

William A. Hoffmann · Edson Rangel da Silva Jr
Gustavo C. Machado · Sandra J. Bucci
Fabian G. Scholz · Guillermo Goldstein
Frederick C. Meinzer

Seasonal leaf dynamics across a tree density gradient in a Brazilian savanna

Received: 11 November 2004 / Accepted: 7 April 2005 / Published online: 18 June 2005
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Abstract Interactions between trees and grasses that influence leaf area index (LAI) have important consequences for savanna ecosystem processes through their controls on water, carbon, and energy fluxes as well as fire regimes. We measured LAI, of the groundlayer (herbaceous and woody plants < 1-m tall) and shrub and tree layer (woody plants > 1-m tall), in the Brazilian cerrado over a range of tree densities from open shrub savanna to closed woodland through the annual cycle. During the dry season, soil water potential was strongly and positively correlated with grass LAI, and less strongly with tree and shrub LAI. By the end of the dry

season, LAI of grasses, groundlayer dicots and trees declined to 28, 60, and 68% of mean wet-season values, respectively. We compared the data to remotely sensed vegetation indices, finding that field measurements were more strongly correlated to the enhanced vegetation index (EVI, $r^2 = 0.71$) than to the normalized difference vegetation index (NDVI, $r^2 = 0.49$). Although the latter has been more widely used in quantifying leaf dynamics of tropical savannas, EVI appears better suited for this purpose. Our ground-based measurements demonstrate that groundlayer LAI declines with increasing tree density across sites, with savanna grasses being excluded at a tree LAI of approximately 3.3. LAI averaged 4.2 in nearby gallery (riparian) forest, so savanna grasses were absent, thereby greatly reducing fire risk and permitting survival of fire-sensitive forest tree species. Although edaphic conditions may partly explain the larger tree LAI of forests, relative to savanna, biological differences between savanna and forest tree species play an important role. Overall, forest tree species had 48% greater LAI than congeneric savanna trees under similar growing conditions. Savanna and forest species play distinct roles in the structure and dynamics of savanna–forest boundaries, contributing to the differences in fire regimes, microclimate, and nutrient cycling between savanna and forest ecosystems.

Communicated by Jim Ehleringer

W. A. Hoffmann (✉)
Department of Botany, North Carolina State University,
Campus Box 7612, Raleigh, NC 28695-7612, USA
E-mail: william_hoffmann@ncsu.edu
Tel.: +1-919-5137668
Fax: +1-919-5153436

E. R. da Silva Jr · G. C. Machado
Departamento de Engenharia Florestal,
Universidade de Brasília,
Caixa Postal 04357, Brasília, DF 70919-970, Brazil

Present address: E. R. da Silva Jr
Instituto Brasileiro do Meio Ambiente e dos Recursos Naturais
Renováveis (IBAMA) SCEN trecho 02 – LPF,
Ed.sede Brasília, DF, Brazil

S. J. Bucci · G. Goldstein
Department of Biology, University of Miami,
Coral Gables, Florida 33124, USA

F. G. Scholz · G. Goldstein
Laboratorio de Ecología Funcional,
Departamento de Ciencias Biológicas,
Facultad de Ciencias Exactas y Naturales,
Universidad de Buenos Aires, Ciudad Universitaria,
Nuñez, Buenos Aires, Argentina

F. C. Meinzer
USDA Forest Service, Forestry Sciences Laboratory,
3200 SW Jefferson Way, Corvallis, OR 97331, USA

Keywords Cerrado · Leaf area index · Phenology ·
Tropical forest · Water potential

Introduction

Leaves are the primary site for the exchange of water, carbon, and energy between terrestrial vegetation and the atmosphere. Therefore, leaf area index (LAI) is a primary determinant of ecosystem function and governs net primary productivity, water balance, and energy balance (Bonan 2002; Asner et al. 2003). Soils and

climate exert strong controls on LAI, but understanding these controls is made difficult by spatial and temporal changes in species and life-form composition.

The role of species composition in modulating environmental controls on LAI should be particularly important in tropical savannas, characterized by a continuous grass layer interspersed with trees. Trees and grasses differ greatly in rooting depth, and consequently in leaf phenology, so the relative abundance of deep-rooted trees versus shallow-rooted grasses will largely determine seasonality in LAI. Furthermore, the groundlayer comprises a diversity of growth forms in addition to graminoids, including herbaceous dicots, subshrubs and juvenile shrubs and trees. Despite their low stature, these groundlayer dicots can have deep roots (Rizzini and Heringer 1961; Moreira and Klink 2000), which might permit them to maintain leaf area during the dry season, though there appears to be little information about the phenology of this component.

Interactions between trees and grasses are likely to influence leaf dynamics in ways not expected based on simple mixing of species of different phenological patterns. Trees can have negative effects on grasses through competition for light, nutrients, and water (Belsky 1994; Le Roux et al. 1995; Ludwig et al. 2004), but can also have positive effects by increasing resource levels or ameliorating environmental stresses. During the dry season, hydraulic lift, i.e., passive transport of water from deep soil layers to shallow layers, can increase water availability for herbaceous plants (Scholz et al. 2002; Ludwig et al. 2003; Moreira et al. 2003). Shading reduces light availability for grasses, but ameliorates soil and air temperatures, thereby reducing grass water stress and soil water loss. Furthermore, soil beneath savanna trees is often enriched, due to greater deposition of organic matter (Kellman 1979; Weltzin and Coughenour 1990; Isichei and Muoghalu 1992; Mordelet et al. 1993; Hibbard et al. 2001). The relative strength of the various positive and negative effects of trees on grasses is quite variable (Mordelet and Menaut 1995), and is likely to depend on tree density (Scholes and Archer 1997) and season. In the dry season, when grasses are strongly limited by water availability, positive effects of shading and hydraulic lift should be more important, so seasonality in groundlayer LAI might be lower where tree density is greater.

