath adult trees (Clark and Clark 1989; Gillman and Ogden 2003). Since scattered savanna trees are likely to concentrate animal activity through the provision of habitat, shelter and/or food (Manning et al. 2006), apparent competition could play a critical role in limiting recruitment of non-resident woody species.

As woody encroachment progresses, seedlings of non-resident species will have greater chances of being influenced by previously established adults of either the same or other colonising species. Adults of colonising species may also exert nursing or competitive effects on establishing seedlings (Callaway and Walker 1997; Scholes and Archer 1997; Weltzin and McPherson 1999; Dickie et al. 2005; Brooker et al. 2008). In particular, facilitative, synergistic interactions between non-resident woody species have been found to be decisive during colonisation and invasion processes (Yarranton and Morrison 1974; Archer et al. 1988; Verdú and García-Fayos 1996; Simberloff and Von Holle 1999; Milton et al. 2007). In contrast, increasing evidence from forest communities shows that, by harbouring specialised pathogens or herbivores, adult trees can inhibit the establishment of conspecific seedlings in their immediate vicinity (Janzen 1970; Connell 1971; Harms et al. 2000; Packer and Clay 2000; Hille Ris Lambers et al. 2002; Hyatt et al. 2003). If, consistent with the “escape hypothesis” (Howe and Smallwood 1982), such negative intraspecific interactions are frequent during savanna encroachment, we would expect seedling performance of colonising species to be enhanced away from conspecific adult trees.

In this study, we examined the influences of adults of resident and colonising tree species on seeds and seedlings of two riparian woody colonisers during encroachment of a South American humid palm savanna after fire suppression. Fire-dependent savannas at El Palmar National Park, east-central Argentina, have historically been dominated by the palm *Butia yatay* (Mart.) Becc. (hereafter *Butia*), but currently undergo an accelerated lignification process due to invasion by native and exotic woody species (Ciccero and Balabusic 1994; Goveto 2006). Here, we focussed on two native riparian trees, *Allophylus edulis* (A. St.-Hil., A. Juss. & Cambess.) Hieron. ex Niederl. and *Sebastiania commersoniana* (Baill.) L.B. Sm. & Downs (hereafter named by genus). Current landscape distribution of trees within El Palmar National Park suggests that tree colonisation is faster in the absence of fire and in dense palm savannas, and that *Allophylus* is colonising at a much higher rate than *Sebastiania* (Rolhauser 2007; Rolhauser & Batista *in prep.*). Specifically, we asked (1) how do *Butia* palm trees influence seed arrival and seedling establishment of *Allophylus* and *Sebastiania*? (2) Do adult trees of

colonising riparian species affect establishment of conspecific and heterospecific tree seedlings? And (3) what are the primary causes of tree seedling mortality in different savanna microsites? For 2 years, we monitored seed arrival and performance of *Allophylus* and *Sebastiania* seedling transplants under adult tree canopies and in herbaceous savanna openings in two unburned savanna patches.

Materials and methods

Study system

El Palmar National Park occupies 8,500 ha on the west margin of the Uruguay River, in the province of Entre Ríos, Argentina (31°55'S, 58°17'W). Land management in the area prior to Park's creation involved cattle grazing and frequent (annual or biennial) intentional fires (Goveto 2006). In 1970, fires were suppressed and domestic cattle was removed and excluded, a policy that triggered a rapid colonisation process by several shrub and tree species, both native and exotic (Ciccerio and Balabusic 1994). The study species, *Allophylus* and *Sebastiania*, are small- to medium-sized trees (up to 15–20 m of height) living in the understorey of the Paranaense Forest (Argentina, Paraguay and Brazil) and in the overstory of riparian forests that extend southwards along the Paraná and Uruguay rivers (Burkart and Bacigalupo 2005). Propagules of *Allophylus* are one-seeded, drupe-like mericarps (4–6 mm of diameter) dispersed by birds, whereas propagules of *Sebastiania* are sub-ovoid seeds (4.5–5.5 mm long), which are elastically dispersed from three-seeded dehiscent capsules (Burkart and Bacigalupo 2005).

Mean annual precipitation at El Palmar National Park is 1,346 mm and annual average temperature is 19°C. Although rainfall is concentrated in summer, high temperatures induce frequent water deficit increasing the chances of fire events during this period (Goveto 2006). Annual and spring–summer (October–March) rainfalls during the first growing season of this study (2004–2005) were similar to historical records (1,054 and 738 mm, respectively). In contrast, the second growing season (2005–2006) was substantially drier than usual, especially during spring–summer (686 and 326 mm of annual and spring–summer rainfall, respectively).

