



Can native vegetation recover after slash pine cultivation in the Brazilian Savanna?

Rodolfo Cesar Real de Abreu^{a,*}, Geissianny Bessão de Assis^{b,1}, Sergianne Frison^{b,1}, Andrea Aguirre^{c,2}, Giselda Durigan^{a,d,3}

^a Research Center on Water Resources and Applied Ecology, Engineering School of São Carlos, University of São Paulo, Avenida Trabalhador São Carlense, 400, CP 292, CEP 13.560-970 São Carlos, SP, Brazil

^b São Paulo State University, UNESP – Agronomic Sciences Faculty, Natural Resource Department, Rua José Barbosa de Barros, 1780, CP 237, CEP 18610-307 Botucatu, SP, Brazil

^c Department of Biological Sciences, Luiz de Queiroz College of Agriculture, University of São Paulo, Piracicaba, SP, Brazil

^d Forestry Institute of São Paulo State, Assis State Forest, CP 104, CEP 19802-970 Assis, SP, Brazil

ARTICLE INFO

Article history:

Received 12 May 2011

Received in revised form 24 June 2011

Accepted 26 June 2011

Available online 22 July 2011

Keywords:

Forest plantations

Exotic species

Savanna

Pinus elliottii Engelm.

Intermediate disturbance hypothesis

ABSTRACT

There is a widespread view that forest plantations with exotic species are green deserts, unable to sustain biodiversity. Few studies have demonstrated, however, that planted stands of exotic trees have a greater negative effect on the plant diversity of savanna vegetation. We compared the native woody flora under four stands of slash pine of about 45 years old with four stands where the previously existing native Cerrado vegetation was preserved and protected from disturbances for the same period, has changed into dense vegetation – the “cerradão”, at Assis municipality, São Paulo State, Brazil. Aiming at understanding the potential ecological filters driving these communities, we assessed air and soil humidity, light availability and classified the native species on the basis of shade tolerance, dispersal syndrome and biomes in which they occur (Atlantic Forest or Cerrado). We recorded an average of 70 (± 13) species under pine stands and 54 (± 16) species in cerradão. Of the total of 136 species recorded, 78 occurred in both habitats, eight were exclusive to the “cerradão” (shade tolerant and also occurring in forest ecosystems) and 18 were recorded only under pine stands (82% heliophytic, exclusive to the Cerrado biome). Among the functional attributes and abiotic variables analyzed, only light availability explained the floristic differences found. Since richness was higher under pine, we refuted the hypothesis that exotic species constrain the establishment of the native species richness in the understory. On the other hand, the dark environment under the closed-canopy of the “cerradão” acts as a filter inhibiting the establishment of typical Cerrado species. Since pine stands, if managed in long cycle, maintain a reasonable pool of Cerrado endemic species in the understory pine plantations may be a good starting point for savanna restoration.

© 2011 Elsevier B.V. All rights reserved.

1. Introduction

The Cerrado is reported as the most diverse savanna in the world, where more than 12,000 species of vascular plants have been recorded (Mendonça et al., 1998), with a high proportion of endemic species, estimated at 44% (Klink and Machado, 2005). Many species are exclusive to this ecological region, and thus the richness and specificity of habitats reflect the high proportion of rare plants found in this biome (Ratter et al., 2003). The Cerrado (*sensu lato*) vegetation comprises a physiognomic gradient ranging from open grasslands (*clean field*, *dirty field* and *closed field*), with an intermediate savannic physiognomy (*cerrado stricto sensu*) prevailing and the cerradão or *woodland savanna*, which is a forest