Interactions between trees and grasses also play an important role in savanna–forest dynamics. Because of the presence of grasses, savanna vegetation is very flammable, whereas, evergreen forest is not typically flammable due to the dense canopy that excludes grasses and maintains a more humid understory (Uhl and Kauffman 1990). Therefore, most savanna fires do not penetrate far into undisturbed evergreen forest (Kellman and Meave 1997; Biddulph and Kellman 1998). Edaphic conditions are often considered responsible for this difference in tree canopy cover between savanna and forests. Indeed, there is often an association between soil resources and savanna/forest boundaries, though in

many cases the association is weak or altogether non-existent (Furley 1992; Haridasan 1992; Schwartz et al. 1996; Bowman 2000; Fölster et al. 2001).

An alternative hypothesis is that savanna tree species, even when occurring in high density, are unable to develop sufficiently high LAI to exclude savanna grasses through shading. Shade intolerant species often have low LAI (Mourelle et al. 2001; Sterck et al. 2001; Reich et al. 2003), perhaps because shade tolerance is necessary for maintaining positive leaf carbon balance under the intense self-shading occurring with high LAI. Therefore, the maximum LAI attained by savanna species may be limited by their shade intolerance. Maximum LAI may be further limited by the tortuous architecture and irregular branching pattern typical of savanna trees, which should reduce their ability to efficiently display leaves in a way that maximizes light interception.

It is within this context that we examined the spatial and temporal variation in LAI in Cerrado savannas of Brazil. We quantified seasonal variation in leaf area index across a range of tree cover in cerrado savanna. We hypothesized that (1) grass LAI will be more strongly seasonal than tree LAI, (2) grass LAI is negatively correlated with tree LAI, but the seasonal variation in grass LAI is lower in sites with high tree density, and (3) forest tree species develop higher LAI than savanna tree species under similar growing conditions. To test these hypotheses, we quantify the annual cycle in LAI of the woody and herbaceous species across a range of trees densities. Additionally, we compare the LAI of savanna and forest species using phylogenetically independent contrasts based on congeneric species pairs.

Study site

Tree density in the Cerrado region is heterogeneous, with savanna vegetation ranging from open grassland (campo limpo), through a gradient of increasing tree density (campo sujo, campo cerrado, cerrado *sensu stricto*, and cerrado denso) to nearly closed-canopy woodland (cerradão). Across these savanna physiognomies, tree density is somewhat correlated with soil nutrient status (Goodland and Ferri 1979), though it is more strongly associated with topography, with denser formations occurring on deep, well-drained soils of the uplands and more open formations typically occurring on shallow or coarse soils. Evergreen gallery forest occurs along rivers, while evergreen, semideciduous, and deciduous forests occur locally on upland sites.

Data were collected at the Ecological Reserve of IBGE (Instituto Brasileiro de Geografia e Estatística) located near Brasília in the Federal District, Brazil at an elevation of approximately 1,100 m. Mean annual rainfall at the meteorological station in IBGE was 1,426 mm for 1993–2002, with a distinct dry season from May to September and mean annual temperature of 22.5°C.

Five sites were chosen to represent a range of tree densities typical of the cerrado:

1. *Campo sujo*, an open shrub savanna with basal area of $4.3 \text{ m}^2 \text{ ha}^{-1}$ ($15^\circ 56' 02'' \text{S}$, $47^\circ 52' 26'' \text{W}$).
2. *Campo cerrado*, open tree and shrub savanna with basal area of $4.4 \text{ m}^2 \text{ ha}^{-1}$ ($15^\circ 57' 39'' \text{S}$, $47^\circ 53' 05'' \text{W}$).
3. *Cerrado sensu stricto*, 'typical' cerrado, i.e., tree savanna with basal area of $10.7 \text{ m}^2 \text{ ha}^{-1}$ ($15^\circ 57' 19'' \text{S}$, $47^\circ 52' 22'' \text{W}$).
4. *Cerrado denso*, dense tree savanna, with basal area of $18.2 \text{ m}^2 \text{ ha}^{-1}$ ($15^\circ 57' 15'' \text{S}$, $47^\circ 52' 44'' \text{W}$).
5. *Cerradão*, a nearly closed-canopy woodland, with basal area of $26.6 \text{ m}^2 \text{ ha}^{-1}$.

In addition to these intensely studied sites, point measurements were made in three gallery forests, as described below. None of the study sites had burned within several years prior to the study.

Methods

Groundlayer LAI

We estimated groundlayer LAI with a LAI 2000 Plant Canopy Analyzer (LI-COR Inc., Lincoln, Nebraska, USA). The LAI-2000 estimates LAI by comparing light intensity at various angles for measurements performed above and below the canopy (LI-COR, 1992). To estimate groundlayer LAI, the above-canopy measurement was performed above the groundlayer but under tree cover, when present, as described by LI-COR (1992). A 180° view cap was used to block the silhouette of the operator during measurements. All herbaceous plants, as well as woody plants $< 1\text{-m}$ tall were considered to belong to the groundlayer, while larger woody plants were pooled into a single category of trees and shrubs.

