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REGULAR ARTICLE

Savanna soil fertility limits growth but not survival of tropical forest tree seedlings

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Abstract

Background and Aims Cerradão (Brazilian woodland savannas) and seasonally dry forests (SDF) from southeastern Brazil occur under the same climate but are remarkably distinct in species composition. The objective of this study was to evaluate the role of soil origin in the initial growth and distribution of SDF and Cerradão species.

Methods We conducted a greenhouse experiment growing Cerradão and SDF tree seedlings over their soil and the soil of the contrasting vegetation type. We evaluated soil nutrient availability and seedling survivorship, growth and leaf functional traits.

Results Despite the higher nutrient availability in SDF soils, soil origin did not affect seedling survivorship. The three SDF species demonstrated home-soil advantage, enhanced growth with increasing soil nutrient availability and had higher growth rates than Cerradão species, even on Cerradão soils. Growth of Cerradão seedlings was not higher on Cerradão soil and, overall, was not positively correlated with soil nutrient availability.

Conclusions SDF species are fast-growing species while Cerradão trees tend to be slow-growing species. Although savanna soil reduces growth of forest species, our findings suggest that soil chemical attributes, alone, does not exclude the occurrence of SDF seedlings in Cerradão and vice-versa.

Keywords Atlantic forest · Cerrado · Savanna-forest boundaries · Soil fertility · Nutrient availability · Growth strategies

Abbreviations

LAR	leaf area ratio
LD	leaf tissue density
LMR	leaf mass ratio
LT	leaf thickness
NAR	net assimilation rate
RGR	relative growth rate
SDF	seasonally dry forest
SLA	specific leaf area

Introduction

Savannas and forests are the two major vegetation types found in the tropics. In Brazil, the Cerrado savannas and the Atlantic Forest are the second and

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third largest biomes covering about 37% of the country. Due to their threatened status and high species diversity and endemism, both Cerrado and Atlantic Forest belong to the 25 world hotspots and as such are considered the most important areas for biodiversity conservation (Myers et al. 2000). Frequently, these two biomes form vast contact zones (Durigan and Ratter 2006) and this is particularly true in southeastern Brazil, where SDF, a vegetation physiognomy of the Atlantic Forest, and Cerradão, a woodland of Cerrado biome, are among the dominant vegetation types (Kronka et al. 2005).

Climatically, part of the Brazilian Cerrado occurs in areas that could support tropical forests. In fact, southeastern Brazil Cerradão and SDF occur under similar seasonal climates, characterized by a pronounced dry season during the winter, but they are remarkably distinct in structure and floristic composition, with few species occurring in both environments, suggesting species specialization to different habitats.

There are many forest-savanna contact zones across the world, in which factors such as fire (Ratter 1992; Hoffmann 2000; Hoffmann et al. 2003; Banfai and Bowman 2005), light regime (Hoffmann and Franco 2003), soil nutrient status (Ratter 1992; Bowman and Panton 1993; Bond 2010; Wang et al. 2010; Lehmann et al. 2011), and rainfall seasonality (Lehmann et al. 2011) have been reported as drivers or not of savanna-forest boundary dynamics. In the SDF-Cerradão boundaries, previous studies showed that SDF occurs over soils with higher nutrient availability, while Cerradão occurs over nutrient-poor soils (Furley and Ratter 1988; Ratter 1992; Ruggiero et al. 2002). Although these studies suggest soil nutrient availability as the main factor affecting the distribution of SDF and Cerradão in southeastern Brazil contact zones, they were not based on experimental work.

In fact, soil nutrient availability is a key factor determining distribution of species and composition of many tropical forests and woodlands (McGraw and Chapin 1989; Bowman and Panton 1993; Theodose and Bowman 1997; Oliveira-Filho et al. 2001; John et al. 2007). Soil-related habitat specialization has been documented in Amazon forests (Fine et al. 2004), dipterocarp rainforests (Palmiotto et al. 2004) and in sandstones (ridges) and alluvium (valley) soils of Borneo (Baltzer et al. 2005).

While there is evidence that soils are important for maintaining savanna-forest boundaries, there has been no experimental examination of the role that soil nutrient availability may play in promoting the existence of Cerradão and SDF species in southeastern Brazil contact zones. A mechanistic understanding of how nutrient availability influences the performance of forest and savanna tree seedlings is therefore essential for predicting biome distribution under both current and future climatic conditions. To evaluate experimentally the role of soil origin on the growth and, consequently, the distribution of SDF and Cerradão species, we conducted a greenhouse experiment using tree seedlings that were grown in their native soil and also in the soil of the contrasting vegetation type. We then addressed the following questions: 1) How do Cerradão tree species perform in their native soil versus SDF soil and vice-versa? 2) Is soil nutrient availability a key factor affecting plant functional traits that may in turn limit the early establishment of Cerradão and SDF tree species in the field? 3) Do SDF and Cerradão species have different growth responses in relation to contrasting soil fertility? We hypothesized that if soil nutrient availability (fertility) is a key factor limiting the distribution of species from both vegetation types, then species will show lower survivorship and/or lower growth rates when grown on the soil of the contrasting vegetation type.

Material and methods

Study area and species

Seeds from Cerradão and SDF species were collected in *Estação Ecológica de Assis* (22°32-39′ S, 50°22-24′W) and in *Estação Ecológica dos Caetetus* (22°22-26′S, 49°40-44′W), respectively. Both sites are protected areas located in the state of São Paulo, southeastern Brazil. Cerradão is best described as a dense woodland with abundant evergreen trees and shrubs. Cerradão vegetation has a semi-closed canopy with tree cover varying from 50–90% (Ribeiro and Walter 1998) and does not have a remarkable grassy understory. The *Estação Ecológica de Assis* has a Cwa Koeppen's climate type, with a mean annual temperature of 22.1°C.

