

Differences in growth patterns between co-occurring forest and savanna trees affect the forest–savanna boundary

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Summary

1. Patterns of growth, activity and renewal of stems and branches are primary determinants of ecosystem function and strongly influence net primary productivity, water and energy balance. Here we compare patterns of leaf phenology, stem radial growth and branch growth of co-occurring savanna and forest trees in the Cerrado region of central Brazil to gain insight into the influence of these parameters in forest–savanna boundary dynamics. We hypothesized that forest species would have higher radial growth rates but later leaf flush than savanna species.

2. We studied 12 congeneric species pairs, each containing one savanna species and one forest species. All individuals were growing in savanna conditions under full sun. We measured specific leaf area (SLA), light-saturated photosynthesis and monthly increments in stem circumference, branch length, leaf flush and leaf fall.

3. Relative to savanna species, forest species had 68% higher diameter growth rates, 38% higher SLA, and displayed a greater crown area for a given basal area. Across species, radial growth was positively correlated with SLA ($r^2 = 0.31$), but not with CO₂ assimilation.

4. Peak leaf production of savanna species was in the late dry season, 1 month earlier than for forest species, which suggests a strategy to avoid nutrient losses during leaf expansion due to herbivory or leaching. However, savanna and forest species did not differ in annual branch growth, number of leaves produced per branch, or in timing of leaf fall.

5. Radial growth was tightly coupled to monthly rainfall in forest species whereas the growth of savanna species ceased before the end of the wet season. The cessation of above-ground growth at a time of active photosynthesis may reflect a shift in allocation to roots and reserves.

6. These results contribute to recent studies showing that savanna and forest species represent different functional types and that despite the limiting resources in savanna environments, forest trees that invade the savanna tend to present higher growth rates and larger and denser crowns, which enhance shading and could promote changes in equilibrium of forest–savanna boundaries.

Key-words: cerrado, ecosystem dynamics, forest–savanna boundaries, leaf phenology, photosynthesis, specific leaf area

Introduction

Tropical savanna–forest boundaries represent the natural limit to the distribution of closed-canopy forest and therefore provide a perspective for understanding how the distribution of tropical forests will respond to changes in climate or disturbance regimes (Cole 1992). At the savanna–forest boundary, there exists a dynamic balance between forest

advance and its retreat in response to disturbances such as fire, herbivory and extreme drought events (Hopkins 1992, Woodward *et al.* 1995). Therefore, forest expansion onto the savanna will depend on the establishment rates of forest tree seedlings, growth rates of established trees, and the intensity and frequency of disturbance.

The tropical savanna–forest ecotone is characterized not only by a sharp transition in tree density, but also in species distributions (Bowman 2000), with few species being common to both environments (Adejuwon & Adesina 1992, Felfili &

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Silva Junior 1992). In the balance between forest advance and retreat, one can postulate that the success of forest tree species should play a more important role than the success of savanna trees. Establishment and growth of forest tree species within savanna might convert it to a forest, but the invasion of the forest by savanna trees would not substantially change the structure of the forest. Even if savanna species did successfully establish in the forest, their low stature, low canopy density and shade intolerance make it unlikely that they could competitively exclude forest species (Hoffmann *et al.* 2004).

In the absence of fire, it is uncertain whether communities composed entirely of savanna tree species can attain a forest physiognomy (Hoffmann *et al.* 2005a) or whether growth and crown development in savanna trees are so slow that, in the absence of fire, invasion by forest species would typically occur before complete canopy closure occurs in savanna sites. There is little comparative data on growth rates of forest and savanna species (Prior *et al.* 2004), however, the characteristics of savanna species suggest that above-ground growth rates may be inherently lower than those of forest species. Specifically, forest species invest a greater proportion of their biomass to stems and have higher leaf area ratios (total leaf area/plant mass) than savanna species, at least as seedlings (Hoffmann & Franco 2003). Specific leaf area (SLA) also tends to be higher among forest species for both seedlings (Hoffmann & Franco 2003) and adults (Hoffmann *et al.* 2005b). These traits should confer higher stem growth rates for forest species under typical growth conditions, as was found for savannas and forests in Australia (Prior *et al.* 2004), however this may not be true for forest trees invading savanna, where soil and water resources have been found to be limiting (Haridasan 1992).

Plant carbon balance and growth are intimately related to the patterns of leaf flush (LFL) and senescence (Reich 1995). In highly seasonal environments, such as savanna regions, there should be a strong selective pressure acting upon the timing of growth and leaf production to maximize survival and productivity (Meloche & Diggle 2001, Damascos *et al.* 2005). Low water availability can potentially limit leaf production due to insufficient cell turgor required for leaf expansion, but this appears not to be typical in humid savannas and evergreen forests, where leaf expansion is widespread before the first rains of the wet season (Wright & van Schaik 1994, Williams *et al.* 1997, Damascos *et al.* 2005, Franco *et al.* 2005). Instead, there is some evidence that LFL in these environments can be triggered by photoperiod (Stubblebine *et al.* 1978, Rivera *et al.* 2002, Williams *et al.* 2008), whereas the timing may be under selection by factors other than soil water availability. Various hypotheses exist to explain the evolution of leaf flushing in the dry season including the potential use of the higher light availability at the end of dry season (Wright 1996), prevention of leaching of nutrients during leaf development (Sarmiento *et al.* 1985) and herbivory avoidance during leaf development (Marquis *et al.* 2001, 2002).

These different hypotheses explaining dry-season LFL lead to contrasting predictions regarding the timing of leaf production in savanna and forest species. If early leaf production has arisen largely to make use of high light availability at the

end of the dry season, the advantage should be greatest for species of light-limited environments, such as those in forest. However, if loss of nutrients due to herbivory or leaching is the primary selective force, the advantage should be greatest for species of nutrient-limited environments, such as humid savannas.

