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Constraints to seedling success of savanna and forest trees across the savanna-forest boundary

Abstract Tropical savannas and closed forests are characterized by distinct tree communities, with most species occurring almost exclusively in only one of the two environments. The ecology of these two groups of species will largely determine the structure and dynamics of the savanna-forest boundary, but little is known about the ecological and physiological differences that might control their distributions. We performed field and nursery experiments to compare seedling establishment success, predawn leaf water potential, biomass allocation, and root carbohydrate concentration of congeneric species, each composed of one savanna species and one forest species. Seedling establishment of savanna and forest species responded differently to vegetation cover, with forest species having lowest establishment success in the open savanna and savanna species having lowest success in forest. Subsequent survival followed similar patterns, resulting in even greater differences in cumulative success. The low survival of forest species in the savanna appears related to drought stress, as seedlings of forest species had lower predawn leaf water potential than savanna species. Seedlings of savanna species had greater root: shoot ratios and root total nonstructural carbohydrate (TNC) concentration, particularly among evergreen genera. Among evergreen genera, root TNC per shoot mass, which may largely determine resprout capacity, was seven times higher in savanna species than forest species. Although water availability and microclimate may reduce the success of forest species, these factors appear unable to completely exclude forest seedling establishment in savanna. Fire, on the other hand, appears to be a much more absolute constraint to success of forest species in savanna.

Keywords Carbohydrate · Cerrado · Fire · Tropical forest · Water potential

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Introduction

Much of the seasonal tropics is composed of a mosaic of savanna and closed-canopy forest at landscape and regional scales. The distribution of these two vegetation types is often associated with soil properties or hydrology, with forest occurring on sites of greater nutrient or water availability (Furley 1992; Ruggiero et al. 2002). While such patterns suggest that the distribution of savanna and forests is edaphically determined and therefore somewhat stable, other evidence indicates that savanna-forest boundaries are not always stable. Palynological and isotopic studies show that savanna-forest boundaries have shifted in the past (Kershaw 1992; Desjardins et al. 1996; Schwartz et al. 1996; Sanaiotti et al. 2002), and continue to do so (Hopkins 1992; Schwartz et al. 1996; Bowman et al. 2001). Often, soil properties across the savanna-forest boundary are not perfectly associated with vegetation type (Gillison 1983; Furley 1992; Haridasan 1992; Schwartz et al. 1996; Bowman 2000; Fölster et al. 2001). And when they are, it is not always clear whether the soil properties determine the vegetation or whether the vegetation determines soil properties. Tree cover can favor the accumulation of soil organic matter and nutrients (Belsky et al. 1989; Kellman 1979; Kellman and Miyanishi 1982; Mordelet et al. 1993) while the frequent burning typical of savanna may reduce these (Neary et al. 1999), so improved soil status may often be the result of rather than the cause of forest vegetation (Bowman 2000).

In cases where savanna-forest boundaries have shifted in the past, fire has often played a particularly important role, with forest expanding during extended fire-free periods (Hopkins 1992; Swaine et al. 1992) and retreating under frequent fire or human disturbance (Bowman 1992; Hopkins 1992; Kershaw 1992). The rate of forest retreat is likely determined by fire frequency and intensity, while the rate of forest expansion will be determined by tree establishment, survival and growth in the savanna environment. These in turn, may be limited by the high temperature, drought stress, high light stress, low nutrient availability, frequent fire, and competition with grasses typical of savannas.

To understand the dynamics of savanna-forest boundaries, it is important to emphasize that these two vegetation types differ not only in the tree density, but also in their species composition (Adejuwon and Adesina 1992; Felfili and Silva Junior 1992), with most tree species occurring predominantly in one environment or the other. In the balance between forest advance and retreat, the success of forest tree species probably plays a more important role than does the success of savanna trees. Establishment and growth of forest tree species within savanna might convert it to forest, but invasion of savanna trees within forest would not substantially change the structure of the forest. If savanna species did successfully establish in forest, their shade intolerance and low stature (Hoffmann et al. 2003) make it unlikely that they could competitively exclude forest species.

Therefore we focus primarily on understanding the constraints to establishment and survival of forest species. However, to demonstrate that the environment limits the success of forest trees in savanna, it is necessary to demonstrate that forest species are more sensitive than savanna species to the savanna environment. Therefore we rely on phylogenetically independent comparisons between savanna and forest species to test for differential responses to the environment. Furthermore, comparisons of traits of savanna and forest species permit us to infer what adaptations have evolved in response to their respective habitats. Very few studies have compared the performance of tropical savanna and forest species in natural conditions (Hoffmann 1996, 2000), and to our knowledge none have ensured phylogenetic independence.