Mean annual rainfall is 1,440 mm and elevation is 505 m. The main soil type is a deep, well-drained and sandy dystrophic red Latosol with low water availability during the driest months (Juhász et al. 2006). SDF is a closed canopy vegetation type with abundant deciduous and semi-deciduous trees and shrubs. During the driest months, canopy trees may lose up to 50% of their leaf area (Veloso 1992). The *Estação Ecológica dos Caetetus* has the same climate type (Cwa), but mean annual temperature and rainfall of 21.3°C and 1,460 mm, respectively. Its mean elevation is 522 m. The main soil type is a well drained and sandy clay loam Ultisol. In both vegetation types, less than 25% of total annual precipitation falls during April to September, indicating a strong seasonality of rainfall and the existence of a dry season during this period. Although only 100 km apart and possessing similar climates, the Cerradão and SDF sites have structurally and floristically distinct vegetation types. The Cerradão site has almost the double of stems per hectare compared to SDF but the SDF trees have a mean diameter at breast height almost four times higher. Total number of woody species with DBH>5 cm in the two study sites is 268, but only 18 species are shared between them.

The seeds of all studied species were collected in the field from Jul-2007 to Oct-2007. We selected three woody species based on seed availability and endemism to one of the vegetation types. The chosen species are also widespread and abundant over their respective vegetation type (Oliveira-Filho 2006). The three SDF species were: *Balfourodendron riedelianum* (Engl.) Engl., *Cariniana estrellensis* (Raddi) Kuntze, *Centrolobium tomentosum* Guillemin ex Benth.), and the Cerradão species: *Dimorphandra mollis* Benth., *Machaerium acutifolium* Vogel, *Stryphnodendron obovatum* Benth. All species, except *B. riedelianum* (Rutaceae) and *C. estrellensis* (Lecythidaceae) from SDF, are legumes with potential for associating with N_2-fixing bacteria (Sylvester-Bradley et al. 1980, Faria et al. 1984, SM Faria personal communication 2009).

Cerradão and SDF soils used as the growth media for the greenhouse experiment were collected from the 0–20 cm depth layer, in six different locations at *Estação Ecológica de Assis* and *Estação Ecológica dos Caetetus*. To provide better representation of horizontal variation in soil characteristics from both vegetation types, each of the six locations were treated as independent samples in our experiment. In both sites, the soil was collected at randomly selected points, at least 500 m apart from each other. After the soil was collected, it was sieved to eliminate plant material such as foliage, branches and other large debris and placed into opaque polyethylene pots 11 cm in diameter and 25 cm deep.

Prior to the beginning of the greenhouse experiment, a subsample (*ca.* 500 g) of each soil collected in the field was analyzed for its chemical properties at a private soil analysis laboratory (Pirasolo—Laboratório Agrotécnico Piracicaba), located in Piracicaba, SP, Brazil. To account for total soil inorganic N, N-NO_3 and N-NH_4 were extracted in KCl and determined by ultraviolet spectrophotometry and by flow injection analysis (FIA) followed by spectrophotometry at 650 nm respectively. Soil pH was determined by potentiometry in $CaCl_2$ solution, Al was extracted in KCl and determined by acid–base titulation, and H+Al was extracted in SMP buffer and determined by potentiometry (van Raij et al. 2001). P, K, Ca, and Mg were extracted in ion exchange resin; Cu, Fe, Zn and Mn were extracted in DTFA and B was extract in $BaCl_2$ (EMBRAPA 1997). Soil cations were determined by spectrophotometry, P and B by colorimetry and S-SO_4 by turbidimetry (van Raij et al. 2001). Organic matter was determined by the method of Walkley and Black (Allen 1989).

Greenhouse experiment

Seeds were sown into sand boxes and after seedling germination and emergence, each plant was transplanted into pots containing either their home-soil or the soil of the contrasting vegetation type. Transplanting occurred between Nov-2007 and Dec-2007. All seedlings were 5–10 cm at the beginning. Evaluations were made at 5 and 9 months after transplantation of each species. Each species was transplanted into 240 replicate pots, with each one of the 12 soil locations containing 20 seedlings. The experiment was performed in a greenhouse located in the “Luiz de Queiroz” College of Agriculture, Piracicaba, Brazil; there was no temperature or light control but during the experiment, temperature within the greenhouse varied between 12°C and 34°C and relative humidity varied between 35–100%. Water was supplied every day to insure constant water availability to the seedlings. No additional nutrients were added to soil. Pots were randomly placed and regularly relocated to minimize the effect of potential environmental heterogeneity inside the greenhouse.

Survivorship, growth and leaf traits measurements

Five months after transplanting, plants were evaluated for survivorship, total plant leaf area and dry mass. Survivorship per species within each soil location (%) was calculated dividing the number of surviving seedlings by the initial number of seedlings (20), and then multiplying this number by 100. For leaf area and dry mass quantification, five randomly selected plants per soil location were harvested and separated into leaves, stems and roots. For the compound-leaved species (all except *B. riedelianum* and *C. estrellensis*), only the leaflets were included for the leaf area and mass calculations. After the measurement of leaf area with a digital portable area meter (Li-Cor, LI-3000A), all the parts were oven dried for at least 48 h at 60°C and weighed separately using an analytical balance.