To better understand how savanna and gallery forest trees species contribute to the dynamics of savanna–forest boundaries and whether any differences in growth patterns have evolved in response to their respective habitats of origin, we performed a comparative study of radial growth rates of 12 congeneric species pairs from different taxonomic families, each containing a savanna and a forest species. We hypothesized that forest species would exhibit higher growth rates than savanna species, even when both are growing in savanna environments, which should be associated with higher photosynthetic rates on a mass basis and higher SLA. We also studied the seasonal patterns of branch extension and leaf phenology to compare the timing of critical growth events in relation to rainfall seasonality. We expected that savanna trees would flush earlier than forest trees because the low nutrient availability in the savanna environment should select for earlier LFL as a strategy to avoid loss of nutrients caused by leaching and herbivory. All comparisons were performed on individuals growing in open savanna conditions. This was made possible by long-term fire suppression which allowed forest species to invade savanna environments at the study site.

Materials and methods

STUDY SITE

The study was carried out at the Ecological Reserve of IBGE (Instituto Brasileiro de Geografia e Estatística) near Brasília in the Federal District, Brazil, located at 15°56'41" S and 47°53'07" W and at an elevation of approximately 1100 m above sea level. The average annual rainfall recorded at the meteorological station of IBGE from 1993–2002 was 1462 mm, with a distinct dry season from May to September and a mean annual temperature of 22.5 °C. Rainfall records were obtained from the meteorological station of IBGE (Fig. 1a; www.recor.org.br), with total rainfall of 1460 mm during the period of July 2006 to May 2007. No rainfall was recorded from June to September 2007. This amount of rainfall is high compared to savannas in Africa (where most savannas receive < 1200 mm; Sankaran *et al.* 2005), but similar to some savanna sites in Australia (1710 mm; Prior *et al.* 2004). To rule out microhabitat differences in soil nutrient availability, a soil sample was collected from the surface layer (0–10 cm) in the immediate vicinity of three individuals of each species. No differences were found except for 44% higher Mn in soils under forest species (see Table S1 in Supporting Information).

METHODS

Twelve species pairs were selected based on availability at the study site (Table 1). Each pair consisted of one savanna species and one forest species of the same genus; no two genera were selected from the same family. Classification of the study species into forest or savanna groups was based on floristic lists of gallery forests (Silva-Júnior

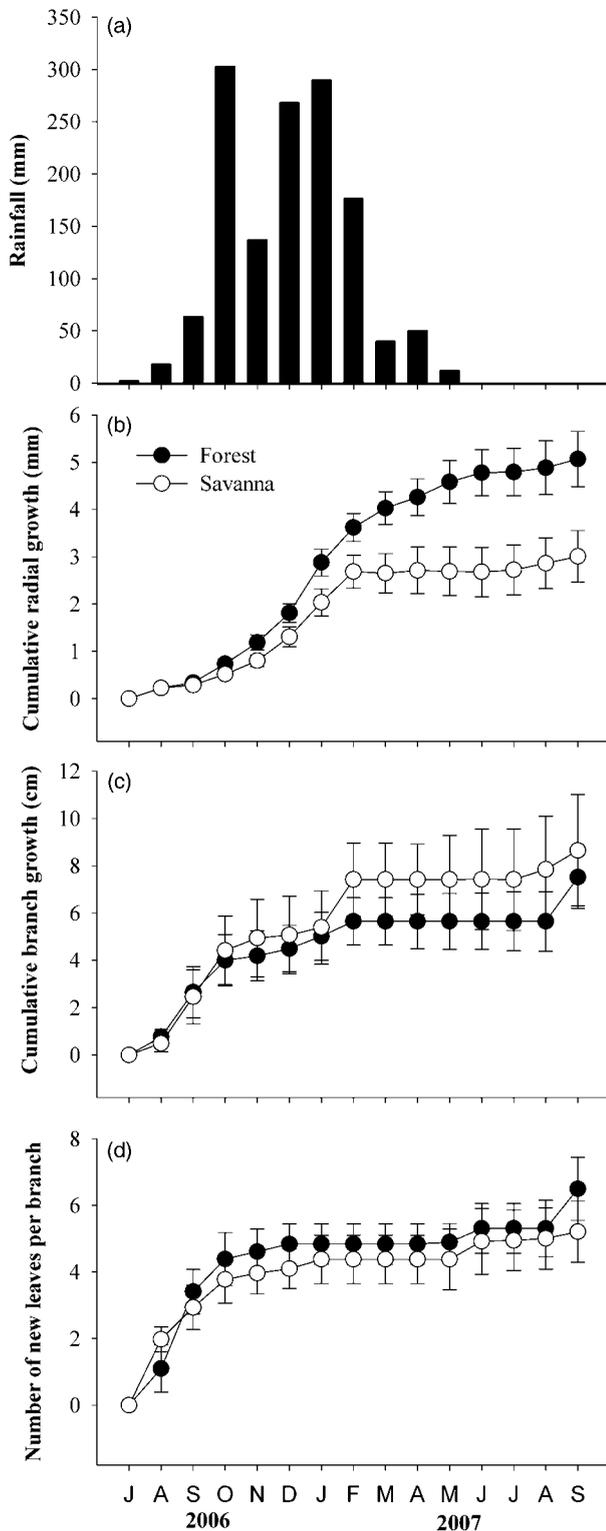


Fig. 1. (a) Seasonal changes in monthly rainfall during the study period; (b) Cumulative diameter growth for forest (full circles) and savanna (open circles) species from July 2006 to September 2007. Error bars represent standard errors based on variation among species means ($n = 12$ species for each plant functional type). Patterns of branch growth (c) and leaf production (d) for forest and savanna functional types during the study period (July 2006–September 2007). Error bars represent standard errors based on variation among species means ($n = 10$ species for each functional type).

et al. 1998) and savanna (Medonça *et al.* 1998). The use of congeneric species pairs from different families ensures phylogenetic independence by assuring that the divergence into savanna and forest species has occurred independently in each genus. Five individuals were sampled for each species with the exception of *Aegiphila sellowiana*, where only three individuals were available. We selected only individuals growing within the savanna environment. For most species these were naturally occurring individuals, except for *Hymenaea martiana* and *Tabebuia impetiginosa*; in this case we utilized individuals planted in savanna at least 20 years before, with no management at least for the past 15 years or longer. Although many of the individuals were large enough to be sexually mature, none were observed to flower during the study period. Savanna trees averaged 7.24 ± 0.50 cm in initial diameter and forest trees averaged 8.11 ± 0.56 cm, with both groups ranging between 5 and 11 cm. A factorial ANOVA indicated that stem diameter did not differ among genera ($F = 2.8410$; $P = 0.078$) or between savanna and forest species ($F = 1.9462$; $P = 0.1939$). However there was a genus \times plant-origin interaction ($F = 3.4373$; $P = 0.0001$).