Here we compare various aspects of seedling ecology of savanna and forest species to test the following hypotheses:

Seedling establishment of savanna and forest species responds differently to tree cover, with savanna species having greater establishment success in open grassland sites and lower establishment success in forest sites, relative to forest species. Establishment of forest species is limited within the savanna environment, and is facilitated by the presence of nurse trees (Kellman and Miyanishi 1982; Kellman 1985; Hoffmann 1996), suggesting that the savanna environment is harsh for the establishment of forest species. However it is unclear if they differ from savanna species in this regard, as some (Hoffmann 1996), but not all (Hoffmann 1996; Kanegae et al. 2000), savanna species also exhibit low establishment in open savanna relative to shaded sites.

Seedlings of forest species exhibit greater water stress than seedlings of savanna species under similar conditions. It is widely asserted that deep roots permit savanna species to maintain favorable water status during dry periods by permitting access to moist soil layers. In potted seedling studies, savanna species allocate more biomass to coarse roots than forest species (Paulilo and Felippe 1998; Hoffmann and Franco 2003). If this corresponds to greater rooting depth, savanna species should exhibit greater seedling survival and reduced drought stress, as measured by predawn water potential. A previous study (Hoffmann 2000) did not detect differences in survival between savanna and forest species in unburned conditions, but by using phylogenetically independent comparisons, we expected to increase statistical power to detect differences.

Seedlings of savanna species have greater concentrations of root total nonstructural carbohydrates (TNC) and greater total mass of root TNC per shoot mass than forest species. Seedlings of savanna species are more able to survive fire than forest species (Hoffmann 2000). Since root carbohydrate reserves are essential for surviving fire, the greater survival of savanna species might be explained by greater root TNC concentrations, greater total root biomass, or both.

Materials and methods

Savannas and forests of central Brazil

This study was performed in the Cerrado region of Brazil, a region of nearly 2,000,000 km^2 originally covered predominantly by savanna and identified as one of 25 global biodiversity hotspots (Myers et al. 2002). The savanna formations range from open grassland to dense woodland and are collectively referred to as "cerrado" or "cerrado *sensu lato*." At regional scales, the transition from cerrado to forest is a mosaic, with enclaves of savanna occurring within forest and a variety of forest types occurring within the Cerrado region (Eiten 1972). Upland forests in the Cerrado region are referred to as either dry forest (Ribeiro and Walter 2001) or mesophytic forest (Oliveira-Filho and Ratter 2002) and are classified as deciduous, semideciduous and evergreen. These forest types occur locally throughout the Cerrado region and at the transitions with the Amazonian and Atlantic forests. Additionally, gallery forests occur as corridors along streams and rivers. This forest type can be divided into the downslope portion with seasonally or permanently waterlogged soils, and the upslope portion on well-drained soils.

Within the savanna formations of cerrado, there are no clear transitions in the tree and shrub species from the more open forms to the more closed forms (Eiten 1972). Although many species become more or less abundant with increasing tree density, most common species occur along the entire gradient from open shrub savanna (campo sujo) to dense woodland (cerradão; Goodland and Ferri 1979). Similarly, there is a strong overlap in species composition among the various forest types in the region (Oliveira-Filho and Ratter 1995). In contrast, there is clear distinction between savanna and forest communities, with little or no species overlap occurring between savanna and forest (Felfili and Silva Junior 1992). An important exception occurs in cerradão, a dense woodland that may contain both savanna and forest species. Cerradão can occur as patches within a savanna-dominated landscape, but sometimes also occurs at the savanna-forest boundary (Oliveira-Filho and Ratter

2002), resulting in a diffuse, poorly defined transition. In other cases, especially in the case of gallery forests, the transition can be very sharp, with savanna grading into forest over a few meters.

In this study we focus primarily on the transition between savanna and gallery forest, though we include a few species typical of other forests, due to seed availability. Gallery forests are a useful system for studying the savanna-forest boundaries because they share many tree species with other forest types of Central Brazil, as well as Amazonian and semi-deciduous Atlantic forests (Oliveira-Filho and Ratter 1995, 2002). Furthermore, it is plausible that during dry periods of large-scale forest retreat, forest refugia were similar to modern gallery forests so the processes occurring there should yield insight into forest-savanna dynamics during such times.

Study species

All experiments were performed on congeneric species pairs, each composed of one forest species and one savanna species from the same genus. Three species pairs were used in experiments one and two, while eight species pairs were used for experiment three. Due to seed availability, different species pairs were utilized for the various experiments (Table 1). Seeds of all savanna species were collected in natural cerrado in the vicinity of Brasília, DF, Brazil. Seeds of the forest species were obtained from gallery forests around Brasília, with the exception of *E. contortisiliquum* and *A. subincanum* collected in dry forest, and *D. nigra* (typical of Atlantic forest) collected from planted individuals in the campus of the University of Brasília, *G. graciliflora* collected in closed-canopy woodland (cerradão), and *B. rubescens* from transitional Amazonian forest. All of these, with the exception of *D. nigra* and *B. rubescens* also occur in gallery forests in the region (Felfili et al. 2001). All species are trees except the subshrub *J. ulei* and all are evergreen except *Enterolobium* spp. and *Aspidosperma* spp.