type (Eiten, 1972; Ribeiro and Walter, 1998). The “cerradão” is almost closed woodland with canopy cover of 50–90% (Oliveira-Filho and Ratter, 2002). A number of natural factors, such as depth, texture, nutrient and water availability in soil, as well as human disturbances such as fire, grazing, selective logging, etc., have been reported as possible conditioning factors influencing that gradient (Goodland and Ferri, 1979; Coutinho, 1990; Eiten, 1994; Oliveira-Filho and Ratter, 2002; Hoffmann and Franco, 2003; Henriques, 2005; Ribeiro and Walter, 2008; Assis et al., 2011). Among these factors, fire stands out by affecting the density of the woody layer of Cerrado vegetation. While frequent fires favor the ground layer and produces more open physiognomies, the protection from fire allows the woody vegetation to increase in biomass (Oliveira-Filho and Ratter, 2002). With the exception of some species of the “cerradão”, which are restricted to this forest physiognomy (Furley and Ratter, 1988), plant species of the Cerrado are mostly heliophytic, xeromorphic and fire adapted. Such attributes give the Cerrado a high resilience, quickly and easily recovering naturally even after major disturbances in many situations (Durigan, 2003; Hoffmann, 1999).

* Corresponding author. Tel.: +55 16 3373 8253.

E-mail addresses: rodolfodeabreu@gmail.com, rcra@sc.usp.br (R.C.R. Abreu), giselda@femane.com.br (G. Durigan).

¹ Tel.: +55 14 3811 7132.

² Tel.: +55 19 3429 4431.

³ Tel.: +55 18 3325 1066.

Considered as a diversity hotspot on a global scale (Myers et al., 2000), the Cerrado (Brazilian savanna) covered approximately 2 million square kilometers, mainly in central Brazil (Klink and Machado, 2005). Currently, in approximately half of that area, the native vegetation was severely modified or eradicated, replaced by different forms of cultivation, including forestry, which occupies an area of 3,165,436 ha, estimated from satellite images of 2002 (Sano et al., 2009). Forestry, if carried out with invasive alien species, as is the case of *Pinus* genera in various regions of the world (Almeida et al., 2010; Richardson et al., 1994; Zanchetta and Pinheiro, 2007; Zalba and Villamil, 2002), can cause diversity losses, over and above those normally arising from the conversion of natural areas for forestry.

There is a widespread view that forest plantations with exotic species are green deserts (Lima, 1996). However, in different regions of the world, studies have shown that such planted forests can catalyze the natural regeneration of native species in the understory, including sustaining rare and endemic species (Camus et al., 2006; Pawson et al., 2010; Viani et al., 2010). The hypothesis that the cultivated exotic species could catalyze natural regeneration of native species was confirmed by Modona et al. (2010) under pine plantations in the riparian zone in the cerrado region, close to areas of this study. In a recent review, Viani et al. (2010) indicate that successful regeneration under commercial stands can be determined by factors such as: (1) the management and land use history of the area (Lemenih and Teketay, 2005), (2) proximity of fragments of native vegetation (Yirdaw and Lukkanen, 2003), (3) age of the plantation (Geldenhuys, 1997), (4) the species planted (Geldenhuys, 1997) and (5) canopy density (Bone et al., 1997; Barbosa et al., 2009). Management practices of the cultivated species also exert influence, since cleaning the understory is widely used in forest plantations (Camus et al., 2006). Although these studies demonstrate the potential for regeneration of native vegetation under commercial stands, the mechanisms by which the alien species influence the community assemblage in the understory are not yet understood. In addition, these studies, in general, lack comparison with reference ecosystems, to check the representativeness of the regional pool of species under the exotics.

Brazilian environmental laws and conservation policies have undergone recent changes. Thus, large areas of commercial cultivation of exotic trees on public and private lands must be reverted to native vegetation. The question posed by this demand is: can the native vegetation naturally reestablish itself under pure plantations of exotic species or are interventions necessary for its restoration? The question is examined here for the savanna vegetation of southeastern Brazil (the Cerrado). This study was conducted to evaluate the potential for natural regeneration of native cerrado vegetation under cultivated stands of *Pinus elliottii*, and to understand the mechanisms influencing the plant community assemblage. Considering that management practices cause impact to the pine understory and that the structure of the planted forest is considerably different from the native vegetation, we start from the premise that the planted forests would act as a filter, hindering the entry of the native species of cerrado. Based on these assumptions, we raise two hypotheses: (1) the plant species richness under pines is lower in comparison to the native vegetation, and (2) the species assemblage of the two habitats is functionally distinct, and that it is driven by ecological filters.