Band dendrometers were used to measure monthly increments in stem circumference. The dendrometers were made manually with stainless steel tape and a stainless steel spring, as described by Cattellino *et al.* (1986). They were mounted at 30 cm from the ground, except where stem irregularities required installation slightly above or below this height. Dendrometers were installed 2 months before the initial measurements, in May 2006, to allow for stabilization. Measurements were performed approximately in the middle of the month from July 2006 (which was set as zero) to September 2007, always in the morning to avoid problems associated with daily fluctuations in stem diameter due to changes in plant water status. The measurements were taken with a digital caliper (Mitutoyo®) with a resolution of 0.01 mm. To convert circumference growth into diameter increments, all values were divided by π . The projected crown area of each individual was estimated in November 2008 from measurements of the major and minor axis by assuming the crown to be an ellipse. We also re-measured stem diameters of the trees at this time to compute the allometric relationship between basal area (calculated as the area of a circle) and crown area. To increase the range of variation in these two traits, we measured three additional individuals of each species.

Leaf production, leaf fall (LFA) and branch tip elongation were measured on the same trees fitted with dendrometers. The phenological data were not obtained for *Piptocarpha* and *Aegiphila*. We marked five terminal branches of each individual in the middle of the dry season (July 2006) prior to the flush of leaf production that typically occurs at the end of the dry season and beginning of the wet season. Branch elongation, leaf production, and LFA were assessed on these branches at the same monthly intervals utilized for measurements of diameter growth.

LFL and LFA at crown level were assessed with the Fournier Intensity Index (Fournier 1974). This method consist of monthly visual estimates of the percentage of the crown area of each individual that was flushing new leaves and the percent of the crown that was devoid of leaves, utilizing a scale of five categories: 0, 1, 2, 3 and 4. These categories were converted to percentage values; 0: 0%; 1: 1–25%, 2: 26–50%, 3: 51–75% and 4: 76–100%.

Maximum photosynthetic rates were measured in three different occasions during the rainy season (November 2006, January 2007 and March 2007) on the same congeneric pairs, with the exception of *Piptocarpha* and *Aegiphila*, which were not measured. Measurements were performed on the same individuals as before, with an open gas exchange system (LCA4–ADC, Hoddesdon, UK). We took

Table 1. Congeneric species pairs included in this study. Leaf phenology classification is based on Franco *et al.* (2005) and field observations (D = Deciduous; BD = Brevideciduous; E = Evergreen). Diameter (cm) is the average \pm (SE) initial diameter of studied trees

| Family | Forest Species | Phenology | Diameter | Savanna Species | Phenology | Diameter |
|-----------------|--|-----------|------------|---------------------------------------|-----------|------------|
| Lamiaceae | <i>Aegiphila sellowiana</i> Cham.* | D | 8.1 (0.5) | <i>A. lhotskiana</i> Cham.* | D | 7.7 (0.5) |
| Malpighiaceae | <i>Byrsonima laxiflora</i> Griseb. | E | 5.9 (0.2) | <i>B. crassa</i> Nied. | BD | 4.8 (0.4) |
| Nyctaginaceae | <i>Guapira areolata</i> (Heimerl) Lundell | BD | 5.1 (0.6) | <i>G. noxia</i> (Netto) Lundell | D | 6.6 (0.7) |
| Fabaceae | <i>Hymenaea martiana</i> Hayne | BD | 9.3 (0.9) | <i>H. stigonocarpa</i> Mart. ex Hayne | BD | 8.3 (0.9) |
| Melastomataceae | <i>Miconia cuspidata</i> Naudin | E | 7.1 (0.4) | <i>M. pohliana</i> Cogn. | E | 6.7 (0.4) |
| Myrtaceae | <i>Myrcia rostrata</i> DC. | E | 10.5 (0.6) | <i>M. tomentosa</i> (Aubl.) DC. | BD | 11.1 (0.5) |
| Myrsinaceae | <i>Myrsine ferruginea</i> (Ruiz & Pav.) Spreng | E | 7.5 (0.9) | <i>M. guianensis</i> (Aubl.) Kuntze | E | 6.2 (0.4) |
| Asteraceae | <i>Piptocarpha macropoda</i> (DC.) Baker* | E | 9.1 (0.6) | <i>P. rotundifolia</i> Baker* | BD | 8.1 (0.8) |
| Styracaceae | <i>Styrax pohlii</i> A.DC. | BD | 5.9 (0.5) | <i>S. ferrugineus</i> Nees & Mart. | BD | 6.4 (0.9) |
| Symplocaceae | <i>Symplocos mosenii</i> Brand | BD | 9.5 (0.6) | <i>S. rhamnifolia</i> A.D.C. | D | 9.0 (1.0) |
| Bignoniaceae | <i>Tabebuia impetiginosa</i> Standl. | D | 7.8 (1.0) | <i>T. ochracea</i> (Cham.) Standl. | D | 5.0 (0.8) |
| Vochysiaceae | <i>Vochysia tucanorum</i> Mart. | E | 11.6 (1.4) | <i>V. thyrsoidea</i> Pohl. | E | 7.0 (0.5) |

*Utilized only in radial growth study.

measurements on three leaves of each of five individuals per species during the period of 08:00 to 11:30 h. Light intensity of 1200–1300 $\mu\text{mol m}^{-2} \text{s}^{-1}$ was provided by a halogen light source. The assimilation values on a area basis were used to calculate assimilation on a mass basis (A_{mass}) (the product of SLA ($\text{m}^2 \text{kg}^{-1}$) and assimilation in area basis ($\mu\text{mol m}^{-2} \text{s}^{-1}$)).

We measured SLA of three fully-expanded leaves, without the petiole (or leaflets in the case of *Hymenaea* and *Tabebuia*), per individual in each of three different occasions during the rainy season (November 2006 and January and March of 2007). We also collected 5 leaves of each individual to measure the area of the leaf lamina in April 2008. For SLA and leaf area, each leaf was scanned on a flatbed scanner and its area determined using the free software Area (Caldas *et al.* 1992). To determine SLA, the leaf was then dried at 70 °C for three days and weighed.