Study site

This study was performed at the experimental station, Fazenda Água Limpa (FAL), of the University of Brasília. FAL is located at approximately 15°46′S, 47°57′W at an elevation of 1,100 m. Mean annual rainfall at a meteorological station located at the adjacent IBGE Ecological Reserve was 1,426 mm for 1993–2002, with a distinct dry season from May to September. Mean temperature was 22.5°C with mean annual minimum and maximum temperatures of 6.0 and 34.0°C.

Experiment 1. Seedling establishment and survival

To compare seedling establishment across the savanna-forest boundary, 48 plots were established within FAL. Each was located in open savanna, closed savanna or forest, with 16 plots in each cover type. The first two cover types were in cerrado sensu stricto ('typical' savanna), with the open savanna sites lacking tree cover and the closed savanna sites being under the cover of one or more tree crowns. The forest plots were in closed-canopy gallery forest, with equal numbers in the upslope and downslope portions of the forest. These were distributed in the gallery forests of three different streams, and the savanna plots were distributed over distances of several km. No two plots of the same cover type were placed within 50 m of each other. In tropical savanna, burning tends to reduce seedling establishment (Hoffmann 1996; Setterfield 2002), so all plots were established in locations that had not burned for several years.

Each seedling plot was divided into six 0.5 m ×0.5 m subplots, one for each of six species (Table 1). Seeds were sown by scattering seeds over the subplot and lightly ruffling the grass layer, when present, to facilitate settling of the seeds. Seeds of *Hymenaea* spp. were scarified before sowing. The number of seeds per plot varied from 20 for *H. stigonocarpa* to 35 for *G. aurea*. Seeds were sown early in the wet season (November and December), 2001, with both species of each genus sown on the same date. Censuses of establishment and survival were performed in May 2002 and June 2003 (early dry season).

Experiment 2. Dry season drought stress

A field experiment was performed to test the hypothesis that forest species experience greater dry-season drought stress than savanna species. In an area of open shrub savanna (campo sujo), six blocks were delimited and each was divided into six 1 m ×1 m plots, with one plot for each of six study species (Table 1). Soil psychrometers (Wescor PST-55-30 SF) were installed at 15, 30, and 60 cm depth in one randomly chosen plot per block. Each plot was planted with 16 newly germinated seedlings early in the rainy season (December 1998). These plots were irrigated manually during rain-free periods to improve survival until the beginning of the dry season, with the last irrigation being on 16 June 1999. Irrigation was performed eight times, each with 10 mm of water in all plots.

Measurements of pre-dawn leaf water potential were performed periodically on the seedlings during the dry season with a Scholander-type pressure chamber (Model 3005-1422, Soil Moisture Equipment, Santa Barbara, Calif., USA). Initially, measurements were made on at least one individual per species per plot in every

Table 1 Species used in this study

Savanna species	Forest species	Family	Experiment in which species were used		
			Experiment 1	Experiment 2	Experiment 3
Aspidosperma macrocarpon Mart.	*A. subincanum* Mart.	Apocynaceae		X	X
Brosimum gaudichaudii Trec.	*B. rubescens* Taub.	Moraceae		X	X
Dalbergia miscolobium Benth.	*D. nigra* (Vell.) Britt.	Leguminosae	X		
Enterolobium gummiferum (Mart.) MacBride	*E. contortisiliquum* (Vell.) Morong	Leguminoseae (Mimosoideae)			X
Guapira noxia (Netto) Lundel.	*G. areolata*[a]	Nyctaginaceae	X		X
Hymenaea stignocarpa Mart. Ex Hayne	*H. courbaril* (Hayne) Lee et Lang.	Leguminosae (Caesalpinoideae)	X	X	X
Jacaranda ulei Burm. & K. Schum.	*J. puberbula* Cham.	Bignoniaceae			X
Ouratea hexasperma (St. Hil.) Bail.	*O. castaneaefolia* (St. Hil.) Engl.	Ochnaceae			X
Salacia crassifolia (Mart.) G. Don.	*S. elliptica* (Mart.) G. Don.	Hippocrateaceae			X

[a]This species was used for experiment 1. For experiment 3, the forest species was *G. graciliflora* (Mart. Ex J.A. Schmidt) Lunde

block at each sample date. As the dry season progressed, seedling death or loss of leaves sometimes reduced the number of samples.