2. Material and methods

2.1. Study area

The Assis State Forest and the Assis Ecological Station form a continuous area of 4480 ha located in the southwestern region of São Paulo state, between coordinates 22° 33' 20" to 22° 37' 41" S,

and 50° 24' 48" to 50° 21' 27" W, with an average altitude of 562 m above sea level. Four soil types occur in the whole area (Juhász et al., 2006), from which we selected for this study only patches of Oxisol, located on the upper slopes (Max et al., 2007). The area is in a transition zone between the climate types Cwa and Cfa, according to Köppen's classification, which is defined as humid subtropical climate. Average annual rainfall is about 1300 mm, the length of the dry season varies between years (Gênova et al., 2007), and severe frosts can occasionally occur.

All the studied areas were occupied by Cerrado *lato sensu* vegetation and used as pasture until the early 1960s, when the native vegetation started to be replaced by forestry with exotic species, mostly *P. elliottii* var. *elliottii* – slash pine. *P. elliottii* is a fast-growing tree species originally from Florida, USA that was introduced to Brazil in 1936 (Kronka et al., 2005). It is native from pine Flatwoods, a kind of wet savanna where arboreal stratum is composed mostly by pine trees that are capable of change light availability to the assemblages of the lowers strata (Brewer, 1998). When the pine plantations started, some stands of native vegetation were maintained, where the plant community has changed considerably in its structure over the last decades, suffering an increase in biomass after suppression of fire and cattle grazing. Typical savanna (cerrado *sensu stricto*) is confined at present to less than 5% of the area (Pinheiro and Durigan, 2009), mostly evolving towards the cerradão (forest physiognomy), which has a basal area >20 m² ha⁻¹ (Assis et al., 2011). The matrix around these fragments is fully occupied by stands of pine and eucalyptus, which have been managed for resin or timber production (Max et al., 2007). The landscape, at present, is a mosaic of forestry and native vegetation stands.

Data collection for this study was carried out in February and March 2010, in four replicates of two different habitats or vegetation types: (1) commercial stands of slash pine and (2) fragments of cerradão, used for comparison. The stands of *P. elliottii* were planted between 1962 and 1964, after cerrado deforestation by using huge chains pulled by two bulldozers, which was the usual practice at the time. This operation was followed by conventional tillage – plowing and harrowing. The planted pine forest plots underwent four thinnings for timber exploitation since the 1970s, and the native vegetation sprouting in the understory was cut once a year, since it was inconvenient for resin exploitation. These interventions have been suspended in the last 15 years, and the current density of pine trees is approximately 300 individuals ha⁻¹, with an average height estimated in 18 m.

2.2. Floristic and functional composition

A rapid botanical inventory was carried out in each area, on the basis of the method adopted by Filgueiras et al. (1994) and Ratter et al. (2001), considered as the most efficient to survey the cerrado floristic composition (Walter and Guarino, 2006). By this method, all species observed in intervals of 15 min are recorded, until the stabilization of the curve species vs. time, with the registration of less than three new species in the last interval.

Since the planted stands and the native fragments had different size, the smallest with 7 ha, and in order to minimize the influence of this variation, none of them were surveyed beyond an area of 10 ha. All woody species comprising shrubs, palms and trees were recorded in each area. Species whose identification in the field were not possible were collected for later identification with the support of literature, herbaria or specialists, and were deposited in the local botanical collection.