STATISTICAL ANALYSIS

We used a factorial ANOVA to test for effects of genus and functional type (savanna vs. forest) on mean cumulative branch growth, mean number of leaves produced, leaf area, crown area and mean cumulative radial growth through September 2007. In this analysis, genus was designated as a random factor and functional type as a fixed factor to ensure that species, rather than individuals, were treated as the sampling unit. Linear regression was used to test for the relationships between annual diameter increment, CO_2 assimilation, and SLA. Linear regression was also used to test for the relationship between basal area and crown area and between monthly rainfall and monthly changes in stem diameter. Differences in slope and elevation between savanna and forest species were tested with the SMATR software (Warton *et al.* 2006). To compare how much of the overall interspecific variance of a trait can be attributed to differences among genera or to differences between functional types, we calculated the partial r^2 values for each trait. These were calculated from factorial ANOVAs, following Rosenthal & Rosnow (1985), where $r^2 = \text{SS}_{\text{factor}}/\text{SS}_{\text{total}}$; $\text{SS}_{\text{factor}}$ is the sum of squares for a factor (plant origin or genus) and SS_{total} is the total sum of squares.

We used ANCOVA to test for the influence of initial diameter on the diameter increment after controlling for species effects, and also to test if SLA or A_{mass} accounted for the observed differences in annual growth between savanna and forest species. To test whether Fournier intensity index of LFL and LFA occurred uniformly throughout the

year or in a specific period of the year, for both savanna and forest species, we applied the Rayleigh test (Zar 1999). In this analysis, the timing of the annual cycle is represented as angles of a circle, with January 1st corresponding to 0°, February 1st corresponding to 30°, etc. To test for differences between savanna and forest species in the mean dates of LFL and LFA, we applied the Watson–Williams test (Zar 1999) to data from July 2006 to June 2007, considered as the first annual cycle, and for data from March 2007 to February 2008, considered as a second annual cycle. Rainfall, mean temperature and photoperiod records were analysed in a multiple stepwise regression to examine their influence on leaf production and on the Fournier intensity index for crown flush. The data for SLA, radial growth, branch growth and number of new leaves per branch were \log_{10} -transformed to restore normality and the homogeneity of variances (Zar 1999). The software Oriana version 2.02b was used to analyse the phenological patterns and Statistica 99' edition (Statsoft 1999) was used for the other analysis.

Results

STEM GROWTH, SLA AND CO_2 ASSIMILATION

Cumulative radial growth of forest species was 68% greater than for savanna species under similar savanna conditions (Fig. 1b, 5.0 ± 0.45 vs. 3.0 ± 0.54 mm year^{-1} , mean \pm SE (average species value); $P < 0.01$). However, there was considerably more variation among genera within each group than between savanna and forest groups (Fig. 2a). Radial growth rates ranged between 2 and 9 mm year^{-1} among forest species and 1–7 mm year^{-1} among savanna species. The genera that had the highest growth rates for both groups were *Miconia*, *Myrcia*, *Piptocarpha* and *Vochysia*, all of which are evergreens, with the exception of *Myrcia tomentosa* which is brevideciduous.

Within species, there was no relationship between stem diameter and diameter increment (ANCOVA, $F = 0.66$, $P = 0.43$), so the higher growth rate of the forest trees cannot be explained by differences in initial diameter between functional groups.

When tested over all genera, forest trees had higher SLA than savanna trees (113.97 ± 4.89 vs. 82.43 ± 3.97 $\text{cm}^2 \text{g}^{-1}$,

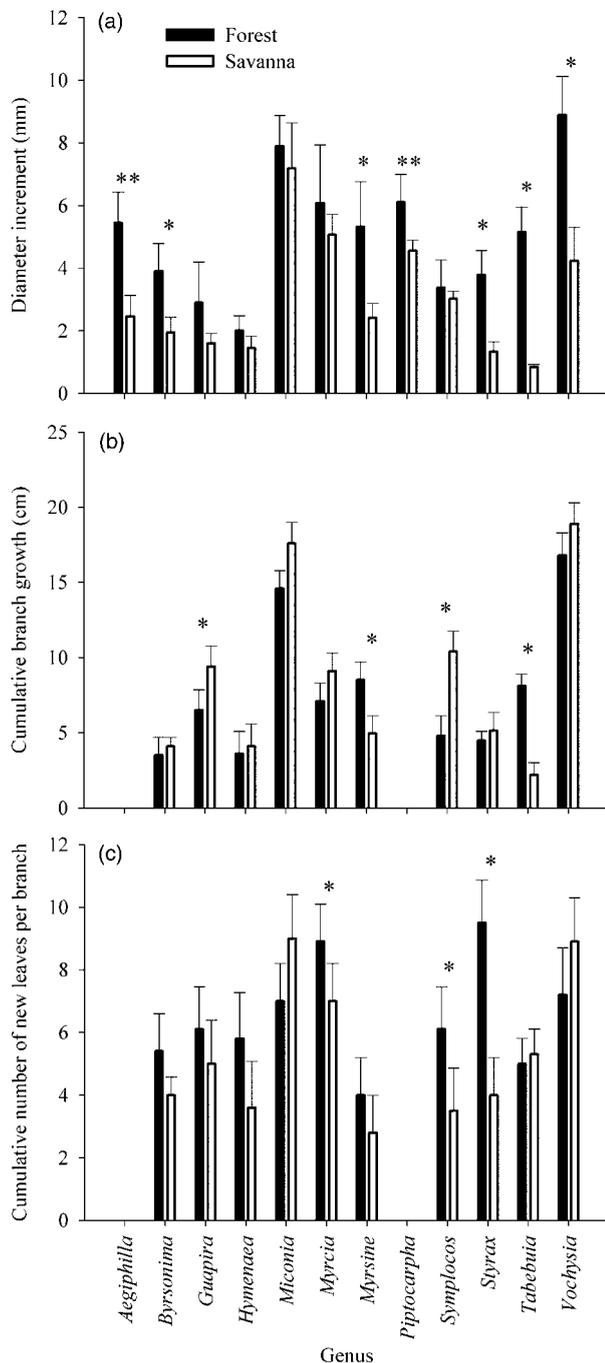


Fig. 2. (a) Mean annual diameter increment for individual species of the two functional types. Standard error bars are shown ($n = 5$, except for *A. sellowiana* where $n = 3$). (b) Mean cumulative branch growth for studied species. Standard error bars are shown ($n = 5$). (c) Mean number of new leaves per branch. Standard error bars are shown ($n = 5$). * $P < 0.05$, ** $P < 0.01$.