Nine months after transplantation, the seedlings were evaluated again for total plant leaf area and dry mass. Additionally, LT, LD, SLA, LAR, LMR, root:shoot ratio and leaf nutrient concentration were determined. Total leaf area and plant dry mass were assessed as mentioned above, except for *M. acutifolium*, where the number of seedlings evaluated per soil location was reduced to only three plants because of high mortality rates. LT was measured on three fully expanded leaves per plant, using digital calipers, avoiding prominent veins. For simple-leaved species three thickness measurements per leaf (lamina base, middle and apices) were made. For compound-leaved species, we measured the middle portion of three leaflets per leaf, with each leaflet representing a position on the leaf: base, middle or apices. LD was calculated by dividing leaf dry mass by the product of leaf area multiplied by LT. SLA was obtained by dividing plant leaf area by leaf dry mass. LAR was calculated by dividing plant leaf area by plant dry mass. LMR was calculated as the ratio of leaf mass to total plant biomass and root:shoot ratio as the ratio of belowground biomass (root biomass) to aboveground biomass (stem and leaf biomass). One leaf nutrient concentration analysis per soil location was performed with a compound sample containing the leaves from all individuals harvested at 9 months. Leaf N, P, K, Ca, Mg and S concentration were analyzed at the Soil Science Department, at “Luiz de Queiroz” College of Agriculture, University of São Paulo, Brazil. N was determined by Kjeldahl distillation, after sulfuric acid digestion. Other nutrients were determined by optical (P) or atomic absorption spectrophotometry (K, Ca, Mg, SO_4), after nitric perchloric digestion.

RGR was calculated as:

$$RGR = (M2 - M1)/(T2 - T1)$$

where, $M2$ and $M1$ are plant dry mass at the second and first harvest, and $T2$—$T1$ the interval in days between first (5 months) and second (9 months) evaluation times. NAR, which represents the net result of dry mass gained via photosynthesis and lost in respiration by unit of leaf area, was calculated as:

$$NAR = (M2 - M1)(\ln A2 - \ln A1)/(T2 - T1)/(A2 - A1)$$

where, $A2$ and $A1$ are plant leaf area at the second and first harvest, respectively, and the other are as described above for RGR calculation.

Data analysis

Differences in soils attributes between the two vegetation types were tested by an unpaired Student's *t*-test, using each soil location as a replicate of its respective vegetation type. Within species, effect of soil origin over plant traits was assessed by an unpaired Student's *t*-test, with each soil location being considered a replicate of its soil origin. Overall effect of soil origin (Cerradão and SDF) and species over plant survivorship, growth parameters, morphological traits and nutrient leaf concentration were analyzed by a two-factor Analysis of Variance, considering soil and species as factors. Then, a post-hoc analysis was made within species using Tukey's test. Finally, we performed Pearson's correlation analyses to test the relationship between growth parameters and the most relevant soil fertility attributes (inorganic N, P and K+Ca+Mg soil availability). All plant and soil data, except for RGR and NAR, were log-transformed prior to the Analysis of Variance and Student's*t*-test analyses, in order to achieve normality and homogeneity of variance assumptions.

Results

Soil characterization

Cerradão and SDF soils are very different with respect to chemical properties and fertility (nutrient availability). SDF soils had lower Al concentrations and higher pH, organic matter, macronutrients, Zn and Mn availability, cation exchange capacity and base saturation than Cerradão soils (Table 1).

Seedlings performance

Seedling survivorship after 5 months, was significantly different among species ($F_{5,60}$=60.83; P<0.001) but was not affected by soil origin (Cerradão or SDF) ($F_{1,60}$=0.86; P=0.357), even when each species was evaluated individually (Fig. 1a). At 9 months, all growth variables and plant functional traits had diverged among species (Table 2). In general, growth variables (biomass, leaf area, RGR and NAR) had higher values for SDF species, while for most of the plant functional traits there is no clear pattern in the variation between Cerradão and SDF species (Appendix 1). Overall (regardless of species origin), plants accumulated more biomass and had higher total leaf area in SDF soils (Table 2). Individually, seedlings of the three SDF species (*B. riedelianum*, *C. estrellensis* and *C. tomentosum*) had higher biomass and leaf area when growing over their home-soil (Fig. 1b-c). Cerradão species (*S. obovatum*) also had more biomass when compared with their biomass on SDF soil (Fig. 1b). Moreover, the three SDF species accumulated more biomass than did Cerradão species, regardless of soil type (Fig. 1b).

Table 1 Mean (± SE) values of chemical and physical attributes for Cerradão and SDF soils

Attributes	Cerradão	SDF
pH *	3.78±0.02	4.85±0.38
Organic matter (g dm^{-3})*	18.50±1.36	36.00±7.81
Inorganic N (mg dm^{-3})*	3.81±0.55	13.62±3.12
P (mg dm^{-3})*	4.67±0.33	9.17±0.83
K (mmol$_c$ dm^{-3})*	0.13±0.03	1.72±0.32
Ca (mmol$_c$ dm^{-3})*	1.33±0.21	38.83±14.5
Mg (mmol$_c$ dm^{-3})*	1.33±0.21	10.33±2.86
H+Al (mmol$_c$ dm^{-3})	42.83±3.89	31.50±5.88
Al (mmol$_c$ dm^{-3})*	6.33±0.33	2.50±1.59
Bases added [a] (mmol$_c$ dm^{-3})*	2.80±0.44	50.88±17.63
CEC[b] (mmol$_c$ dm^{-3})*	45.63±3.41	82.38±13.68
Base saturation (%)*	6.34±1.16	54.15±12.78
Al saturation (%)*	69.94±3.16	15.23±9.64
SO_4 (mg dm^{-3})	9.67±1.28	12.83±1.01
Cu (mg dm^{-3})	0.65±0.23	0.48±0.03
Fe (mg dm^{-3})	103.17±10.66	72.67±16.83
Zn (mg dm^{-3})*	0.27±0.02	1.45±0.46
Mn (mg dm^{-3})*	2.28±0.52	21.25±3.99
B (mg dm^{-3})	0.43±0.03	0.42±0.03