The LAI-2000 does not distinguish between leaves and stems, so it yields an estimate of vegetation area index (VAI), i.e., living and dead LAI plus stem area index (SAI). To estimate green graminoid LAI and green dicot LAI, we multiplied the VAI by the fraction of the vegetation area composed of green graminoid and green dicot leaves, respectively. To do this we estimated the fraction of green graminoid leaf, green dicot leaf, and nonphotosynthetic leaves and stems in the groundlayer at 80 points at 1-m intervals along four 20-m transects in each site at each sampling date. At each point, a 1-m thin metal rod painted with white rings at 1.0-cm intervals was inserted vertically into the groundlayer vegetation. All contacts between the vegetation and any of the white rings were tabulated as green graminoid leaf, green dicot leaf, or nonphotosynthetic material. The sum of these counts for the 80 points was used to estimate the fractional composition of these three components. Measurements were performed nine times between September 2002 and October 2003.

We compared data obtained with this approach with destructive harvests of groundlayer vegetation. Grass and dicot green LAI was estimated as described above within 14 $0.5\text{-m} \times 0.5\text{-m}$ plots located to represent a range of LAI values. VAI was estimated in each plot with five replicated measurements with the LAI-2000, and the fraction of graminoid leaf, dicot leaf, and nonphotosynthetic area was determined with the graduated rod at 20 points within the plot. All groundlayer vegetation was harvested from the plot, and the area of dicot and grass leaves was determined with a CI-202 area meter (CID, Inc., Vancouver, WA, EUA).

Tree and shrub LAI

The LAI-2000 tends to underestimate LAI, when vegetation is strongly aggregated (LI-COR 1992), posing a problem for estimating tree LAI in savanna. To avoid this problem, we made measurements only under tree canopies at points where the entire angle of view intercepted one or more tree or shrub crowns. Since these measurements yield the leaf area per unit crown area, we refer to this as crown LAI. Subsequently, to obtain an estimate of overall LAI, the crown LAI value was multiplied by the fraction of ground area covered by tree and/or shrub crowns (Asner et al. 1998).

In each physiognomy, we permanently marked 50 locations that permitted measurements including only tree or shrub crowns. Measurements at these locations were performed with a 45° view cap and only during periods of diffuse sunlight, such as on cloudy days or at dusk or dawn. Measurements were performed within a few days of each of the nine sampling dates for the groundlayer LAI, with an additional set of measurements performed in November 2003.

To validate this approach to estimating LAI, we compared estimates performed with the LAI2000 and subsequent destructive measurements of LAI for 14 trees and shrubs. Crown area was estimated from measurements of the major and minor axis by assuming the crown to be an ellipse. Five measurements of LAI were performed for every individual with the LAI 2000. All leaves were collected from the tree, and stem area index (SAI) of the defoliated tree was estimated with the LAI-2000 using the same procedure. The area of a subsample of approximately 30 leaves was measured with a CI-202 area meter. The subsample and the remaining leaves were dried to constant mass at 70°C and total leaf area determined using the ratio of leaf area to leaf mass determined from the subsample. Total leaf area was converted to crown LAI by dividing by the crown area.

We use repeated-measures ANOVA to test for differences in seasonality of leaf display among plant types (trees, groundlayer dicots, and groundlayer graminoids). We used vegetation type as the blocking factor (von Ende 1993), with month and plant type as fixed factors. Mean squares were calculated with JMP 5.1 and the appropriate F values were calculated manually accord-

ing to Steel and Torrie (1980). All LAI values were Log_{10} transformed prior to analysis to ensure that comparisons of seasonality were based on relative changes in LAI rather than absolute changes.

Soil water potential

Soil psychrometers (Wescor PST-55-30 SF) were installed at depths of 10, 20, 30, 60, and 100 cm at four locations in each of the five intensively studied sites. Water potential was recorded with a Campbell CR7 data logger that was rotated among the five sites at approximately weekly intervals from June to November 2002, and was kept continuously at the cerrado denso site from April to August 2003. To relate soil water potential to LAI, we used published rooting distributions for tropical savanna (Jackson et al. 1997) to obtain a depth-weighted mean water potential for each date.

Comparisons between savanna and forest species

In November 2003 (wet season), we compared the LAI of congeneric savanna and forest trees under similar growing conditions. We made measurements only on genera containing both a savanna and a forest species to ensure phylogenetic independence, an important condition for inference in comparative studies (Felsenstein 1985), and to improve the statistical power of comparisons between the two groups (Ackerly 1999). One exception is that we included two species from two genera of the family Myrtaceae (Table 1). However, since no other genus from this family was included in the study, phylogenetic independence is maintained.

To control for site differences, we only measured individuals that had established within the savanna environments at either the IBGE reserve or at a nearby

site of native cerrado vegetation. In the case of forest species, this was possible because long-term fire protection at IBGE has permitted forest species to establish in savanna. For *H. martiana*, we used individuals planted in cerrado soils at least 20 years previously, with no management for at least the past 15 years and perhaps longer, allowing savanna grasses to recolonize the site.