mean \pm SE; $P < 0.01$); and higher CO_2 assimilation on a mass basis (83.72 ± 4.94 vs. $70.15 \pm 4.50 \mu\text{mol kg}^{-1} \text{s}^{-1}$, mean \pm SE; $P = 0.044$). Annual diameter increment was significantly correlated with SLA across all species (Fig. 3; $r^2 = 0.31$, $P = 0.009$), but was not correlated with mean CO_2 assimilation on a leaf mass basis (A_{mass} ; $r^2 = 0.04$, $P = 0.356$), nor with CO_2

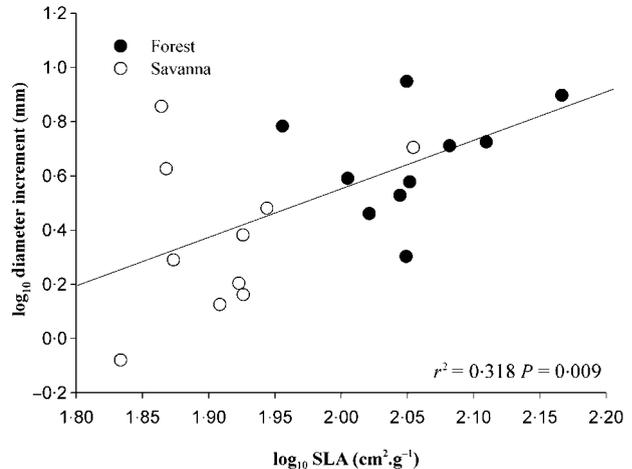


Fig. 3. Relationship between diameter increment (DI) and specific leaf area (SLA). Full circles represent forest species and open circles savanna species. Equation: $\text{DI} = 1.86 + 0.17 \text{ SLA}$, $r^2 = 0.318$, $P = 0.009$. Relationship was obtained with \log_{10} transformed values. SLA effects were still significant after ANCOVA analysis ($F = 17.57$, $P = 0.00$).

assimilation on a leaf area basis (see Fig. S1, Supporting information). However, the relationship between SLA and diameter increment was not significant when tested among only forest species ($r^2 = 0.131$, $P = 0.29$) or only savanna species ($r^2 = 0.04$, $P = 0.54$). Despite this weak relationship between SLA and annual diameter increment, when diameter growth was analysed with SLA as a covariate in an ANCOVA, there was no difference between functional groups ($F = 0.59$, $P = 0.45$), while SLA continued to have a significant effect on diameter increment ($F = 17.57$, $P < 0.01$). Differences between functional groups remained ($F = 9.72$, $P = 0.008$), when A_{mass} was used as a covariate.

Monthly diameter increments exhibited strong seasonality, with stem expansion starting at end of the dry season (August–September), and continuing until February in savanna trees and as late as June in forest species (Fig. 1b). Monthly diameter increment was positively correlated to rainfall (Fig. 4) both for forest ($r^2 = 0.74$, $P = 0.001$) and savanna species ($r^2 = 0.56$, $P = 0.0012$). The two groups shared statistically similar slopes, but differed statistically in their elevations (Fig. 4). Monthly temperature and day-length were not correlated with diameter increment ($r^2 < 0.05$, $P > 0.20$).

SEASONAL PATTERNS IN LEAF PHENOLOGY AND BRANCH ELONGATION

The two functional groups differed in timing of LFL but not in LFA; patterns of leaf phenology for these groups in the 2 years of study (2006–2007 and 2007–2008) are depicted in Fig. 5. In the first year, the Fournier intensity index for forest trees was not uniformly distributed throughout the year for LFL ($z = 60.76$; $P < 0.01$) and LFA ($z = 21.08$; $P < 0.01$), indicating that these phenomena occur in a specific period of the year. This was also the case for savanna trees, both in

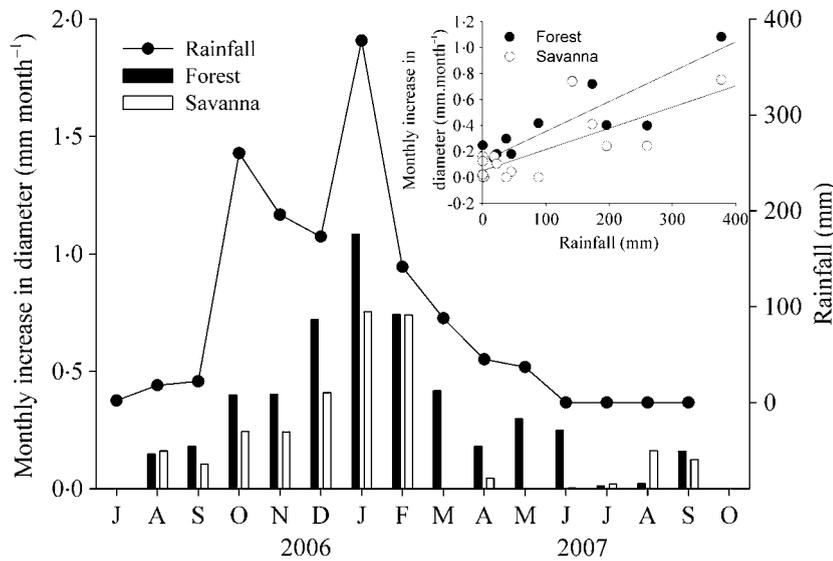


Fig. 4. Monthly diameter increment and rainfall during the study period. Bars indicate mean growth rates for forest species (black) and savanna species (white). Equation for forest: $Y = 0.1261 + 0.0023x$, $r^2 = 0.7427$, $P = 0.0001$. Equation for savanna: $Y = 0.0528 + 0.0016x$, $r^2 = 0.5665$, $P = 0.0012$. The slopes of the regression lines were not statistically different, but the intercepts differed statistically (Wald Statistic = 4.054, $P = 0.044$).