Experiment 3. Root carbohydrate concentration

Seeds of eight congeneric species pairs (Table 1) were sown in opaque black polyethylene sacks, 10 cm in diameter and 25 cm deep, with perforated bottoms, in a substrate of oxisol subsoil collected from a cerrado site. Chemical analysis on this soil revealed (mean $\pm$ SE, n=6) pH =4.9$\pm$0.1, N (%) =0.28$\pm$0.11, P (ppm) =0.72, K (ppm) =6.7$\pm$1.8, Ca (ppm) =19.0$\pm$3.2, Mg (ppm) =2.5$\pm$0.8. The sacks were placed in full sun and were irrigated daily to supplement precipitation, when needed. No fertilizer was applied.

Three seedlings of each species were harvested 150 days following emergence and were dried to constant mass at 70°C. The plants were separated into coarse roots, fine roots, stems and leaves, and were weighed. Coarse roots were defined as those with clear signs of secondary growth and lignification.

The coarse roots were separated and finely ground. The ground material was extracted with water (30 mg dry mass ml^{-1} distilled water) for 1 h at 100°C. After centrifuging, the supernatants were used for the determination of total non-structural soluble carbohydrates by the Anthrone assay (Scott and Melvin 1953). The insoluble residue was used for starch determination. After threefold extraction with 80% ethanol the starch was degraded by a heat-stable α-amylase (EC 3.2.1.1, Sigma) and amyloglucosidase (EC 3.2.1.2, Merck) into its monomer glucose which was determined enzymatically by the hexokinase-glucose-6-phosphate-dehydrogenase assay (Bergmeyer 1970).

Statistical analysis

For every variable examined, analyses were performed for each genus, as well as for all genera after pooling all data. For experiment 1, seedling establishment success was transformed with the arcsin transformation as suggested by Cokal and Rohlf (1995) for proportions. Then a factorial ANOVA was performed to test for effects of species type and tree cover for each species. Similar analyses were performed to test for effect of species type and date on predawn water potential in experiment 2. For both the establishment and water potential data, additional ANOVAs were performed on the pooled data for all species, including genus as an independent variable. Here, genus was included as a random factor because we are interested in generalizing about differences between savanna and forest species whereas all others were considered fixed factors. For comparisons between the savanna and forest types, this mixed-model ANOVA is equivalent to a paired t-test applied to species means (Zar 1999). Analyzing the data in this manner treats each species as a statistical replicate as is appropriate in comparative studies, and as would be done with a paired t-test. In contrast, prescribing genus as a fixed factor would have treated each individual plant as a replicate, greatly inflating the error degrees of freedom.

Loglinear analysis was performed to test for effects of species type (savanna vs forest) and cover type (open savanna, closed savanna and gallery forest) on establishment within each genus.

Results

Experiment 1. Seedling establishment and survival

Seedling establishment, which we define here as the fraction of sown seeds that produced seedlings that survived until the end of the first growing season, was highly dependent upon cover type ($F_{2,270}$=16.05,

P<0.0001), with highest establishment in sites of intermediate cover. When tested over all genera, savanna and forest species types responded differently to cover (Type $\times$ Cover interaction; $F_{2,4}$=9.02, P=0.03), with savanna species having lowest establishment in gallery forest and forest species having lowest establishment in open sites (Fig. 1). Although this pattern was significant over all species, and apparent in each of the three genera, when tested within each genus, this Type $\times$ Cover interaction was significant for *Dalbergia* ($F_{2,90}$=10.56, P<0.001) and nearly significant for *Guapira* ($F_{2,90}$=2.80, P=0.066).

A similar response to tree cover was observed in subsequent survival (Fig. 2). For the 1-year period beginning at the end of the first growing season, forest species had greater mortality than savanna species in open savanna sites, whereas in the forest sites the savanna species had higher mortality than forest species, when tested over all genera (χ^2=26.79, P<0.001). When tested within each genus, this trend was significant for *Dalbergia* (χ^2=11.12, P=0.004) and *Guapira* (χ^2=20.23, P<0.001).