Experimental setup

We selected two large sites (blocks) representative of open palm savannas at El Palmar National Park, which had not been burnt since the creation of the Park in 1965. Within each site, we randomly selected ten replicates of each of four microsite types: *Butia* adult (“palm”), *Allophylus*

adult, *Sebastiania* adult, and herbaceous openings with no woody vegetation. Adult trees of extreme sizes (either too small or too large) were not considered in this selection. In the palm microsites, the herbaceous layer was dominated by 30- to 50-cm-tall grasses, mostly *Paspalum juergensii*, whereas the ground cover under *Allophylus* and *Sebastiania* adults and in the openings was largely made up of the fern *Adiantopsis chlorophylla* (50–60 cm tall). Herbaceous, woody-less openings had a radius of at least 2 m. The minimum distance separating two experimental microsites was 4 m between adult tree microsites (measured from crown edge) and 7 m between adult tree microsites and herbaceous openings.

In September 2004, we randomly selected half the replicates of each microsite type within each block, and in each microsite we placed a seed trap at ground level, for a total of 40 seed traps ($n = 5$ per microsite type and block). Seed traps were rectangular, 23 × 33 cm trays protected from predators with a 1-cm mesh wire screen.

To assess individual survival and growth of *Allophylus* and *Sebastiania* offspring in different microsites, we obtained plantlets of both tree species by agamic propagation under greenhouse conditions (Hartmann et al. 1990). This method was preferred to that of growing seedlings from seed due to the low availability of seeds of *Sebastiania* at the field, and because it ensured a greater homogeneity of the experimental plants. We acknowledge that agamic plantlets may be more rustic and perform better than true seedlings of similar size. Thus, our results will be fairly conservative as constraints on tree establishment imposed by biotic and physical conditions may be even stronger for true seedlings.

In October 2003, basal shoots were cut from two spatially close individuals of *Allophylus* and from three *Sebastiania* trees. Harvested shoots were cut into segments of approximately 10 cm (with 2–4 nodes), inoculated with commercial rooting powder (Indole-3-butyric acid, IBA, 3%) and placed in cutting beds. Cuttings were potted immediately after the root length exceeded 10 cm; when necessary, roots were cut to homogenise root length among individuals. After growing in pots for 7 months (August 2004), plantlets were transplanted to the field. Mean basal diameter (2.7 ± 0.3 mm) and height (150 ± 18 mm) of agamic transplants were similar to those of 1-year-old tree seedlings grown from seed under the same conditions (2.9 ± 0.3 and 163 ± 26 mm, respectively). Transplants were randomly assigned to the field microsites so that each tree species occurred in half of all the microsites. Individuals were planted carefully in order to minimise disturbance of the surrounding herbaceous cover. In each microsite, transplants were established in groups of five, leaving 20 cm between adjacent plants. Transplants were individually marked at the stem base to follow their fate

over two consecutive growing seasons. In the tree microsites, the location of the transplants relative to the adult stem was determined by randomly drawing a compass direction; transplants were placed at 70 cm from the adult stem base. Transplants dying within the first month of planting were immediately replaced (only three plantlets in total).

Data collection

Seed traps were visited in October and November 2004, and in February, April and September 2005 (i.e. comprising one full growing season). On each visit, we collected and counted the number of apparently viable seeds of *Allophylus* and *Sebastiania* present in each trap.

In October and November 2004, in February, April and September 2005, and in July 2006 (i.e. comprising two growing seasons), we recorded the number of transplants in each of three categories: (1) alive, (2) dead due to physical damage (uprooted, trampled, buried, missing associated to micro-disturbance; classified as “damaged-dead”); and (3) dead due to causes other than physical damage (desiccation, damping-off, etc.; classified as “standing-dead”). An additional visit made in December 2006 allowed us to confirm transplant mortality as recorded in July 2006. For each sampling date, we also recorded the length of all branches in each surviving transplant.

In December 2006, we characterised the abiotic environment in each microsite by measuring soil water content and percentage solar radiation reaching the transplants. Four days after a 2-day period of rain, we measured volumetric soil water content to 5 cm depth using a Theta Probe sensor (model ML2x, Delta-T Devices, Cambridge, UK). Photosynthetic photon flux density (PPFD, $\mu\text{mol m}^{-2} \text{s}^{-1}$) was measured using a 65-cm-long radiation ceptometer (“Cavadevices BR-R1”, Buenos Aires; www.cavadevices.com). In each microsite, we measured PPFD above transplant height (30 cm) and at the nearest unshaded spot to obtain a single relative measure of light levels reaching the transplants. All light measurements were taken around noon (1030–1330 hours) during a clear day.