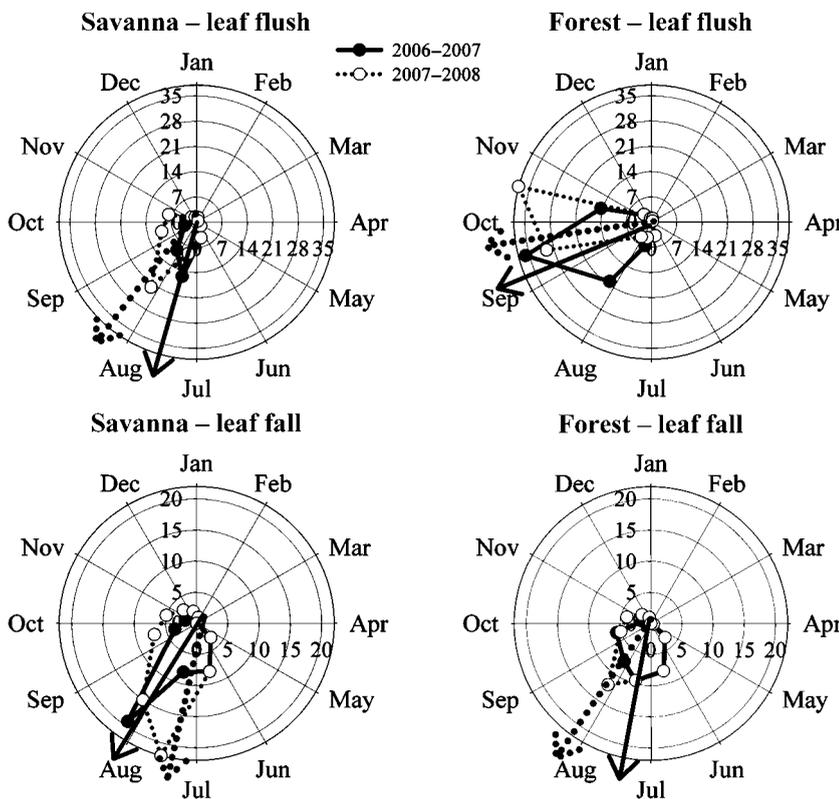


Fig. 5. Patterns of leaf flush and leaf fall for the two functional types. Arrows represent the mean angle for phenological patterns; the solid arrows represent the period of July 2006 to June 2007 and the dotted arrows represent the period of March 2007 to February 2008.

terms of LFL ($z = 22.13$; $P < 0.01$) and LFA ($z = 25.47$; $P < 0.01$). Mean angle for LFL in forest species was 248° , which corresponds to the end of the dry season (September), and for LFA was 199° (middle of July), while mean angle for LFA for savanna trees was 202° (the end of July) and for LFL was 210° (August). Although mean angles of LFL differed between forest and savanna species ($F = 26.01$; $P < 0.01$), the mean angle for LFA did not ($F = 0.07$; $P = 0.78$).

Similar patterns were observed in the second year of study. LFL and LFA were not uniformly distributed throughout the year, for forest ($z = 59.97$, $P < 0.01$ for LFL and $z = 31.43$,

$P < 0.01$ for LFA) or savanna ($z = 46.06$, $P < 0.01$ for LFL and $z = 45.92$, $P < 0.01$ for LFA) trees. As in the first year of study, LFL occurred earlier in savanna species than in forest species ($F = 20.76$, $P < 0.01$), but there was no difference in LFA ($F = 0.049$, $P = 0.89$).

The majority of forest and savanna species followed a similar pattern of branch growth, beginning at end of the dry season with almost no growth in the late wet season and most of the dry season (Fig. 1c). In fact, by December, branch elongation continued in only a few species, all evergreens (*Myrsine guianensis*, *Myrsine ferruginea* and *Miconia cuspidata*).

The average cumulative branch growth was statistically similar between forest (7.52 ± 1.29 cm) and savanna (8.65 ± 1.32 cm) species ($P = 0.20$), with both species within a genus usually having similar values (Fig. 2b). Branch elongation was not correlated to monthly rainfall, mean monthly temperature or day-length for either group ($r^2 < 0.05$, $P > 0.20$).

Production of new leaves in the marked branches was concentrated in the late dry season, simultaneously with branch elongation (Fig. 1d). New leaves in most savanna and forest species were first observed in August 2006 and the production of new leaves extended for a period of 1–2 months; only the evergreens *Miconia* and *Myrsine* continued producing new leaves throughout the rainy season (data not shown). Mean cumulative leaf production per branch was similar between the two functional groups ($P = 0.61$), with a mean of $5.31 (\pm 0.74)$ newly produced leaves per branch in forest and $4.92 (\pm 0.98)$ in savanna species. The production of new leaves was quite variable among genera ($P < 0.05$). The evergreen *Vochysia* and *Miconia* produced the greatest numbers of new leaves per branch while *Hymenaea* and *Styrax* produced the fewest (Fig. 2c). In general, leaf production per branch was not correlated with day-length, mean monthly temperature or monthly precipitation for forest or savanna species ($P > 0.20$, see Table S2). The Fournier index for crown flushing was correlated with photoperiod only for savanna species ($r^2 = 0.51$, $F = 12.75$, $P = 0.005$) (see Table S3). There were no differences ($P = 0.19$) in the area of the leaf lamina (Fig. S2) between forest (52.79 ± 4.46 cm²) and savanna trees (64.43 ± 4.12 cm²), nor among genera ($P = 0.33$).

VARIANCE EXPLAINED BY PHYLOGENY AND GENUS

For most variables, more of the overall interspecific variance was explained by differences among genera than by differences between savanna and forest species (Table 2). However, for SLA and CO₂ assimilation on a mass basis, species type, rather than genus, accounted for more of the total variance.

BASAL AREA IN RELATION TO CROWN AREA

On a log₁₀ basis, basal area was tightly correlated with crown area for both forest and savanna species (Fig. 6). In contrast to the similarity between the slopes, the intercepts were significantly different between the two functional groups (Wald Statistic = 36.034, $P = 0.000$). Thus, forest species displayed a greater crown area for a given basal area.