In order to investigate possible functional patterns in the floristic composition of each habitat, species were classified according to functional groups based on the following attributes: (1) dispersal syndrome (anemochory, or zoochory or autocory) and (2) shade tolerance (Batalha et al., 1997; Weiser and Godoy, 2001; Durigan

et al., 2004; Tannus et al., 2006). Species were also classified by their ecological range, as occurring in the Cerrado or the Atlantic Forest, based on a previous study on the flora of the study area (Durigan et al., 2004). Species occurring only in the Cerrado were considered as endemic to this biome.

Proportion of functional traits was calculated for the whole list of species surveyed in the eight areas, and later for groups of species which were exclusive to one vegetation type or the other, more suitable for the identification of filters. We considered as exclusive those species occurring in at least two areas with similar vegetation. Species occurring in only one of the eight areas were not included in the analyses.

2.3. Abiotic factors

Air temperature (°C), soil moisture (%), relative humidity (%), and canopy openness (%) were recorded in the eight areas, as explanatory variables for the performance of any filters on the community assemblage. The relative humidity and air temperature were measured simultaneously during 24 continuous hours, using eight digital thermohygrometers (Impac TH02), installed at a distance of 50 m from the edge inwards. The devices were installed above the canopy of the cerradão and above the canopy of native vegetation under *P. Elliottii*, at an approximate height of 10 m. Soil moisture was determined by gravimetry (Catani et al., 1955; EMB-RAPA, 1997), with three samples (composed by ten sub-samples), collected at intervals of seven days after rain in all areas. Canopy cover was obtained in each area by taking hemispherical photographs, using fisheye lens (Nikkon FC-E9), and positioned 1 m from the surface with a tripod. Four photographs were obtained for each of the eight areas, totaling 32 images. The photographs were taken before sunrise or just after sunset, with homogeneous sky, to avoid overestimation of brightness. Each photograph was handled in software Sidelook 1.0 (Nobis, 2005), auto-mode threshold, with the maximum contrast of blue. After converting images to black and white, the photos were analyzed by the Gap Light Analyzer 2.0 software (Frazer, 1999).

2.4. Data analysis

From a binary matrix (presence/absence) of species and the eight areas, a cluster analysis was performed, adopting the Jaccard's similarity index with average groups using vegan package in R (Oksanen et al., 2010). Two plant communities were considered floristically similar if the Index value surpassed 0.25 (Mueller-Dombois and Ellenberg, 1974). Chi-square tests were performed to compare the frequency of each functional group or species origin, between the two vegetation types. For this analysis, we considered that the expected frequency of each attribute for the set of species in each environment should be equal to the frequency of the attribute among all species in the eight areas together (null hypothesis). After verifying the normality of data and transforming proportion data using the arcsine of the square root, parametric tests were performed to test differences in abiotic variables between areas of cerradão and pine stands. For air relative humidity (%), mean temperature (°C) and canopy openness (%), a *t*-student test was applied. For soil moisture a MANOVA was performed, where the three-day samples in the same area were considered dependent. Multivariate analysis and graphics were made using R software (R Development Core Team, 2009).

3. Results

A total of 136 species were recorded (Table 1), distributed among 51 families. Under *P. Elliottii* stands, 122 species were

recorded in the four areas, with an average of 70 (± 13) species per sampled area. In the four cerradão fragments, 96 species were surveyed, with an average of 54 (± 16) species per area. From the total, 78 species were common to both vegetation types. Eight species were found exclusively in the cerradão and 18 species exclusively in the understory of pine stands. The sampling effort was similar in all the sampled areas (Fig. 1).