Data analysis

We examined differences in soil water content and percent light levels among the four microsite types using ANOVA models (proc GLM; SAS Institute 1999). Treatment means were separated by Fisher’s least significant difference method. Data were log-transformed to meet ANOVA assumptions (Sokal and Rohlf 1995).

Seed arrival data were compared based on the Poisson distribution. We calculated confidence intervals for the mean number of tree seeds captured per trap in each

microsite type over the first growing season (2004–2005) for each colonising tree species separately. We followed a method based on the link between the Poisson distribution and the chi-square distribution (Ulm 1990). Upper and lower confidence limits were calculated as $\text{UCL} = \chi^2_{2(n+1), 1-\alpha/2}$ and $\text{LCL} = \chi^2_{2n, \alpha/2}$, where n is the total number of seeds captured for each microsite type and colonising tree species, $\chi^2_{v, \alpha}$ is the chi-square quantile for upper tail probability on v degrees of freedom and q is the number of replicates (Ulm 1990). This method allowed us to calculate confidence limits for seed arrival in all microsite types, even for those where no arrival was detected.

Patterns in transplant fate were evaluated using logit models fitted by maximum likelihood procedures (Agresti 1996; proc CATMOD; SAS Institute 1999). We used logit models to test for the effect of microsite type on the proportion of transplants alive, damaged-dead, and standing-dead at the end of the study (July 2006), and on the proportion of damaged-dead and standing-dead transplants between growing seasons. Separate analyses were conducted for each tree species.

To evaluate differences in transplant growth, we calculated the relative growth rate of each individual transplant as $\text{RGR} = \ln(\Sigma_t/\Sigma_0)/t$. Here, Σ_t is the summed length of all branches at the end of the study (July 2006), or at the time of death; Σ_0 is the initial summed length of all branches (October 2004); and t is the time (in months) either to death or to the end of the study. We compared mean RGR values across microsite types for each tree species using linear mixed models fitted by maximum likelihood procedures (proc MIXED; SAS Institute 1999). This approach allowed us to deal with variance heterogeneity and unbalanced data derived from differential mortality of transplants across microsite treatments (Littell et al. 1996). Data for each colonising tree species were analysed separately.

Results

Microsite abiotic conditions

Transplants in herbaceous openings and palm microsites received more sunlight than those in *Allophylus* and *Sebastiania* microsites (Table 1). However, soil water content was higher in palm microsites than in herbaceous openings. *Allophylus* microsites were, on average, more shaded and humid than *Sebastiania* microsites (Table 1).

Seed arrival

Seeds of both riparian tree species were dispersed during October and November (data not shown). For both species, seed arrival was highest near conspecific adults, although

Table 1 Topsoil water content (0–5 cm) and percentage light penetration (photosynthetic photon flux density) at transplant height in four savanna microsites

Microsite	Light penetration (%)	Soil water content (%)
Opening	51.3 ± 4.2 a	12.8 ± 0.5 bc
Palm	44.8 ± 3.6 a	15.2 ± 0.8 a
<i>Allophylus</i>	11.7 ± 3.0 c	13.9 ± 0.7 ab
<i>Sebastiania</i>	24.1 ± 4.3 b	11.4 ± 0.7 c

Values are means ± SE ($n = 20$). Microsite types were defined by the presence of different adult trees

Different letters within columns indicate significant differences ($P < 0.05$)

the mean number of seeds trapped was substantially higher for *Allophylus* (113.6 seeds/trap, 95% CI = 106.7–120.2) than for *Sebastiania* (1.7 seeds/trap, 95% CI = 0.99–2.72). No seeds of the focal species were found in herbaceous openings or near adults of the other colonising species (95% CI = 0–0.37). Remarkably, a few *Allophylus* seeds (all of them lacking outer fleshy parts) were trapped in palm microsites (0.8 seed/trap, 95% CI = 0.35–1.58), accounting for an arrival rate that is significantly different from zero.

Transplant survival

After 2 years, transplant survival for both species was generally high (from 0.38 to 0.98 depending on microsite and target species). Mortality of *Allophylus* transplants was largely accounted for by physical damage throughout the study (Fig. 1a). *Allophylus* mortality by physical damage was strongly concentrated near palm trees, where overall survival of this species was the lowest (Fig. 2a). *Allophylus* survivorship did not significantly differ among savanna openings and microsites of riparian conspecific or heterospecific adult trees. However, the proportion of standing-dead *Allophylus* plants was higher in openings and near conspecific adults than near heterospecific, *Sebastiania* adults (Fig. 2a).