[*] significant difference between the mean of each vegetation type (*t*-test, *df*=1,10; P≤0.05)

[a] bases added is the sum of K, Ca, and Mg

[b] CEC: cation exchange capacity (bases added+H+Al)

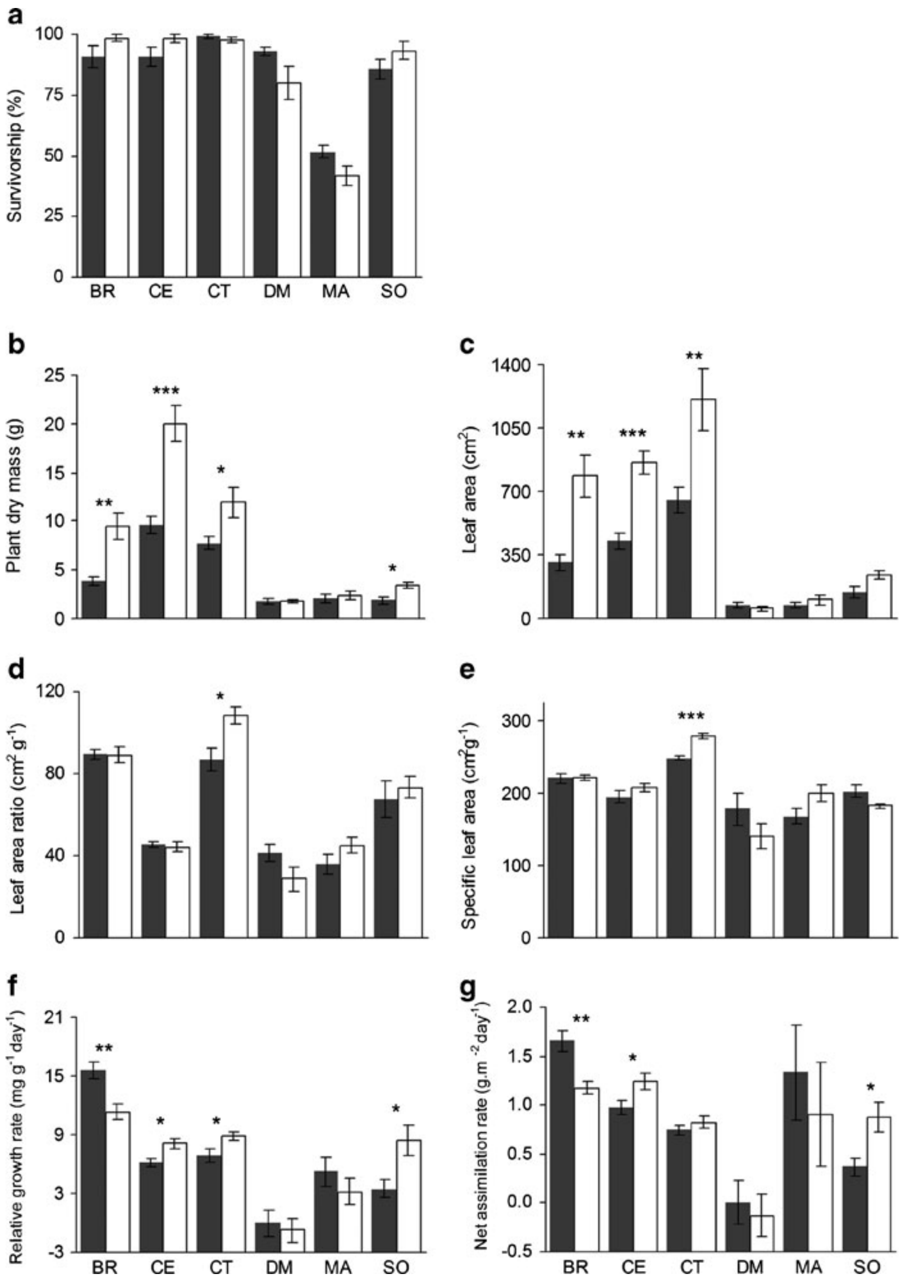
Soil type had no influence on most of the plant functional traits we measured, when all species were considered (Table 2). In contrast, some plant functional traits were affected by soil origin within species. For example, LAR and SLA for *C. tomentosum* were higher for seedlings growing on SDF soil compared with the Cerradão soil (Fig. 1d-e). Growth variables and plant functional traits for the Cerradão species *D. mollis* and *M. acutifolium* were similar for seedlings growing on either SDF or Cerradão soil (Fig. 1).

Overall, concentration of all nutrients, except N and S, were higher in leaves of seedlings growing on SDF soil (Table 2). Although there was no difference in leaf N concentration according to the soil type for any of the studied species (Fig. 2a), seedlings of the three SDF species accumulated more N in their leaves, when leaf nutrients was converted to total nutrient content, considering total plant's leaf biomass (Fig. 2b). The same result was found for the three SDF species and *S. obovatum* with respect to leaf P concentration and total content.