Using the methods described above for measuring crown LAI, we only measured LAI of individuals in savanna sites where unobstructed measurements of LAI of a single species was possible. Two to 15 individuals (mean = 9.2) were measured per species. All four species with fewer than seven measured individuals were forest species for which we were unable to locate additional individuals that had established in savanna. We used the *t* test to compare LAI of the savanna and the forest species within each genus. Additionally, to test for a difference between savanna and forest species across all genera, we performed a paired *t* test on species means, with pairings being based on genera.

In November 2003, we also measured LAI of gallery forests along three different streams, locally known as the Pitoco, Taquara, and Monjolo forests. LAI was measured at 25 points in each forest, located at 5-m intervals along five transects placed perpendicular to the forest edge.

Remote sensing

We compared our ground-based estimates of LAI with two vegetation indices derived from Moderate Resolution Imaging Spectroradiometer (MODIS) images (<http://modis.gsfc.nasa.gov/>). We used 16-day composites of the MODIS enhanced vegetation index (EVI) and the MODIS normalized difference vegetation index (NDVI) products (Huete et al. 2002) at 500-m resolution. The densest site (cerradão) was excluded because the extent of this vegetation type at the study site was

Table 1 Congeneric species pairs studied

| Savanna species | Forest species | Family |
|---|---|---------------------|
| <i>Aegiphilia lhotzkiana</i> Cham. | <i>A. sellowiana</i> Cham. | Verbenaceae |
| <i>Aspidosperma tomentosum</i> Mart. | <i>A. subicanum</i> Mart. | Apocynaceae |
| <i>Byrsonima crassa</i> Nied. | <i>B. laxiflora</i> Griseb | Malpighiaceae |
| <i>Erythroxylum suberosum</i> St. Hil. | <i>E. daphnites</i> Mart. | Erythroxylaceae |
| <i>Guapira noxia</i> (Netto) Lundell | <i>G. areolata</i> (Heimerl) Lundell | Nyctaginaceae |
| <i>Hymenaea stignocarpa</i> Mart. Ex Hayne | <i>H. martiana</i> Hayne | Leguminosae – Caes. |
| <i>Miconia pohliana</i> Cogn. | <i>M. acuminata</i> (Steud.) Naudin | Melastomataceae |
| <i>Ouratea hexasperma</i> (St. Hil.) Bail. | <i>O. castaneaeifolia</i> (St. Hil.) Engl. | Ochnaceae |
| <i>Blepharocalyx salicifolius</i> (H.B.K.) Berg. | <i>Myrcia rostrata</i> DC. | Myrtaceae |
| <i>Myrsine guianensis</i> (Aubl.) O. Kuntz | <i>M. ferruginea</i> (Ruiz and Pav.) Spreng. | Myrsinaceae |
| <i>Pouteria ramiflora</i> (Mart.) Radlk. | <i>Pouteria</i> sp. | Sapotaceae |
| <i>Symplocos lanceolata</i> (Mart.) A. DC. | <i>S. mosenii</i> Brand. | Symplocaceae |
| <i>Vochysia thyrsoidea</i> Pohl. | <i>V. tucanorum</i> (Spreng.) Mart | Vochysiaceae |

much smaller than the resolution of the MODIS data products.

Results

The relationship between destructively measured LAI and values measured with the LAI 2000 did not vary significantly from a 1:1 line for the groundlayer (Fig. 1a, $t_{27}=1.66$, $P=0.11$). However, the LAI2000 significantly underestimated tree and shrub LAI (Fig. 1b, $t_{14}=2.69$, $P=0.018$), so the raw data from other measurements on trees and shrubs were multiplied by a scaling constant of 1.174, as determined from the regression relationship shown in Fig. 1b.

For the destructively harvested individuals, stem area index (SAI) estimated with the LAI2000 was

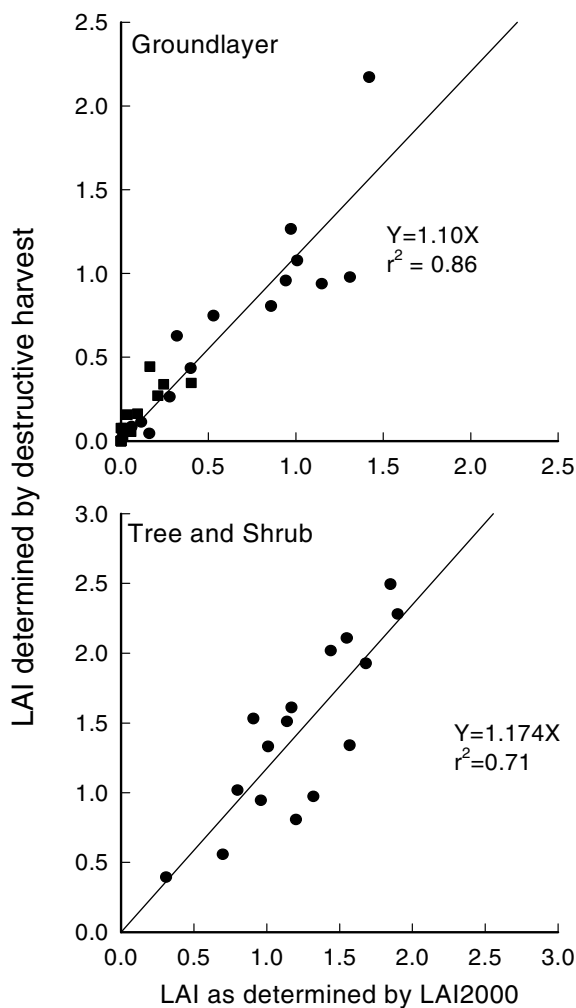


Fig. 1 Relationship between LAI measurements made with the LAI-2000 and those determined by destructive harvests. **a** Groundlayer LAI. *Circles* represent graminoids and *squares* represent dicots. The relationship did not deviate significantly from a 1:1 line. **b** LAI of woody plants over 1-m tall. Measurements with the LAI-2000 significantly underestimated woody plant LAI ($P=0.02$)