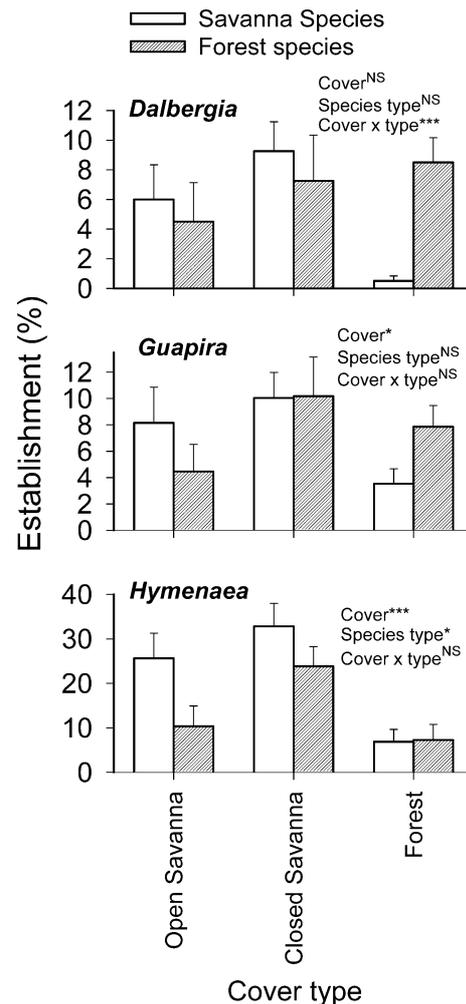The combined effect of establishment and survival resulted in even more accentuated differences in final

Fig. 1 Effect of tree cover on seedling establishment of savanna and forest species (mean$\pm$SE; n=16 plots per treatment). When tested over all genera, there was a significant Cover $\times$ Type interaction
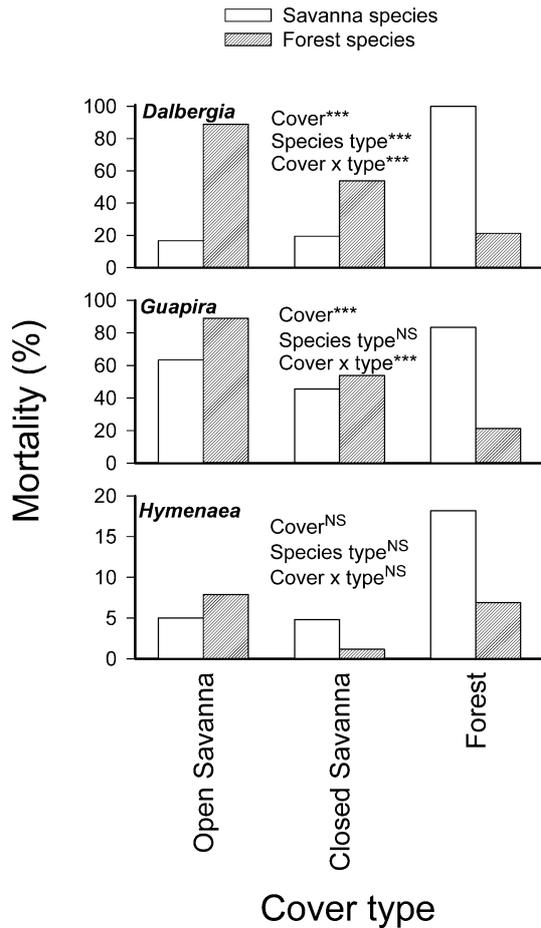
Fig. 2 Effect of tree cover on seedling survival of savanna and forest trees for May 2002 (end of first growing season) to June 2003
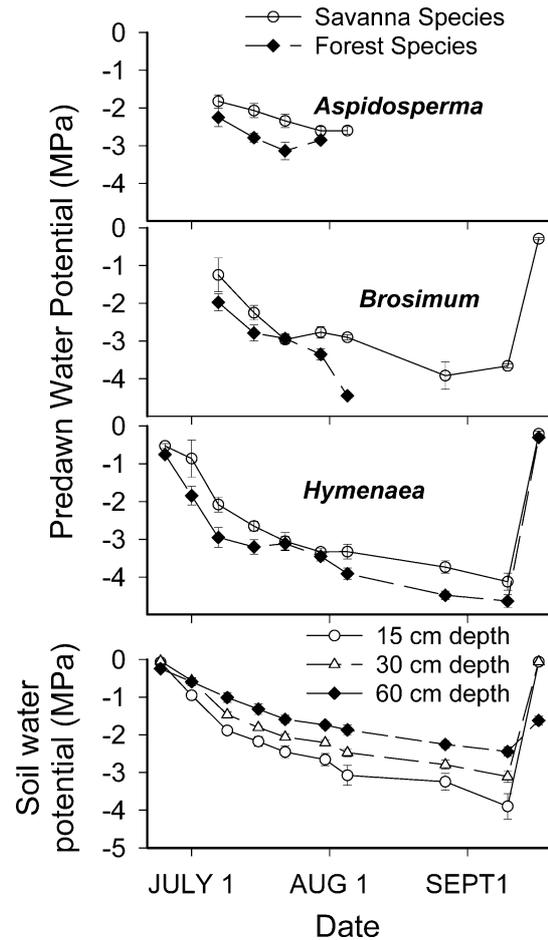