Plant functional traits and soil nutrient availability relationships

Total foliar N, P, K, and Mg were positively correlated with the respective soil nutrient availability for the

Fig. 1 Soil origin effect over mean (± SE) survivorship **a**, growth parameters **b**, **c**, **d**, **f**, **g** and specific leaf area **e** of Cerradão and SDF seedlings growing over Cerradão (*filled bars*) and SDF soils (*open bars*). * $P<0.05$, ** $P<0.01$, *** $P<0.001$ for soil origin effect within species (*t*-test; *df*=1,10). SDF species: BR: *Balfourodendron riedelianum;* CE: *Cariniana estrellensis;* CT: *Centrolobium tomentosum*. Cerradão species: DM: *Dimorphandra mollis*; MA: *Machaerium acutifolium*; SO: *Stryphnodendron obovatum*



three SDF species and *S. obovatum* (Cerradão) (Table 3). A similar positive correlation was also found for Ca, except in *B. riedelianum*. In addition, plant dry mass was positively correlated with soil P, inorganic N and the sum of cation bases (K+Ca+Mg) availability for the three SDF species overall (Fig. 3) and individually (Table 4). For Cerradão species, plant biomass was positively correlated only with inorganic N and P availability for *S. obovatum* (Table 4).

Overall, both RGR and NAR were not affected by soil origin (Table 2). However, when considering species individually, the SDF species *C. estrellensis* and *C. tomentosum*, and the Cerradão species *S. obovatum* showed higher RGR when growing on the SDF soil. Interesting, the SDF species *B. riedelianum* contradicted our initial predictions and showed higher RGR and NAR on the Cerradão soil (Fig. 1f-g). Due to the loss of leaves from the first to the second

Table 2 Mean (± SE) values for plant traits of seedlings grown on Cerradão and SDF soil, and significant level of soil origin and species for each variable evaluated

Variable	Mean (± SE)		Effect		
	Cerradão soil	SDF Soil	Soil origin	Species	Interaction
Biomass (g)	4.44±0.56	8.11±1.18	**< 0.001**	**< 0.001**	**0.038**
Leaf area (cm^2)	275.92±38.89	535.96±80.38	**0.002**	**< 0.001**	**0.047**
RGR ($mg\ g^{-1}\ day^{-1}$)	6.20±0.89	6.53±0.80	0.589	**< 0.001**	**< 0.001**
NAR ($g\ m^{-2}\ day^{-1)}$	0.85±0.13	0.82±0.12	0.813	**< 0.001**	0.263
SLA ($cm^2\ g^{-1}$)	202.12±6.35	205.12±7.81	0.940	**< 0.001**	**0.014**
LT (mm)	0.09±0.01	0.09±0.01	0.139	**< 0.001**	0.680
LD ($g\ cm^{-2}$)	0.61±0.04	0.68±0.08	0.394	**< 0.001**	0.063
LAR ($cm^2\ g^{-1}$)	61.12±4.14	64.86±4.99	0.178	**< 0.001**	**0.022**
LMR	0.30±0.02	0.30±0.02	0.766	**< 0.001**	0.166
Root:shoot ratio	1,29±0,12	1,10±0,10	**0.016**	**< 0.001**	0.293
Leaf N (%)	2.69±0.13	2.58±0.11	0.390	**< 0.001**	0.628
Leaf P (%)	0.09±0.004	0.10±0.004	**< 0.001**	**< 0.001**	0.144
Leaf K (%)	0.71±0.06	0.84±0.05	**< 0.001**	**< 0.001**	**0.026**
Leaf Ca (%)	0.47±0.04	0.98±0.09	**< 0.001**	**< 0.001**	**< 0.001**
Leaf Mg (%)	0.12±0.01	0.16±0.01	**< 0.001**	**< 0.001**	**0.002**
Leaf S (%)	0.42±0.07	0.36±0.07	**< 0.001**	**< 0.001**	**0.003**

Bold values indicate significant effect ($P<0.05$; factorial Analysis of Variance; soil origin *df*=1,60; species: *df*=5,60)

evaluation, *D. mollis* showed a negative NAR and consequently, a negative RGR on both soil types (Fig. 1i-j).

RGR and plant dry mass after 9 months did not correlate with leaf N concentration ($r=0.18$, $P=0.121$). Surprisingly, we found an overall negative correlation between plant dry mass after 9 months of growth and leaf N concentration ($r=-0.584$; $P<0.001$). This result was overly influenced by one species, however, *C. estrellensis*, which possessed the highest biomass after 9 months (Fig. 1), but also the lowest leaf N concentration (Fig. 2).