Mortality of *Sebastiania* was mostly associated to desiccation-like causes, as reflected by the proportion of standing-dead transplants. This pattern became only apparent during the second, drier growing season (Fig. 1b). Survival of *Sebastiania* transplants was greater near heterospecific, *Allophylus* adults than in any of the other three microsites (Fig. 2b). In addition, the proportion of standing-dead plants of *Sebastiania* was highest near conspecific adults and lowest (nil) near *Allophylus* adults (Fig. 2b). A small proportion of *Sebastiania* transplants were killed by physical damage in openings and palm microsites (Fig. 2b).

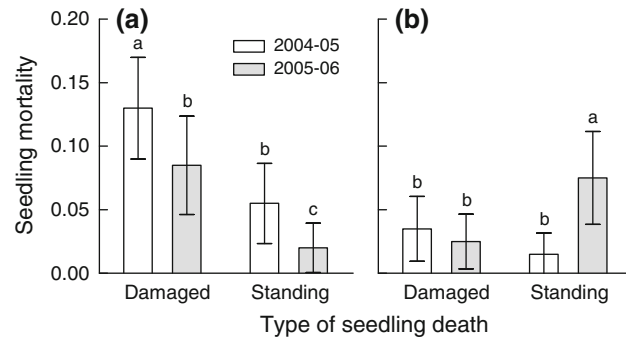


Fig. 1 Proportion of **a** *Allophylus* and **b** *Sebastiania* transplants killed by physical damage (damaged) or by other causes (standing) during two growing seasons (2004–2005 and 2005–2006). Bars indicate 95% confidence intervals. Different letters above bars indicate significant differences ($P < 0.05$) for each tree seedling species

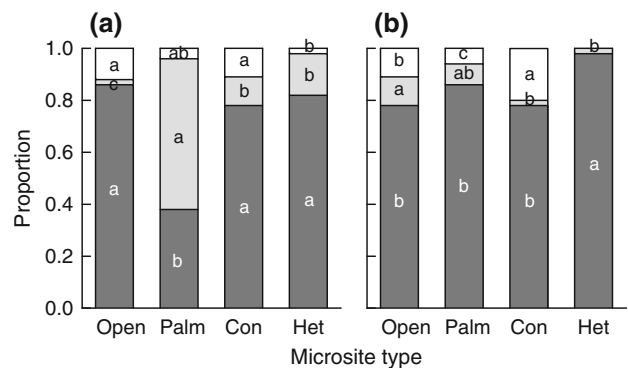


Fig. 2 Fate of **a** *Allophylus* and **b** *Sebastiania* transplants in four savanna microsites defined by the presence of different adult trees: standing-dead (white), damaged-dead (light grey) and alive (dark grey). Data integrated two growing seasons (October 2004–July 2006). Open opening, Con conspecific adult, Het adult of the other colonising species. Different letters within each fate class indicate significant differences ($P < 0.05$) for each tree seedling species

Transplant growth

The relative growth rate of *Allophylus* transplants was significantly lower near conspecific adults than in all other microsites (Fig. 3a). *Sebastiania* transplants exhibited significantly lower growth rates beneath conspecific adults than in openings and *Allophylus* microsites (Fig. 3b).

Discussion

Early colonisation stage—influence of resident palms

Resident *Butia* palm trees exerted qualitatively different influences on the establishment of the two riparian tree species. Adult palms had small or neutral effects on seed

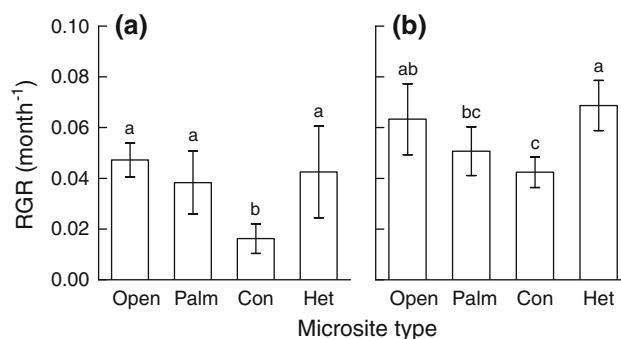


Fig. 3 Relative growth rate (RGR) of **a** *Allophylus* and **b** *Sebastiania* transplants in four savanna microsites defined by the presence of different adult trees. *Open* opening, *Con* conspecific adult, *Het* adult of the other colonising species. Bars indicate 95% confidence intervals. Different letters above bars indicate significant differences ($P < 0.05$) for each seedling species