$13.9 \pm 1.6\%$ (mean \pm SE) of the total vegetation area index. This represents the percentage of vegetation area index attributable to stems at the time of maximum leaf display during the wet season. To estimate the contribution of stems to total VAI, we assumed that this same percentage is representative of all sites during the wet season, and that SAI does not vary seasonally.

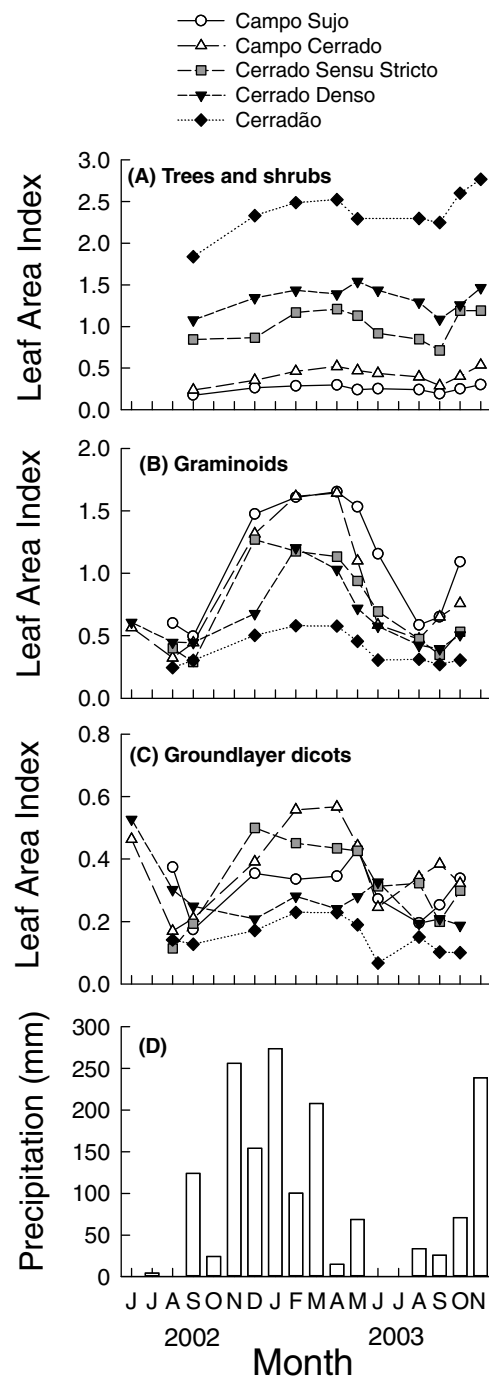


Fig. 2 Seasonality of LAI and precipitation at the study site. **a** Green LAI of woody plants taller than 1 m. **b** Green LAI of graminoids. **c** Green LAI of groundlayer dicots. **d** Monthly precipitation

The three plant types (graminoids, groundlayer dicots, and trees) differed significantly in their seasonality of LAI (Fig. 2; type \times time interaction $F_{2,64} = 6.87$, $P \leq 0.001$). Grasses exhibited much greater seasonality than did woody plants (Fig. 2a, b). For trees and shrubs, late dry season LAI (September) averaged 68% of wet season values (February and April), whereas for grasses, late dry season LAI was 28% of wet season values (Fig. 2b). Seasonality of groundlayer dicots was intermediate, with late dry season LAI being 60% of that of the wet season (Fig. 2c). As a result, most of the seasonality in groundlayer LAI can be attributed to graminoids rather than dicots. During periods of soil drying, grass LAI was strongly correlated to soil water potential (Fig. 3, $r^2 = 0.59$, $P = 0.002$), while tree LAI was less strongly correlated (Fig. 3, $r^2 = 0.30$, $P = 0.05$), and LAI of groundlayer dicots was uncorrelated to soil water potential ($r^2 = 0.03$, $P = 0.57$). There was considerable hysteresis in the relationship between LAI and soil water potential; during the wetting phase at the beginning of the wet season, there was no relationship between soil water potential and LAI (Fig. 3). During this period, soil water potential in the top 1 m very quickly approached 0 MPa, while LAI attained maximum values only after several months.