Fig. 3 Pre-dawn water potential of first-year seedlings of savanna and forest tree species and soil water potential during the dry season of 1999. All plots were irrigated frequently until 16 June to ensure survival until the beginning of the monitoring period. Water potentials were not obtainable for the latter part of the dry season both *Aspidosperma* spp. because these are deciduous and no longer retained leaves. No individuals of *Brosimum rubescens* survived beyond early August, so measurements were not possible after this date

seedling number between savanna and forest species. If we now define establishment success as the fraction of seeds producing seedlings that survive to the end of the *second* growing season, there was a significant Type × Cover interaction for both *Dalbergia* ($F_{2,90}$=20.10, P<0.001) and *Guapira* ($F_{2,90}$=8.90, P<0.001), and when tested over all three genera ($F_{2,4}$=10.63, P=0.03; data not shown).

Experiment 2. Dry season drought stress

Overall, savanna species maintained a higher predawn leaf water potential than forest species ($F_{1,2}$=39.40, P=0.02). This difference was significant in every one of the three genera (Fig. 3, F>10.5, P<0.003). Predawn water potential declined steadily during the dry season for all six species (Fig. 3, F>4.2, P<0.01), with a sharp increase at the onset of the wet season. There was a significant type × date interaction only for *Brosimum* ($F_{4,35}$=2.90, P=0.036). For the savanna species, the predawn water potential closely approximated soil water potential at 15 cm depth (Figs. 3 and 4; r^2=0.90). Among the forest species, predawn leaf water potential (ψ_L) was consistently lower than soil water potential at 15 cm (ψ_s) with the relationship being ψ_L=1.12ψ_s −0.48 (r^2=0.94).

Experiment 3. Root carbohydrate concentration

Coarse root TNC concentration was significantly higher in savanna species than in forest species for the evergreen genera *Brosimum*, *Guapira* and *Salacia*, but was higher in the forest species for the deciduous genus *Aspidosperma* (Fig. 5a). When tested over all genera, root TNC concentration was not significantly higher in savanna species than in forest species (29.6% vs 25%; P=0.06). However, among the six evergreen genera, savanna species had significantly greater TNC concentration (Fig. 5a; 25.7% vs 16.9%; P=0.003).

More important for resprout ability is total root nonstructural carbohydrate mass per shoot mass. Coarse roots of savanna species contained an average of 0.91 g of nonstructural carbohydrates per gram of shoot mass, while coarse roots of forest species contained 0.49 g (Fig. 5b; P=0.03). When the deciduous species are excluded, these values become 0.86 and 0.12 g, respectively (Fig. 5b;
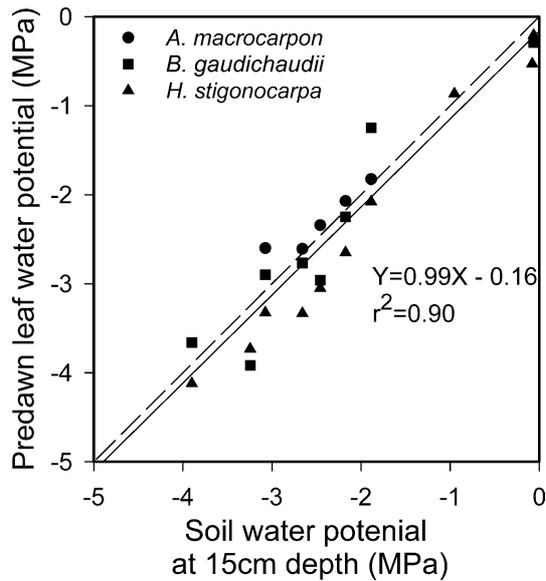
Fig. 4 Relationship between predawn leaf water potential of seedlings of three savanna species and soil water potential at 15 cm. The regression line (*solid line*) is nearly identical to a 1:1 relationship (*broken line*)

$P=0.004$), a seven-fold difference. For four savanna species and one deciduous forest species, the mass of nonstructural carbohydrates in coarse roots was greater than the total aboveground biomass.

The difference in root carbohydrates per shoot mass is largely explained by differences in root:shoot ratio. The ratio of coarse root biomass to shoot biomass is 2.67 for savanna species and 1.28 for forest species (Fig. 5c; $P=0.03$). When the deciduous species are excluded, the ratio of coarse root biomass to shoot biomass is 2.76 for savanna species and 0.66 for forest species ($P=0.009$), a four-fold difference.

Discussion

The results presented here point to clear differences in the seedling ecology of savanna and forest species. Savanna species establish poorly in the dense shade of forest, while forest species establish poorly in exposed sites. Subsequent mortality reinforced this differential establishment, further reducing the number of forest seedlings in open savanna and the number of savanna seedlings in forest.