Discussion

It has been suggested that low nutrient availability of savanna soils (Goodland & Pollard 1973; Haridasan 1992) may limit the growth rates of forest species in savanna. Contrary to these predictions, forest trees, when growing in savanna conditions, exhibited higher radial growth rates than their savanna congeners, which suggests that soil resources alone are not an impediment to the expansion of forest trees into the savanna. The recruitment of these forest species in savanna,

Table 2. Significance values (P) and fraction of total interspecific variance (r^2) that is explained by phylogeny (genus) and by functional type. The r^2 values were calculated from ANOVA sums of squares as explained in Methods. All traits were log₁₀-transformed before analyses

| Trait | P genus | P type | r^2 genus | r^2 type |
|-------------------|-----------|----------|-------------|------------|
| Radial growth | 0.001 | 0.000 | 0.67 | 0.23 |
| Branch growth | 0.031 | 0.527 | 0.26 | 0.01 |
| Leaf production | 0.110 | 0.637 | 0.40 | 0.01 |
| Leaf area | 0.190 | 0.332 | 0.19 | 0.01 |
| Crown area | 0.089 | 0.008 | 0.43 | 0.18 |
| SLA | 0.953 | 0.004 | 0.02 | 0.42 |
| A_{mass} | 0.914 | 0.044 | 0.17 | 0.19 |

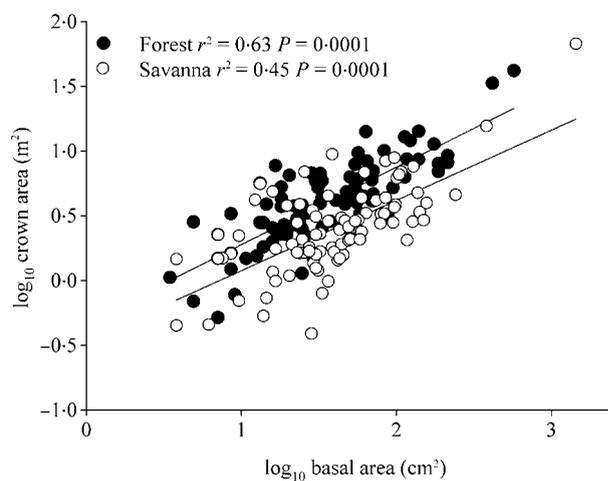


Fig. 6. Allometric relationship between basal area and crown area. Full circles represent forest species and open circles savanna species. Equation for forest: $Y = -0.32 + 0.59x$, $r^2 = 0.6379$, $P = 0.0001$. Equation for savanna: $Y = -0.4641 + 0.54x$, $r^2 = 0.4545$, $P = 0.0001$. Relationship was obtained with log₁₀ transformed values. The scaling exponents did not differ statistically between the two groups, but the elevations were statistically different (Wald Statistic = 36.034 $P = 0.000$).

however, is dependent upon fire suppression (Hoffmann *et al.* 2009), indicating that fire represents a more absolute constraint to the expansion of forest than does water or nutrient availability in savannas of central Brazil.

Our results suggest that savanna and forest species play fundamentally different roles in tree-grass dynamics in the absence of fire. The higher rates of radial growth exhibited by forest species should contribute to a more rapid development of a densely shaded environment at savanna–forest boundaries, a situation that can generate a microclimate that reduces flammability and promotes establishment of more forest seedlings. Tree cover reduces grass production and consequently promotes a less flammable environment (Hennenberg *et al.* 2006). Moreover, forest species have a greater crown area for a given basal area (Fig. 6) and denser crowns (Hoffmann *et al.* 2005a), further enhancing the rate of canopy closure and change in microclimate.

While forest species, as a group, may contribute to more rapid and more complete canopy closure, there is important variation in growth traits within each functional type. In fact, phylogeny (i.e. genus) accounted for more of the interspecific variation in radial growth rates than did functional type (Table 2). The difference in radial growth between savanna and forest species was strongly significant in some genera, such as *Vochysia*, *Piptocarpha* and *Aegiphila*, but not for others, such as *Miconia*, *Hymenaea* and *Guapira*. This suggests that the rate of forest expansion could strongly depend on the local pool of forest species available to establish in the adjacent savanna in the absence of fire. In fact, the rate of forest expansion can be facilitated or enhanced by particular species. At a savanna–forest boundary in Africa, *Anogeissus leiocarpus* Guill. & Perr., a forest tree species, is capable of establishing in savanna habitats and, due to its rapid growth in stem diameter, it promotes canopy closure and facilitates establishment of other forest seedlings (Hennenberg *et al.* 2005).

Forest species exhibit not only higher radial growth rates, but also higher values of A_{mass} and SLA (Fig. 3) and higher concentrations leaf N and P (Hoffmann *et al.* 2005b) than their savanna congeners. This is noteworthy because SLA is recognized to be correlated with a spectrum of traits, including growth, rate of resource extraction (Reich *et al.* 2003), and leaf nutrient concentrations (Reich *et al.* 1999). Savanna and forest trees thus appear to occupy different positions along this universal axis of plant traits, with SLA serving as a useful surrogate for these other traits. In fact there were no significant differences in radial growth or A_{mass} between savanna and forest species once SLA was taken into account with analysis of covariance. In contrast to the other traits studied here, much more of the overall interspecific variance in SLA could be attributed to differences between functional types than to phylogeny (Table 2). This convergence within each functional type suggests that SLA has been subjected to different selective pressures in the savanna and forest environments. SLA is under selection by multiple environmental factors, including light, water, and nutrients (Chapin *et al.* 1993), all of which differ between savanna and forest environments.

Although the savanna trees are shade-intolerant, they differ fundamentally from shade-intolerant species of forest environments. Savanna species have slow growth and low SLA, in contrast to high growth rates and high SLA of shade-intolerant species from moist forests. These contrasting patterns may arise because dry environments may impose fundamentally different tradeoffs and constraints than do moist forests (Poorter 2008). Specifically, shade-intolerant species of moist forests are generally pioneers, which depend on high growth rates to exploit an ephemeral high-light environment, while savanna trees grow in a lasting high-light environment that requires a strategy of persistence under frequent damage by fire (Bond & Midgley 2000). The allocation to storage presumably has a cost of reduced growth (Bond & Midgley 2000), making savanna trees unsuited for exploiting short-lived gaps in forest. Interestingly, however, the narrow crowns of savanna species are consistent with the characteristics of shade-intolerant species from forest (Poorter *et al.* 2006). In both cases this

may reflect a strategy of greater investment in height growth at the expense of reduced crown expansion. The factors that select for maximization of height growth, however, are probably not the same in these two environments; among forest pioneers, growth in height should be particularly important for overtopping competing vegetation (Poorter *et al.* 2006), while for savanna trees, height reduces fire damage to the canopy (Archibald & Bond 2003).