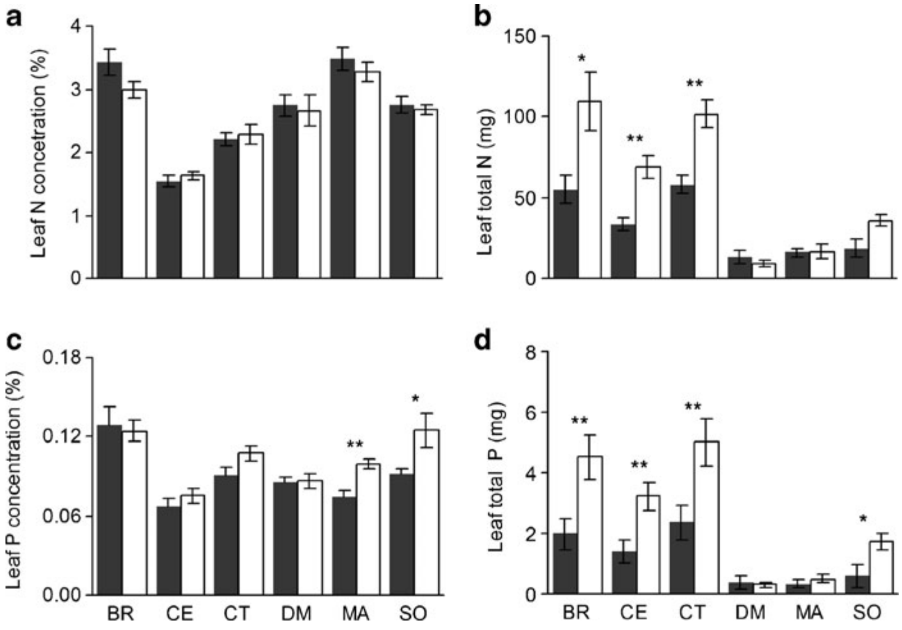


Fig. 2 Mean (+ SE) leaf N **a** and P concentration **c** and their total content **b**, **d** in Cerradão and SDF seedlings growing over Cerradão (filled bars) and SDF soils (open bars). * $P<0.05$, ** $P<0.01$, for soil origin effect within species (*t*-test; *df*=1,10). SDF species: BR: *Balfourodendron riedelianum;* CE: *Cariniana estrellensis;* CT: *Centrolobium tomentosum*. Cerradão species: DM: *Dimorphandra mollis*; MA: *Machaerium acutifolium*; SO: *Stryphnodendron obovatum*

Table 3 Relationship (Pearson's correlation) between soil nutrient availability and total nutrient content in leaf biomass of Cerradão and SDF seedlings

Species	N	P	K	Ca	Mg	S
BR	**0.94 (<0.001)**	**0.77 (0.003)**	**0.77 (0.003)**	0.36 (0.257)	**0.83 (0.001)**	0.32 (0.314)
CE	**0.81 (0.002)**	**0.74 (0.006)**	**0.88 (<0.001)**	**0.78 (0.003)**	**0.77 (0.004)**	0.28 (0.371)
CT	**0.70 (0.012)**	**0.93 (<0.001)**	**0.87 (<0.001)**	**0.80 (0.002)**	**0.79 (0.002)**	**0.64 (0.024)**
DM	−0.48 (0.116)	−0.46 (0.135)	−0.35 (0.260)	0.04 (0.905)	−0.55 (0.062)	−0.24 (0.457)
MA	0.33 (0.298)	0.15 (0.630)	0.12 (0.710)	0.36 (0.252)	0.03 (0.925)	0.21 (0.503)
SO	**0.72 (0.008)**	**0.82 (<0.001)**	**0.87 (<0.001)**	**0.66 (0.018)**	**0.64 (0.026)**	0.33 (0.300)

Significant correlation coefficients ($P<0.05$) are in bold. $n=12$. **SDF species**: *BR Balfourodendron riedelianum, CE Cariniana estrellensis, CT Centrolobium tomentosum*. **Cerradão species**: *DM Dimorphandra mollis*, *MA Machaerium acutifolium*, *SO Stryphnodendron obovatum*

Discussion

The higher fertility of the SDF soil we found is consistent with previous studies that found higher levels of soil nutrients in forests, in other forest-savanna boundaries (Furley and Ratter 1988; Bowman 1992; Ratter 1992; Ruggiero et al. 2002). However, regardless of the differences in nutrient availability between the SDF and Cerradão soils, we did not find differences in seedling survivorship that could be linked to soil origin for any of the plant species we investigated. This indicated that soil nutrient availability alone would not exclude, at least in the early establishment stage of these plants, the presence of seedlings from SDF species on Cerradão soil and vice-versa. Therefore, we reject our first hypothesis that Cerradão and SDF species could not establish on the soil of the contrasting vegetation type.

Except for *D. mollis*, which had a negative RGR, the growth rates we found are within the range of values reported for SDF and Savanna tree species and species from other vegetation types (see Wright and Westoby 1999; Hoffmann and Franco 2003; Scarpa 2007). In addition, except for the higher values for N leaf concentration; in general, leaf nutrient concentration values we found are in the range of values reported in similar greenhouse experiments in other vegetation types (see Sardans et al. 2005, 2006).

Also in contrast to our initial prediction, Cerradão species did not show better performance on their home-soil. Instead, one of the three species we investigated (*S. obovatum*) grew more on the SDF soil and the other two species had similar growth on their native soil than on nutrient-rich SDF soil. SDF species did grow more on their home-soil, however, indicating that SDF species

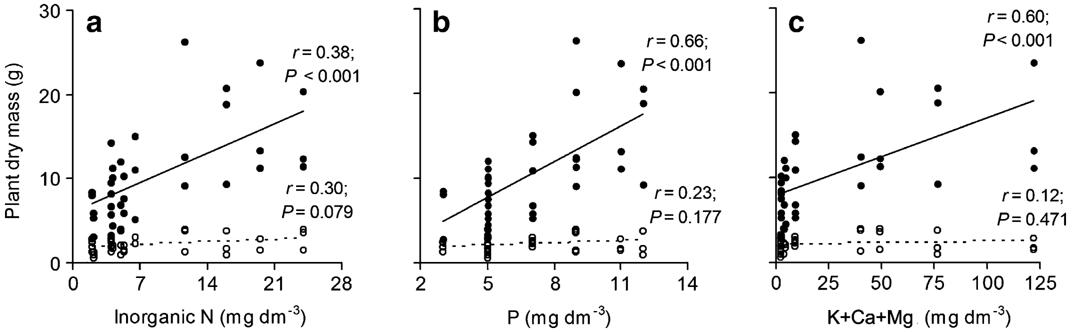


Fig. 3 Relationship between plant biomass and soil inorganic N **a**, P **b** and sum of K+Ca+Mg **c** availability, considering species grouped by vegetation type ($n=36$, 12 for each species). Regression lines are best fits. SDF species: solid lines, filled circles. Cerradão species: dashed lines, open circles