3.1. Functional groups

From the eight species exclusive to the cerradão, most are animal dispersed, shade-tolerant and occur also in the Atlantic Forest (Table 1). On the other hand, the species exclusive to the understory of *P. Elliottii* (18) were mostly zoochorous, shade intolerant (heliophytic) and endemic to the Cerrado biome. The cluster analysis (Fig. 2) of the eight areas showed two groups: four areas of cerradão (C1–C4) on one side, and four pine stands on the other side (P1–P4). The floristic difference between these groups, however, is tenuous. The lowest value of the Jaccard's similarity index between areas was 46%, clearly over the 25% threshold below which two areas should be considered floristically distinct (Mueller-Dombois and Ellenberg, 1974). When analyzed the two sets of species – all species under pine and all species in the cerradão, the floristic similarity between the two environments is even higher (64%; Fig. 2).

There were no differences between the frequencies of dispersal syndromes between vegetation types ($\chi^2 = 5.887$; $\chi^2_{0.05(2df)} = 5.991$), both similar to the expected (null hypothesis accepted). The frequency of Cerrado endemic species in the two vegetation types (Fig. 3A) is different (null hypothesis refuted), being higher under pine and lower than expected in the cerradão ($\chi^2 = 14.264$; $\chi^2_{0.001(1df)} = 10.828$). In addition, the frequency of shade-tolerant species (Fig. 3B) was higher in the cerradão than under pines, based on the entire set of species ($\chi^2 = 50.510$; $\chi^2_{0.001(1df)} = 10.828$) (null hypothesis rejected).

Analyzing only those species exclusive from pine stands or cerradão on the basis of shade tolerance and ecological range, a remarkable difference is observed. From the species recorded only under *P. Elliottii*, 85% are shade intolerant and 82% are endemic to the Cerrado biome. Whereas, all species found only in the cerradão are shade tolerant and also occur in the Atlantic Forest (Table 1).

3.2. Abiotic factors

No differences were observed between pine stands and cerradão concerning the relative humidity ($t = -0.6537$, $P = 0.558$), air temperature ($t = -0.6614$, $P = 0.533$) or soil moisture (MANOVA: Pillai Trace = 0.1487, $F_{3, 20} = 1.1645$, $P = 0.348$). Canopy openness was higher in the pine stands than in the cerradão (Figs. 4 and 5; $t = -4.54$; $P < 0.001$).

4. Discussion

Refuting the hypothesis formulated initially, the richness of woody species was higher under the pine stands than in fragments of native vegetation, the cerradão. The unexpected higher richness under the pine stands led to the formulation of a hypothesis *a posteriori*, that ecological filters should be more restrictive in the shaded environment of the cerradão, limiting the occurrence of heliophytic species, endemic to the Cerrado, which were only recorded under pine.

Beneath the stands of pine, some endemic species of open types of savanna (cerrado *stricto sensu*) were found, which tend to disappear as the thickening of vegetation proceeds (Pinheiro and Durigan, 2009), especially *Annona coriacea*, *Campomanesia adamantium*, *Eugenia punicifolia*, *Handroanthus ochraceus*,

Table 1

Species sampled in the Ecological Station of Assis in February 2010.