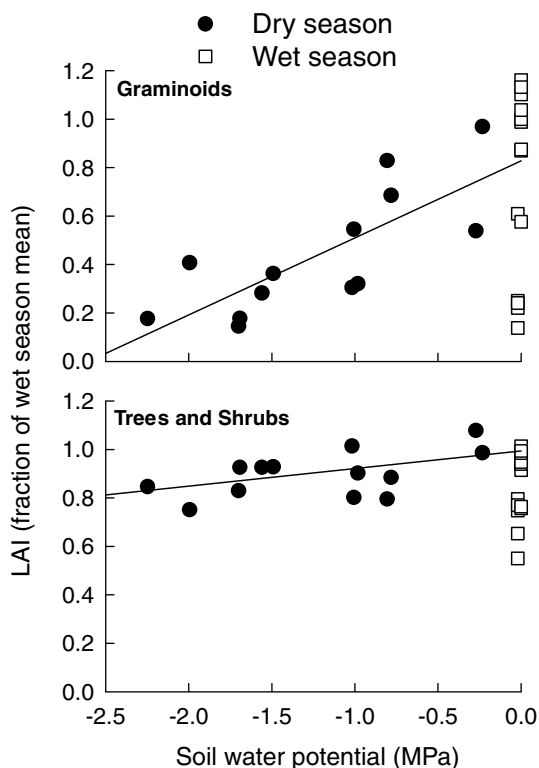


Fig. 3 Relationship between soil water potential and LAI. During the dry season, there was a significant relationship between soil water potential and LAI of graminoids (top, $r^2 = 0.59$, $P = 0.002$) and woody plants (bottom, $r^2 = 0.30$, $P = 0.05$)

Wet-season tree and shrub LAI varied greatly among sites (Fig. 4), primarily due to a sixfold difference in percentage crown cover, which varied from 16% to 91% (Fig. 4a). In contrast, mean wet season crown LAI (i.e. LAI of individual trees and clusters) ranged from 1.37 to 2.59 among sites, less than a twofold difference (Fig. 4b). The net result of these differences is a ninefold difference in ecosystem-level tree and shrub LAI among sites, ranging from 0.28 at the campo sujo site to 2.48 at the cerradão site (Fig. 4c). Wet season LAI of the three gallery forest sites ranged from 3.87 to 4.55 (mean = 4.15).

Total groundlayer green LAI (grass LAI + dicot LAI) was strongly and negatively correlated with tree cover among sites (Fig. 5). Similarly, grass LAI was negatively correlated with tree cover, though

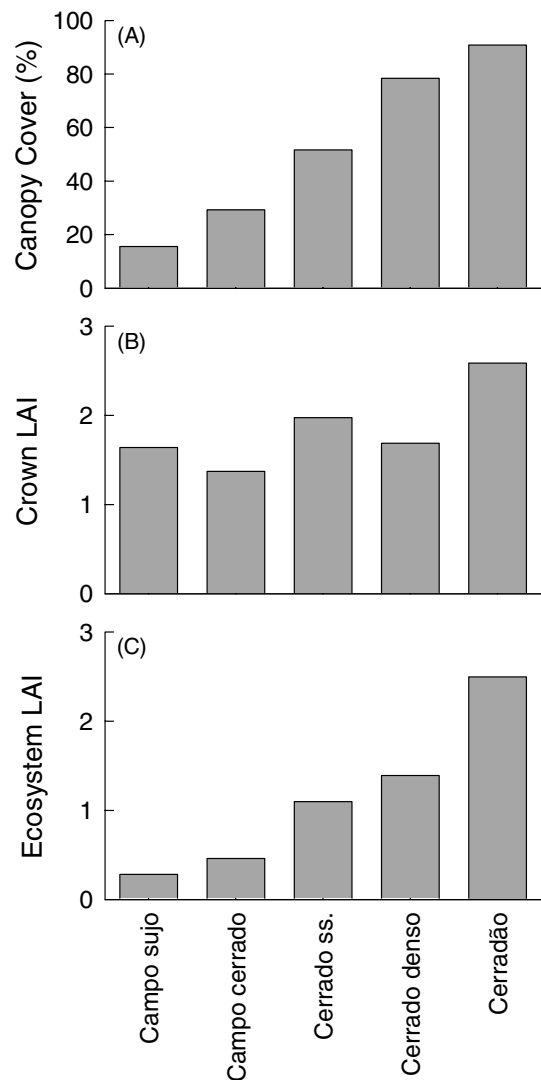


Fig. 4 Components of the among-site variation in wet season tree and shrub LAI. **a** Percentage of ground area covered with tree or shrub crowns, **b** mean LAI of the crowns of individuals and clumps of individuals, **c** overall LAI as obtained by multiplying fractional canopy cover and crown LAI to obtain total tree and shrub LAI