Table 4 Relationship (Pearson's correlation) between soil nutrient availability and seedlings biomass after 9 months

Species	Inorganic N	P	Sum of K+Ca+Mg
BR	**0.96 (<0.001)**	**0.87 (<0.001)**	**0.89 (<0.001)**
CE	**0.81 (<0.001)**	**0.88 (<0.001)**	**0.7 (0.002)**
CT	**0.65 (0.023)**	**0.79 (0.002)**	**0.64 (0.024)**
DM	−0.25 (0.429)	−0.13 (0.688)	−0.22 (0.498)
MA	0.22 (0.494)	−0.06 (0.844)	−0.1 (0.747)
SO	**0.72 (0.009)**	**0.74 (0.006)**	0.54 (0.072)

Significant correlation coefficients ($P<0.05$) are in bold. $n=12$. SDF species: *BR Balfourodendron riedelianum, CE Cariniana estrellensis, CT Centrolobium tomentosum*. Cerradão species: *DM Dimorphandra mollis*; *MA Machaerium acutifolium*, *SO Stryphnodendron obovatum*

show some level of home-soil advantage. Thus, the results we found with respect to growth on the two soils, confirms only part of our initial prediction that seedlings would perform better on their home-soil. This hypothesis was confirmed for SDF species, which performed better in their more fertile soils, but was rejected for savanna species, because no Cerradão species showed a home-soil advantage.

For two of the three Cerradão species, our findings did not corroborate previous studies, which demonstrated that savanna species commonly respond positively to higher levels of nutrient availability (Haridasan 2000; Barger et al. 2002; Kozovits et al. 2007). However, our results do corroborate the ones found for grasses in African savannas (Wang et al. 2010) and support the general hypothesis that growth of wild species from nutrient-poor habitats may not always respond to nutrient additions or higher soil fertility (Chapin et al. 1986). It is also possible that the physiological and morphological adaptations of Cerradão species for being able to grow on nutrient-poor Cerradão soils restrict them to respond when more soil nutrients are made available. Indeed, the ability of a plant to tolerate stress is frequently inversely correlated with its competitive ability (Fine et al. 2004; Liancourt et al. 2005; Brenes-Arguedas et al. 2008).

Our results showed that SDF species have both higher growth rates than Cerradão species in Cerradão soil and home-soil advantage (Fig. 1b). The higher growth rates of SDF species compared to Cerradão species, even on Cerradão soils, corroborate other studies which found that when other factors are controlled, species from more fertile soils tend to show a better growth response not only on their home-soil but also on contrasting soils with lower nutrient availability (Fine et al. 2004). These findings suggest that other factors may be interacting with soil fertility in order to prevent SDF species from outcompeting Cerradão species on savanna patches. Beyond soil nutrient availability, other characteristics such as water availability (Bowman and Panton 1993; Hoffmann et al. 2004), light intensity (Hoffmann and Franco 2003), fire occurrence (Hoffmann et al. 2003), and biological interactions (Bowman and Panton 1993) have been suggested to be important factors controlling the establishment of seedlings and also influencing the dynamics of forest and savanna boundaries. However, the home-soil advantage of SDF species does indicate that the lower nutrient availability of the savanna soil reduces the growth of SDF seedlings, which in turn affects their potential to accumulate biomass at savanna sites. Therefore, our result may not lend support to the idea that soil nutrient availability does not inhibit development of forests on nutrient-poor soils, as proposed by Bond (2010).

One important point to be considered is that we evaluated only plants in their early stage of life. According to Aerts and Chapin (2000), fast-growing species, such as SDF trees, tend to have higher biomass increments early in life compared with slow growing species, even in nutrient-poor environments. However, in the long-term and under nutrient-limited conditions, species with low nutrient loss rates can outcompete species with high nutrient loss rates, even when these species have a greater competitive ability for nutrient uptake (Berendse 1994).

All leaf traits, including leaf nutrient concentration, varied significantly among species (Table 2, Appendix 1). Leaf functional traits are widely variable according to limitations imposed by the environment and hence commonly reflect plants resource investment strategies and aspects of species life history (Wright et al. 2004; Poorter and Bongers 2006). Several studies have also reported that leaf functional traits can be highly plastic when plants are grown in environments with different levels of resources availability (Witkowski and Lamont 1991; Sultan 2000; Hoffmann and Franco 2003, Kozovits et al. 2007). In contrast, in our study most of the leaf functional traits, including foliar N concentration, did not change in response to soil nutrient availability (two soil origins) (Table 2, Fig. 1). Despite this lack of plasticity in leaf functional traits, four of the six species we studied did increase their total leaf area and accumulated more biomass when growing on the soil with higher nutrient availability (SDF soil) (Table 2, Fig. 1). These data strongly suggest that in some cases, the analysis of only a subset of leaf functional traits, such as SLA, LAR and foliar N concentration, may be not as informative as an integrative analysis of plant growth performance that includes analysis of plant biomass and total leaf area. In addition, species increased their root:shoot ratio when were grown on the nutrient-poor Cerradão soil, suggesting morphological plasticity of roots in response to variation in nutrient availability (Jackson et al. 1990; Wang et al. 2006). However, we did not find a consistent pattern of higher root:shoot ratio for savanna species in comparison with forest species (Appendix 1), as found in other studies (Hoffmann et al. 2004).