Species	DS	ST	B	P/ C
<i>Acosmium subelegans</i> (Mohlenbr.) Yakovlev	An	—	Y	II
<i>Actinostemon conceptionis</i> (Chodat and Hassl.) Hochr.	At	+	N	II
<i>Aegiphila lhotskiana</i> Cham.	Z	—	Y	II
<i>Aeschynomene selloi</i> Vogel	At	—	Y	P ^b
<i>Agonandra brasiliensis</i> Miers ex Benth. and Hook. f.	Z	+	N	II
<i>Alibertia edulis</i> (Rich.) A. Rich. ex DC.	Z	+	Y	II
<i>Allagoptera campestris</i> (Mart.) Kuntze	Z	—	Y	P
<i>Amaioua intermedia</i> Mart.	Z	+	N	C
<i>Anacardium humile</i> A. St.-Hil.	Z	—	Y	P ^b
<i>Anadenanthera falcata</i> (Benth.) Speg.	At	—	N	II
<i>Andira anthelmia</i> (Vell.) J.F. Macbr.	Z	+	N	II
<i>Andira humilis</i> Mart. ex Benth	Z	—	Y	P ^b
<i>Annona coriacea</i> Mart.	Z	—	Y	P
<i>Annona crassiflora</i> Mart.	Z	—	Y	C ^b
<i>Annona dioica</i> A. St.-Hil.	Z	—	Y	P ^b
<i>Arrabidaea brachypoda</i> (DC.) Bureau	An	—	Y	C ^b
<i>Aspidosperma tomentosum</i> Mart.	An	—	Y	P ^b
<i>Baccharis dracunculifolia</i> DC.	An	—	N	II
<i>Banisteriopsis stellaris</i> (Griseb.) B. Gates	An	Ø	Ø	P ^b
<i>Bauhinia rufa</i> (Bong.) Steud.	At	—	Y	II
<i>Bowdichia virgiloides</i> Kunth	An	—	Y	II
<i>Bredemeyera floribunda</i> Willd.	An	—	Y	P
<i>Brosimum gaudichaudii</i> Trécul	Z	—	Y	II
<i>Byrsonima intermedia</i> A. Juss.	Z	—	Y	II
<i>Byrsonima laxiflora</i> Griseb.	Z	—	Y	II
<i>Campomanesia adamantium</i> (Cambess.) O. Berg	Z	—	Y	P
<i>Caryocar brasiliense</i> Cambess.	Z	—	Y	II
<i>Casearia sylvestris</i> Sw.	Z	+	N	II
<i>Cissampelos ovalifolia</i> DC.	Z	—	Y	P
<i>Connarus suberosus</i> Planch.	Z	—	Y	II
<i>Copaifera langsdorffii</i> Desf.	Z	+	N	II
<i>Cordia sellowiana</i> Cham.	Z	+	N	II
<i>Couepia grandiflora</i> (Mart. and Zucc.) Benth. ex Hook. f.	Z	—	Y	II
<i>Croton floribundus</i> Spreng.	Z	—	N	P ^b
<i> Cupania tenuivalvis</i> Radlk.	Z	+	N	C
<i>Cybistax antisiphilitica</i> (Mart.) Mart.	An	—	Y	P ^b
<i>Dalbergia miscolobium</i> Benth.	An	—	Y	II
<i>Dalbergia nigra</i> (Vell.) Allemao ex Benth.	An	—	N	P ^b
<i>Daphnopsis fasciculata</i> (Meisn.) Nevling	Z	+	N	C
<i>Davilla elliptica</i> A. St.-Hil.	Z	—	Y	P ^b
<i>Diospyros hispida</i> A. DC.	Z	—	Y	II
<i>Duguetia furfuracea</i> (A. St.-Hil.) Saff.	Z	—	Y	II
<i>Enterolobium gummiferum</i> (Mart.) J.F. Macbr.	At	—	Y	II
<i>Eriotheca gracilipes</i> (K. Schum.) A. Robyns	An	—	Y	II
<i>Erythroxylum campestre</i> A. St.-Hil.	Z	—	Y	P
<i>Erythroxylum cuneifolium</i> (Mart.) O.E. Schulz	Z	+	N	II
<i>Erythroxylum pelleterianum</i> A. St.-Hil.	Z	+	N	II
<i>Erythroxylum suberosum</i> A. St.-Hil.	Z	—	Y	P ^b
<i>Eugenia aurata</i> O. Berg	Z	—	Y	II
<i>Eugenia bimarginata</i> DC.	Z	—	Y	P
<i>Eugenia dysenterica</i> DC.	Z	—	Y	II
<i>Eugenia lambertiana</i> DC.	Z	+	Y	P
<i>Eugenia puniceifolia</i> (Kunth) DC.	Z	—	Y	II
<i>Famea montevidensis</i> (Cham. and Schltdl.) DC.	Z	+	N	C
<i>Gochnatia barrosii</i> Cabrera	An	—	Y	II
<i>Gochnatia polymorpha</i> (Less.) Cabrera	An	—	N	II
<i>Gomidesia affinis</i> (Cambess.) D. Legrand	Z	+	N	C
<i>Guapira noxia</i> (Netto) Lundell	Z	—	Y	II
<i>Guapira opposita</i> (Vell.) Reitz	Z	+	N	C
<i>Handroanthus ochraceus</i> (Cham.) Mattos	An	—	N	P
<i>Heteropterys byrsonimifolia</i> A. Juss.	An	—	Y	P
<i>Hymenaea stigonocarpa</i> Mart. ex Hayne	Z	+	Y	P
<i>Ilex paraguayensis</i> A. St.-Hil.	Z	+	N	C ^b
<i>Jacaranda caroba</i> (Vell.) A. DC.	An	—	Y	II
<i>Lacistema hasslerianum</i> Chodat	Z	+	N	II
<i>Leandra aurea</i> (Cham.) Cogn.	An	+	N	P ^b
<i>Licania humilis</i> Cham. and Schltdl.	Z	—	Y	II
<i>Lippia sidoides</i> Cham.	At	—	Y	C ^b
<i>Luehea candicans</i> Mart.	An	+	N	P ^b
<i>Luehea grandiflora</i> Mart.	An	+	N	II
<i>Mabea fistulifera</i> Mart.	Z	+	N	II
<i>Machaerium acutifolium</i> Vogel	An	—	Y	II
<i>Machaerium brasiliense</i> Vogel	An	—	N	P
<i>Maprounea guianensis</i> Aubl.	Z	+	N	II
<i>Matayba elaeagnoides</i> Radlk.	Z	+	N	II