dispersal and seedling establishment of *Sebastiania*. Conversely, adult palms exerted strong, opposing effects on *Allophylus* seeds and seedlings. Adults of *Butia* promoted the dispersion of bird-dispersed *Allophylus* seeds away from conspecific adults relative to alternative perches (i.e. *Sebastiania* adults), whereas they strongly limited the survival of *Allophylus* transplants (Fig. 4). These results suggest that resident trees were more likely to interact with *Allophylus* than with *Sebastiania* during early stages of colonisation, illustrating the importance of species-specific indirect facilitation in potential vegetation dynamics (Brooker et al. 2008). However, the results of *Allophylus* also show a seed-seedling conflict (sensu Schupp 1995), whereby seeds arriving in palm tree microsites would expose seedlings to a greater risk of mortality. Thus, resident palm trees may not represent “hotspots” for establishment of early colonising riparian trees.

Since palm microsites were moister than openings and no difference was found in light availability, the negative effect of adult palms on *Allophylus* survival cannot be simply attributed to competition for these resources. Remarkably, a relatively high proportion of *Allophylus* transplants placed near adult palms died due to physical damage. Damaged transplants were in all cases surrounded by trampled vegetation and/or associated with small burrows, and there were no signs of shoot damage caused by herbivory or by litter fall from palm trees. These observations suggest that the negative effect of adult palms on *Allophylus* seedlings may have been mediated by non-consumptive animal disturbances (Fig. 4). While the precise agent causing these physical disturbances is unknown, some plausible candidates include introduced wild boars (*Sus scrofa*, abundant at El Palmar National Park), native armadillos (e.g. *Dasypus novemcinctus*, nine-banded armadillo) and native tuco-tucos (*Ctenomys* spp.). Predation of *Butia* seeds and seedlings is presumably carried out

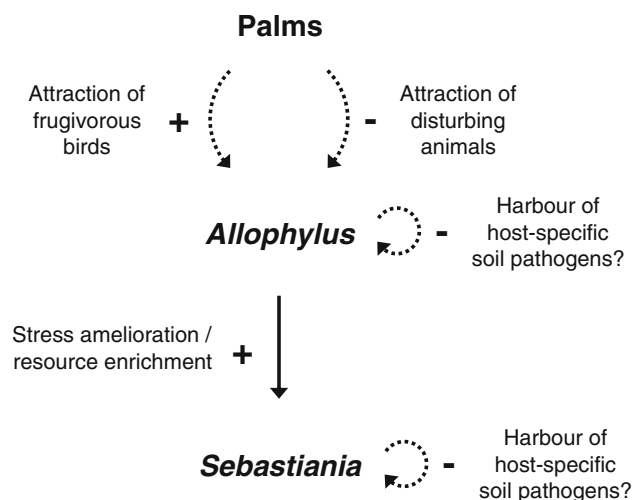


Fig. 4 Diagram of biotic and abiotic factors mediated by con- and heterospecific adults on the establishment of *Allophylus* and *Sebastiania*, two native riparian trees encroaching a humid palm savanna in Argentina. Solid and broken lines correspond to significant direct and indirect influences, respectively: signs indicate whether the interaction is positive or negative. Factors with less evidence supporting the underlying mechanism are followed by question marks. Attraction of frugivorous birds affected seed arrival, whereas the remaining mechanisms acted on seedling establishment

by these mammal species, although direct evidence is lacking. We hypothesise that the negative influence of adult palms on *Allophylus* establishment was mediated by mammalian consumers, which would be attracted to *Butia* microsites while searching for palm seed/seedlings, and thus mechanically damaged (but did not consume) *Allophylus* transplants. This may be seen as a special case of apparent competition mediated by a non-trophic, animal–plant interaction (cf. Connell 1990; Chanton and Bonsall 2000; Orrock et al. 2010). Given the well-known ability of scattered trees to concentrate animal activity (Manning et al. 2006), our results suggest that apparent competition may represent an important, yet generally neglected factor limiting early woody encroachment in savannas.