Cerradão and SDF species have clearly contrasting growth strategies. SDF species increased their growth with increases in nutrient availability (Fig. 3). According to the growth strategies described by Grime (1977), SDF species behaved as competitors, rapidly accumulating aboveground biomass and nutrients. These species evolved in a more competitive environment with higher nutrient and lower light availability, where fast-growing species with higher initial growth tend to be favored. In our study we saw that Cerradão species growth strategies were more variable; *S. obovatum* behaved similarly to SDF species, increasing biomass when more nutrients were available. On the other hand, *D. mollis* and *M. acutifolium* did not increase their growth with increasing nutrient availability, suggesting a “stress tolerant” behavior (Fig. 3). In fact, the Cerradão environment poses greater limitations for plant growth, such as lower nutrient availability and therefore, species which can tolerate these conditions will be more successful. These results confirm, in part, that species from nutrient-rich environments (in our case SDF) tend to be fast-growing species with higher relative growth rates and positive response to increases in nutrient availability, whereas species from nutrient-poor habitats (Cerradão) tend to possess traits typical of slow-growing or stress-tolerant species (Aerts 1999; Aerts and Chapin 2000).

In conclusion, our results demonstrated that Cerradão and SDF soils are remarkably different with respect to soil nutrient availability. We also found that SDF and Cerradão species tend to have distinct growth strategies with respect to soil nutrient availability. Collectively, our results indicate that the chemical attributes of the upper soil layer do not exclude the occurrence of seedlings of SDF woody species in savanna patches and vice-versa, at least in an initial stage of life. It is possible that the mechanisms controlling establishment of Cerradão and SDF seedlings in contact zones may result from the interaction of soil chemical attributes with other site factors such as herbivory, soil water availability, fire and/or light intensity. However, our findings also indicate that the upper soil layer has an effect on growth performance of SDF species, with these species demonstrating some home-soil advantage. This suggests that savanna soil reduces growth of forest species. Finally, in order to confirm our findings and improve our knowledge about the filters that effectively maintain contrasting floras in these forest-savanna boundaries, we suggest reciprocal transplanting and competitive field experiments testing soil and its interaction with other factors such as herbivory, water availability, fire and/or light intensity. A more detailed understanding of the interactions between vegetation, climate and edaphic factors is essential to better predict the impact of future changes in climate in the forest/savanna distribution.

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Appendix

Table 5 Mean (± SE) values for plant traits of tree seedlings grown on a greenhouse experiment with Cerradão and SDF soil. Within lines, means followed by different letters indicate significant differences between species ($P<0.05$, two-way Anova, followed by Tukey's post-hoc test). SDF species: BR: *Balfourodendron riedelianum;* CE: *Cariniana estrellensis;* CT: *Centrolobium tomentosum*. Cerradão species: DM: *Dimorphandra mollis*; MA: *Machaerium acutifolium*; SO: *Stryphnodendron obovatum*

Variables	SDF species			Cerradão Species		
	BR	CE	CT	DM	MA	SO
Biomass (g)	6.51±1.04 c	14.76±1.89 a	9.81±1.04 b	1.79±0.17d	2.25±0.3d	2.54±0.33d
Leaf area (cm^2)	534.61±89.47 b	637.45±76.45 ab	928.36±121.98 a	64.74±11.2d	85.39±16.19d	185.1±25.92 c
RGR (mg g^{-1} day^{-1})	13.45±0.85 a	7.09±0.43 b	7.85±0.5 b	−0.4±0.89d	4.24±1.02 c	5.98±1.14 bc
NAR (g m^{-2} day^{-1})	1.42±0.09 a	1.11±0.07 ab	0.78±0.04 bc	−0.06±0.15d	1.12±0.35 ab	0.62±0.12 c
SLA (cm^2 g^{-1})	220.95±3.97 b	201.47±5.5 bc	263.61±5.09 a	159.48±14.38d	183.87±9.06 c	192.35±5.43 c
LT (mm)	0.075±0.001 d	0.157±0.002 a	0.115±0.006 b	0.073±0.003 de	0.091±0.003 c	0.067±0.002 e
LD (g cm^{-2})	0.67±2.13 b	0.32±1.32 c	0.36±4.69 c	1.05±3.87 a	0.69±3.29 b	0.78±4.93 b
LAR (cm^2 g^{-1})	89.34±4.56 ab	44.94±2.97 c	97.67±6.44 a	34.91±4.27d	40.5±3.28cd	70.58±5.86 b
LMR	0.4±0.01 a	0.22±0.01 b	0.37±0.01 a	0.22±0.02 b	0.21±0.02 b	0.37±0.03 a
Root:shoot ratio	0.54±0.03 e	1.44±0.1 b	0.83±0.08d	1.11±0.06 c	2.12±0.23 a	1.12±0.14 c
Leaf N (%)	3.21±1.31 a	1.59±0.56d	2.25±0.86 c	2.7±1.45 bc	3.38±1.21 a	2.72±0.74 b
Leaf P (%)	0.13±0.08 a	0.07±0.04d	0.1±0.05 bc	0.09±0.03 c	0.09±0.05 c	0.11±0.08 b
Leaf K (%)	1.21±0.56 a	0.62±0.81 c	0.77±0.46 b	0.48±0.48d	0.5±0.25cd	1.07±0.68 a
Leaf Ca (%)	0.41±0.41 b	0.46±1.65 b	0.9±1.38 a	0.46±0.8 b	1.08±1.49 a	1.06±1.19 a
Leaf Mg (%)	0.18±0.23 a	0.19±0.17 a	0.14±0.13 b	0.05±0.03d	0.1±0.04 c	0.16±0.08 ab
Leaf S (%)	0.36±0.25 b	0.16±0.05d	0.12±0.07 e	0.16±0.28 de	0.28±0.33 c	1.28±0.52 a

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