The low success of savanna trees in forest is probably due to low shade tolerance. Additionally, at least some cerrado trees are intolerant of waterlogged soil (Joly and Crawford 1982), which would limit their success in poorly drained sites within gallery forests. And some cerrado species are intolerant of basic soils rich in calcium carbonate (Haridasan 1988), which would exclude them from deciduous dry forest on calcareous substrates, though such soils are not present at the study site.

The greater investment in root biomass by savanna species should also contribute to their greater establishment and survival in open sites, relative to forest species.
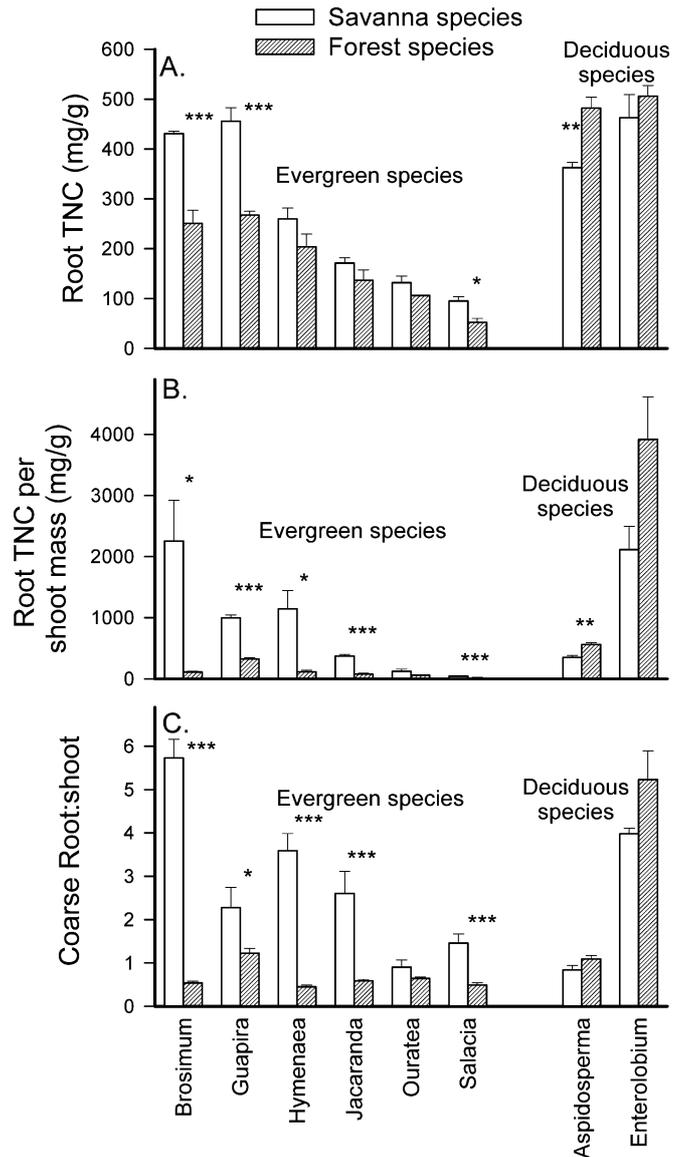

Fig. 5 Biomass allocation and coarse root total non-structural carbohydrate (TNC) content of savanna and forest woody plants 150 days following emergence ($n=3$, mean±SE)

During the rainy season, short rainless periods lasting 5–20 days are common, reducing germination and/or survival of newly germinated seedlings (Hoffmann 1996). Therefore, deep roots early in development should improve establishment in open sites where drying is most intense.

Later, during the dry season lasting several months, even deeper roots will be necessary to ensure survival. During this time, the higher root:shoot ratio of savanna species is manifested as higher predawn water potentials during the dry season (Fig. 3), which probably directly influences seedling survival. Relative to forest species, savanna species also have lower leaf area ratio (leaf area per plant mass; Hoffmann and Franco 2003) which should further improve plant water balance during the dry season.

Predawn water potential of the savanna species closely tracked soil water potentials at 15 cm depth (Fig. 4). If the

predawn seedling water potential was in equilibrium with the soil, then mean depth of fine roots should be approximately 15 cm. Forest species had even lower water potentials, indicating that the mean depth of fine roots was shallower than 15 cm. All three genera used in this experiment have rather large seeds, with seed mass ranging from 0.21 g for *A. subincanum* to 4.18 g for *H. courbaril* (Hoffmann and Franco 2003). Species with smaller seeds are likely to have shallower roots and lower pre-dawn water potentials than the species used here.