Advanced colonisation stage—influence of adult tree colonisers

Growth rates of the two colonising species were lower near conspecific adults than near heterospecific adults (Fig. 4). This pattern is consistent with predictions from the “escape hypothesis” (Howe and Smallwood 1982). Survival of *Sebastiania* was also reduced near conspecific adults, suggesting that detrimental intraspecific effects were stronger for this species, compared to those for *Allophylus*. In addition, transplants of both species were more likely to suffer standing- (desiccation-like) death near conspecific adults than near adults of the other colonising species. In

tropical and temperate forests, where density-dependent mortality of seedlings is pervasive (Harms et al. 2000; Hille Ris Lambers et al. 2002), soil pathogens were identified as a major cause of mortality (Augsburger 1983; Packer and Clay 2000). In our study, the higher proportion of standing-dead plants and limited growth rate of *Sebastiania* under conspecific adults could reflect the activity of host-specific soil pathogens, although more direct evidence is certainly lacking. On the other hand, standing-deaths of *Sebastiania* transplants occurred during the driest (second) growing season and in the driest microsites (near *Sebastiania* adults), suggesting that mortality may have been determined by competition for water. If this was the case, *Allophylus* transplants would have also been inhibited by *Sebastiania* adults, but our results indicated the contrary. We suggest that water stress during the drier season could have increased the negative impact of specific pathogens, which were likely to be more prevalent during the first (and moister) growing season. Our results then illustrate the potential for distance-dependent limitation of seedling performance to operate during advanced stages of woody encroachment in humid savannas.

Our experiment provided evidence for a potential facilitative interaction between riparian tree colonisers (Fig. 4). Survival and growth of *Sebastiania* transplants were enhanced near adults of *Allophylus*, which provided relatively shaded and moist microsites. *Allophylus* adults may have exerted a net facilitation effect on the establishment of *Sebastiania* seedlings through stress amelioration and/or resource enrichment (Scholes and Archer 1997; Manning et al. 2006; Brooker et al. 2008). Nevertheless, no arrival of *Sebastiania* seeds was detected near *Allophylus* adults. Hence, the extent to which *Allophylus* facilitates *Sebastiania* during advanced stages of colonisation would be constrained by the likelihood of *Sebastiania* seeds arriving in *Allophylus* microsites.

Implications for woody plant encroachment in savanna ecosystems

Our results suggest that adult-to-offspring interactions may contribute to shape the dynamics of woody encroachment in savanna systems. Intriguingly, many such neighbourhood interactions appear to be indirect, the most evident being mediated by animal responses to the structural heterogeneity created by resident savanna trees (Fig. 4). Indirect plant–plant interactions may be more important than previously thought in determining the dynamics of woody invasions in grasslands and savannas (White et al. 2006; Milton et al. 2007). Since these indirect effects can have opposing signs, the rate of woody colonisation would be dependent on their relative strength and temporal consistency (Chaneton et al. 2010).

At “El Palmar” National Park, the relatively rapid expansion of *Allophylus* population (Rolhauser 2007) indicates that, so far, positive influences of established trees (on dispersal) outbalanced the negative impacts (on individual establishment) observed in this study. In contrast, the lack of a long-distance dispersal mechanism of *Sebastiania* (perhaps coupled with low seed production) may have largely limited its population expansion over palm savannas from riparian forest sources. Furthermore, the generally high seedling survival rates observed in our experiment could reflect the agamic origin of the transplants (cf. Gignoux et al. 2009 and references therein), which implies that constraints on riparian species establishment discussed here may be even stronger for newly emerged seedlings. Overall, the evidence presented here suggests that facilitation of seed arrival by resident trees may be critical in determining native woody plant encroachment in these savannas after fire suppression. Distance-dependent effects from conspecific and heterospecific adult trees would contribute to shape the subsequent dynamics of woody seedling establishment. We suggest that, along with multifactor interactions among climate, grass competition, fire, and herbivory (Bond 2008), both direct and indirect adult-to-offspring interactions should be considered for a comprehensive understanding of woody plant encroachment in savannas.

Acknowledgments This work was supported by grants from Agencia Nacional de Promoción Científica y Tecnológica (PICT 00-8962) and Universidad de Buenos Aires (UBACyT G011). The Administración de Parques Nacionales of Argentina facilitated our work at El Palmar National Park. All the experiments were conducted in compliance with the current laws of Argentina. Marisa Nordenstahl and several Biology and Agronomy students from UBA provided invaluable field assistance. Many thanks to Marta Divo de César for guidance during plantlet production. We are also grateful to Peter Clarke and two anonymous reviewers for their comments on this manuscript. A.G.R. was supported by a MSc fellowship from Agencia Nacional de Promoción Científica y Tecnológica.

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