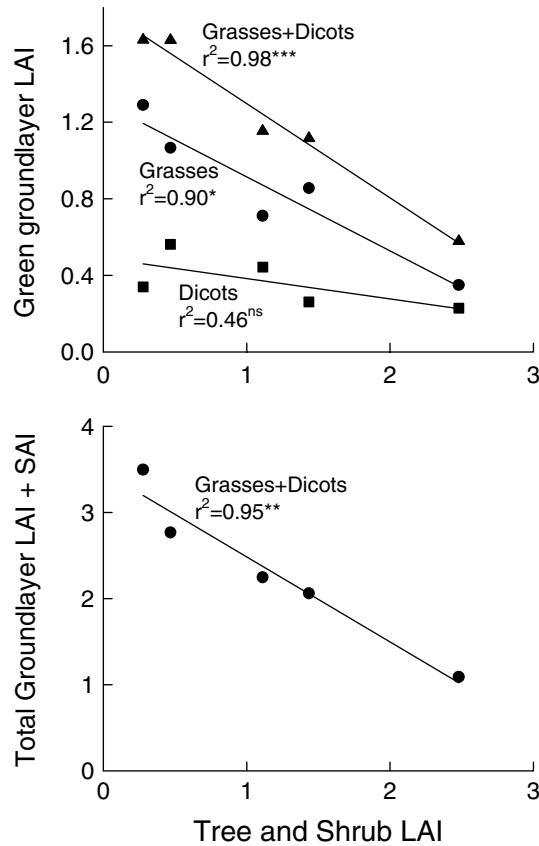


Fig. 5 **a** Relationship between wet-season woody plant LAI and green groundlayer LAI across the five study sites. The regression equations are $y_{total} = 1.79 - 0.49x$, $y_{grass} = 1.30 - 0.39x$ and $y_{dicot} = 0.49 - 0.11x$. **b** Relationship between wet-season woody plant LAI and total groundlayer LAI and stem area index (SAI). These values include all living and dead components of the groundlayer vegetation, including dicots and graminoids. The regression equation is $y = 2.47 - 0.95x$. All values are averages from February and April 2003, the months with peak LAI

that of groundlayer dicots was not (Fig. 5). Total VAI (living and dead LAI plus SAI) of the ground layer was also negatively correlated with tree LAI (Fig. 5).

Sites with less tree cover tended to have a greater relative decline in total LAI during the dry seasons ($r^2 = 0.92$, $P = 0.01$). This was due primarily to the greater contribution of the more seasonal grasses to overall LAI in open sites ($r^2 = 0.92$, $P = 0.01$). There were trends towards reduced seasonality of LAI with increasing tree density for trees ($r^2 = 0.75$, $P = 0.056$) and the groundlayer ($r^2 = 0.48$, $P = 0.19$). Though not statistically significant, these trends nevertheless contributed somewhat to the lower overall seasonality of LAI in denser sites.

In 6/12 genera, the savanna species had significantly lower crown LAI than forest species under similar growing conditions (Fig. 6). When compared over all genera, LAI was 46% greater for forest species (paired $t_{11df} = 3.37$; $P = 0.006$). Mean LAI of forest species was

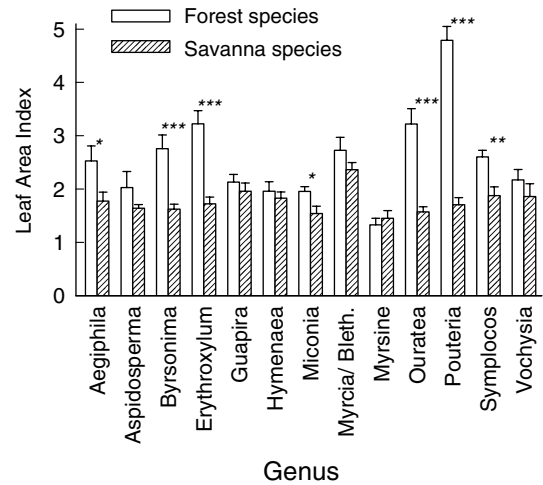


Fig. 6 Mean (+ SE) LAI of congeneric savanna and forest species growing in open savanna environments. * $P < 0.05$, ** $0.01 < P < 0.05$, *** $0.005 < P < 0.01$ for comparisons between savanna and forest species within a genus. Overall forest species had 46% greater LAI than savanna species ($P = 0.006$)

2.57 ± 0.24 , while mean LAI of savanna species was 1.76 ± 0.06 (mean \pm SE).

Both EVI and NDVI were positively correlated to LAI, but the relationship was stronger for EVI (Fig. 7).

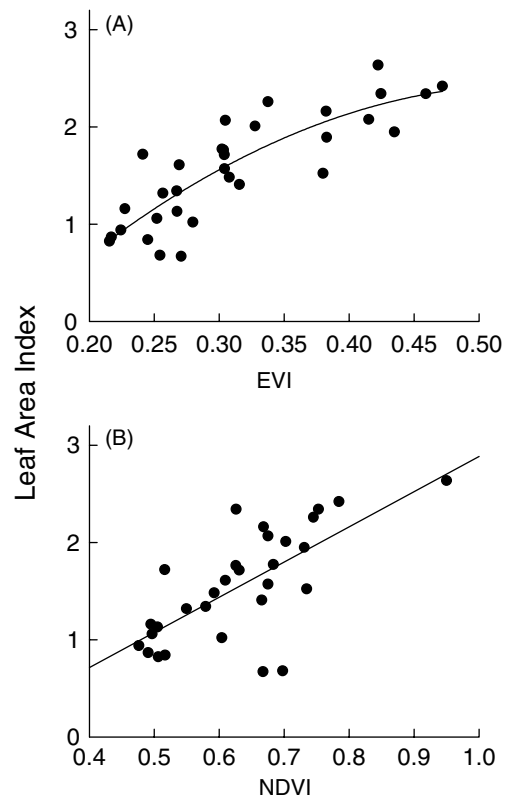


Fig. 7 Relationship between LAI and MODIS vegetation index products. Each point represents one site at one measurement date. **a** Enhanced vegetation index (EVI). $LAI = -15.08EVI^2 + 16.33EVI - 1.98$, $r^2 = 0.71$. **b** Normalized difference vegetation index (NDVI). $LAI = 3.62NDVI - 0.73$, $r^2 = 0.49$

Discussion

Tree cover clearly exerts a strong influence on grasses in these savannas. The negative relationship between tree LAI and grass LAI indicates that the negative effects of trees on grasses substantially outweigh any positive effects over the range of tree densities examined here. Although tree cover was shown to stimulate grass production in some savannas (Belsky et al. 1989; Weltzin and Coughenour 1990; Belsky 1994; Mordelet and Menaut 1995), tree cover usually reduces grass production in savannas receiving $> 800 \text{ mm year}^{-1}$ of precipitation (Mordelet and Menaut 1995). The mean precipitation at the study site is over $1,400 \text{ mm year}^{-1}$, so a negative effect on the ground layer is expected.