The deepest seedling roots of the savanna species undoubtedly reached depths greater than 15 cm, as Moreira and Klink (2000) found that root length of 150-day-old seedlings of seven savanna species ranged from 30 to 60 cm. In the present study, water potential at these depths reached values of −3.1 and −2.4 MPa, respectively, at the end of the dry season (Fig. 3). In contrast to seedlings, predawn leaf water potential of adult cerrado trees is typically −0.3 to −0.8 MPa (Meinzer et al. 1999; Franco 2002), with roots reaching as deep as 17 m (Rawitscher et al. 1943). Thus mechanisms to cope with the seasonal drought will be particularly important for seedlings, with adult plants being less constrained by water availability.

The greater root:shoot ratio of savanna trees also has important consequences for fire tolerance. Among evergreen genera, the higher root:shoot ratio and higher root TNC concentrations of savanna species (Fig. 5) provides them with seven times greater root nonstructural carbohydrate reserves per shoot biomass, relative to forest species. This should provide savanna species with greater ability to replace their aboveground biomass following burning, and corroborates observations that seedlings of savanna species are more tolerant of fire than forest species (Hoffmann 2000; Hoffmann and Moreira 2002). This difference in fire tolerance continues through maturity, as evergreen forest trees experience greater mortality rates than savanna trees (Hoffmann and Moreira 2002; Fensham et al. 2003). As adults there appears to be little difference in root TNC content of savanna (14.1%) and gallery forest trees [12.7%; Hoffmann et al. (2003)], with concentrations being approximately half of the values observed here for seedlings. As adults, however, savanna species retain a much higher ratio of belowground: aboveground biomass than forest species (Castro and Kauffman 1998), thus improving resprout capacity. Furthermore, savanna species have thicker bark than gallery forest species, (Hoffmann et al. 2003), providing better insulation against fire.

The two deciduous genera, *Aspidosperma* and *Enterolobium*, did not follow the same pattern as the six evergreen genera. For the two deciduous genera, the forest species tended to have greater root-shoot ratios and root TNC concentrations. Although both of these deciduous forest species can occur in gallery forests (Felfili et al. 2001), which are dominated by evergreen species, they are much more prominent in deciduous dry forests. These results may reflect adaptations to dry deciduous forest which, relative to evergreen forest, may be more fire-prone

and commonly subjected to greater drought stress because it commonly occurs in shallow soils over limestone. For these two species typical of relatively nutrient-rich soils, nutrient availability may limit success in savanna more than fire or water.

The results presented here indicate that forest species can establish in the cerrado savannas, but with lower success than exhibited by savanna species. While this lower establishment and survival may slow the rate of forest encroachment into savanna, it appears unable to cease it together. Other studies have also demonstrated that forest species can indeed establish in savanna (Bowman 1993; Bowman and Panton 1993; Hoffmann 1996).

Low nutrient availability will probably also limit the growth of forest species in savanna soils, thereby slowing the rate of forest advance. However, Hoffmann and Franco (2003) found that growth of forest species was not more sensitive than savanna species to nutrient availability. Nevertheless, biomass of forest is much greater than savanna, therefore succession to forest will require greater total nutrient stocks than what is available in typical cerrado sites (Haridasan 1992). In this case, succession to forest may require considerable time for sufficient atmospheric and biotic nutrient inputs.

Fire appears to be a much more absolute constraint to the expansion of forest than either water or nutrient availability. Humid savannas commonly burn at 2–3 year intervals, so seedlings must reach a fire-tolerance size quickly to establish under such conditions. Because of the much lower investment in belowground biomass and root TNC, evergreen forest species may often require more time than is available between successive fires. In fact, for three evergreen forest species from the cerrado region, at least 2 years are required to reach fire-tolerance (Hoffmann 2000), whereas 11 of 12 species of cerrado savanna species are able to survive fire when less than 1 year old (Oliveira and Silva 1993; Matos 1994; Franco et al. 1996; Hoffmann 2000; Andrade et al. 2001). In many tropical forests, some species are incapable of resprouting even as adults (Fensham et al. 2003; Gould et al. 2002; Kauffman 1991).

Due to the greater sensitivity of forest seedlings to fire, gallery forest expansion seems unlikely under frequent burns now typical of cerrado. When fire is excluded, gallery forest can invade nearby areas (Ratter 1992), though it is unclear how much time is required for these areas to become sufficiently dense to create the microclimatic conditions that greatly reduce the risk of fire propagation (Biddulph and Kellman 1998).

In conclusion, as predicted, there were clear difference in the ecology of savanna and forest species with forest species having lower root: shoot ratios, lower root nonstructural carbohydrate, lower predawn water potentials during the dry season, and lower seedling establishment and survival in savanna, relative to savanna species. Although water availability and microclimate may reduce the success of forest species in the cerrado savannas, these factors are unable to eliminate forest seedling establish-

ment entirely. Fire, on the other hand, appears to be a much more absolute constraint to success of forest species.

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