Radial growth in both functional types exhibited strong seasonality. However, radial growth was more tightly correlated to monthly rainfall in forest species than in savanna species. The weaker relationship was observed for savanna species because growth declined dramatically prior to the end of the wet season, when water was still abundant. The lack of stem growth and leaf production at a time of year with a full canopy of actively-photosynthesizing leaves suggests that assimilate was being diverted to carbohydrate stores and/or root growth. Overall, savanna tree species invest more assimilate to roots and reserves (Castro & Kauffman 1998; Paulilo & Felipe 1998; Hoffmann & Franco 2003; Franco 2004), allowing savanna species to buffer the effects of seasonal changes in water availability (Franco *et al.* 2005) and to resprout after fire (Hoffmann & Moreira 2002, Hoffmann *et al.* 2003). If the decline in stem growth results from a shift in allocation then this could rather explain the counter-intuitive result of stem growth of forest species continued longer into the dry season. The less extensive root system of forest species, while presumably reducing access to deep soils would represent a smaller sink of assimilates.

In contrast, neither branch elongation nor leaf production per branch was correlated to day-length, mean monthly temperature or monthly precipitation for forest or savanna species. In all species, branches started elongating and producing new leaves at the end of the dry season, but for some species, these processes continued until 2 or 3 months into the wet season. Phylogeny explained substantially more of the interspecific variation in total branch growth and number of leaves produced per branch than did functional type, providing no evidence that savanna and forest environments impose different selective pressures on these two traits.

Patterns of LFA were also similar between the two functional types. The peak in LFA occurred in the middle of the dry season, as commonly found among trees in these Brazilian savannas (Franco *et al.* 2005; Lenza & Klink 2006), in the Australian savannas (Prior *et al.* 2004) and forests of dry regions (Rojas-Jiménez *et al.* 2007). This pattern suggests that water availability represents a substantial constraint to leaf display, for example, adjustments in leaf area in response to seasonal availability of soil water and the evaporative demand of the atmosphere (Goldstein *et al.* 2008).

The timing of LFL differed between the two functional types. Although both functional types flushed new leaves during the dry season, peak leaf production of savanna species was 1 month earlier than for forest species. Branch elongation and leaf flushing at the end of the dry season has been described as a strategy to take advantage of the high light availability characteristic of this time of the year (Wright

1996, Eamus 1999) and probably enhances leaf carbon uptake because the trees can quickly achieve full crown development and maximal carbon gain when the rainy season starts (Franco *et al.* 2005). This explanation does not appear compatible with the later flushing among forest species, which presumably evolved under more light-limited environments. In contrast, arguments involving strategies for conserving resources may better explain differences in the timing of leaf production between savanna and forest species. Species from low-nutrient environments such as the cerrado savannas should be under stronger natural selection to produce leaves well before the first rains, which can leach substantial amounts of nutrients from immature leaves (Sarmiento *et al.* 1985). Similarly, low-nutrient environments tend to select more strongly for strategies that protect tissues from herbivory (Coley *et al.* 1985). Dry-season LFL should reduce leaf damage by herbivores, as the most vulnerable stage of development (the new leaf stage) has already passed by the time the herbivorous insect activity begins (Marquis *et al.* 2002). This strategy may depend on stronger regulation of water balance in savanna trees, which is made possible with a deeper root system. This could allow whole-plant rehydration and leaf flushing earlier in the dry season, while flushing of forest species would be more affected by rainfall seasonality. Although we provide some evidence, detailed studies of seasonal changes in plant water balance and growth of congeneric cerrado and forest trees coupled with studies of root distribution are necessary to better elucidate the mechanisms that allows an earlier LFL in cerrado trees.

In contrast, loss of nutrients due to herbivory or leaching may not be a strong selective factor to forest trees when growing in their natural environment. Although the savanna and forest species studied here were all growing in similar nutrient-poor soils, forest species generally grow in soils with higher content of nutrients than savanna soils (Haridasan 1998, Silva *et al.* 2008), and their phenology is likely to have evolved under this higher nutrient availability.

Conclusions

When growing under similar environmental conditions, radial growth rates of forest species were greater than for savanna species, which could be related to allocation, carbon assimilation, or leaf architecture and density. The combined effect of higher growth rates and larger and denser crowns under savanna conditions implies that under fire suppression, forest trees should contribute to a more rapid canopy closure and exclusion of grasses. Although the timing of LFL was similar between forest and savanna trees, the peak of LFL occurred approximately 1 month earlier in the dry season among savanna species, relative to forest congeners. Leaf expansion before the rains should minimize resource loss from expanding leaves due to herbivory or leaching. Thus, herbivory and leaching of leaf nutrients are probably more important than water or light availability as selective pressures acting upon the timing of growth and leaf production for humid savanna species in central Brazil.

Acknowledgements

The authors would like to thank Mundayatan Haridasan and Sybil Gotsch for critical review of this manuscript, Lucas C.R. Silva for soil analysis, Lourens Poorter, Elmar Veenedaal and an anonymous referee for helpful suggestions. This research is based upon work supported by the National Science Foundation Grant No. DEB-0542912, AW Mellon Foundation, CNPq and CAPES.

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Received 25 August 2008; accepted 9 March 2009

Handling Editor: Lourens Poorter

Supporting Information

Additional Supporting Information may be found in the online version of this article:

Fig. S1. Relationship between diameter increment and CO₂ assimilation on an area basis.

Fig. S2. Mean values of leaf area for forest and savanna types.

Table S1. Soil analysis

Table S2. Multiple regression of branch leaf production

Table S3. Multiple regression of Fournier crown index

Table S4. Mean values of radial growth for congeneric species pairs

Table S5. Mean values of branch growth for congeneric species pairs

Table S6. Mean values of leaf production for congeneric species pairs

Table S7. Mean values of specific leaf area for congeneric species pairs

Table S8. Mean values of CO₂ assimilation on a mass basis for congeneric species pairs

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