Extrapolating the relationship between tree LAI and grass LAI indicates that savanna grasses should not tolerate environments where tree LAI exceeds 3.3. In the gallery forest sites, where mean wet season tree LAI was 4.15, well over the value that should exclude grasses, savanna grasses are indeed absent. The higher LAI in gallery forest may partly result from greater water or nutrient availability, but species composition also plays an important role. Overall, forest species had 46% greater LAI than congeneric savanna species growing under similar conditions. This has important implications for fire occurrence and the dynamics of savanna–forest boundaries, since grasses are the primary fuel in tropical savannas, with groundlayer VAI being strongly correlated to fine fuel mass (Hoffmann et al. 2004a). The lack of grasses and the more humid understory afforded by the closed canopy greatly reduce the risk that savanna fires penetrate far into forest (Kellman and Meave 1997; Biddulph and Kellman 1998). Evergreen forest trees are more sensitive to fire than savanna species (Hoffmann and Moreira 2002), largely due to thinner bark (Hoffmann et al. 2003) and smaller below-ground reserves of nonstructural carbohydrates (Hoffmann et al. 2004b), so exclusion of grasses is essential for persistence of remaining evergreen forest within savanna landscapes.

The higher LAI of forest species appears to play an important role in cerradão, where forest and savanna species coexist. The presence of forest species should permit stands to attain higher values of LAI than in more open forms of cerradão. In fact, crown LAI was highest in cerradão (Fig 4b), largely due to the presence of forest species with dense foliage such as *Ocotea pomaderroides* and *Emmotum nitens* (W. Hoffmann, personal observation). Although species composition of the tree layer may contribute to the higher LAI of cerradão and gallery forest, it did not seem to play an important role in determining the differences in LAI among the four most open sites. Although tree species composition tends to change over the gradient in tree density represented by these four sites (Moreira 2000; Ribeiro and Tabarelli 2002), this appears not to contribute to the differences in LAI, since crown LAI varied little among these sites.

We expected savanna trees to exhibit lower crown LAI than forest species based on findings that shade-tolerant species often have higher LAI than shade-intolerant species (Mourelle et al. 2001; Sterck et al. 2001; Reich et al. 2003). Shade tolerance should permit species to develop greater LAI because their leaves can maintain a positive carbon balance under greater self-shading due to a lower light compensation point for photosynthesis. Fully expanded leaves are unable to upload carbohydrates from the phloem (Turgeon 1989), so a leaf will eventually senesce if it receives insufficient light to maintain a positive carbon balance. While the degree of shade tolerance should restrict the maximum LAI that a species can develop, it would not constrain the minimum LAI of a species. Because of this, along with the fact that many forest species are shade intolerant, we should not expect that all genera would show a significant difference in LAI between savanna and forest species. In fact, for half of the genera there was no difference in mean LAI between savanna and forest species.

Across sites, wet season green LAI of the groundlayer declined by approximately 0.5 units for every 1.0 unit increase in woody plant LAI (Fig. 4). Since the decline in groundlayer LAI does not entirely offset the increase in tree LAI, total LAI in the wet season is highest in sites with the greatest tree cover. The role of tree cover in determining spatial variation in total LAI becomes even more important in the dry season, when groundlayer LAI is greatly diminished. We expect similar patterns in transpiration and primary productivity, whereby sites with greater tree density should exhibit greater maximum fluxes, as well as greater seasonality.

Grass LAI tracked soil water potential during the dry season, but these became quickly uncoupled after the onset of rains when LAI lagged behind soil water potential. Soil water potential has been successfully used as the primary determinant for modeling leaf phenology in tropical savannas (Jolly and Running 2004), but it is not clear whether soil water potential is an important cue for phenology of trees. Leaf fall of savanna trees often occurs before the beginning of the dry season (Simioni et al. 2004), while leaf flush commonly occurs before the first rains at the end of the dry season (Gouveia 1998; Prior et al. 2004; Simioni et al. 2004). To discern what environmental cues are drivers of tree phenology, long-term monitoring of inter-annual variations will be necessary. NDVI has been frequently used to monitor phenology of tropical savannas (Fuller and Prince 1996; Jolly and Running 2004), but here EVI was more strongly correlated to LAI. This suggests that EVI is a more appropriate vegetation index for this purpose, corroborating the results of Ferreira et al. (2003). Although EVI is useful for monitoring leaf phenology at the ecosystem level, it does not distinguish between tree and grass LAI and therefore does not capture the complexity of tree–grass interactions in tropical savanna.

Acknowledgements We thank Augusto C. Franco for comments on the manuscript and Mercedes Bustamante for use of the LAI2000 Plant Canopy Analyzer. This work was supported by a grant from the National Science Foundation (USA) grant# 0296174. This work complies with Brazilian law.

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