Table 1 (continued)

Species	DS	ST	B	P/ C
<i>Memora axillaris</i> K. Schum.	An	—	Y	II
<i>Miconia albicans</i> (Sw.) Steud.	Z	+	Y	II
<i>Miconia fallax</i> DC.	Z	+	Y	II
<i>Miconia langsdorffii</i> Cogn.	Z	+	N	P ^b
<i>Miconia ligustroides</i> (DC.) Naudin	Z	+	Y	II
<i>Miconia sellowiana</i> Naudin	Z	+	N	II
<i>Miconia stenostachya</i> DC.	Z	+	Y	II
<i>Mimosa dolens</i> Vell.	Ø	—	Y	P
<i>Myrcia bella</i> Cambess.	Z	—	Y	II
<i>Myrcia fallax</i> (Rich.) DC.	Z	+	N	II
<i>Myrcia guianensis</i> (Aubl.) DC.	Z	—	N	II
<i>Myrcia lingua</i> (O. Berg) Mattos and D. Legrand	Z	—	Y	P
<i>Myrcia multiflora</i> (Lam.) DC.	Z	+	N	II
<i>Myrcia venulosa</i> DC.	Z	+	N	II
<i>Myrciaria floribunda</i> (H. West ex Willd.) O. Berg	Z	+	N	II
<i>Nectandra cuspidata</i> Nees and Mart.	Z	+	N	II
<i>Ocotea corymbosa</i> (Meisn.) Mez	Z	+	N	II
<i>Ormosia arborea</i> (Vell.) Harms	At	+	N	C ^b
<i>Ouratea spectabilis</i> (Mart. ex Engl.) Engl.	Z	—	Y	II
<i>Pavonia guerkeana</i> R.E. Fr.	At	—	Y	P ^b
<i>Pera obovata</i> (Klotzsch) Baill.	Z	+	N	II
<i>Peritassa campestris</i> (Cambess.) A.C. Sm.	Z	—	Y	II
<i>Persea wilddenovii</i> Kosterm.	Z	+	N	II
<i>Pinus elliottii</i> ^a Engelm.	An	—	N	II
<i>Piptocarpha rotundifolia</i> (Less.) Baker	An	—	Y	P
<i>Plathymenia reticulata</i> Benth.	At	—	Y	II
<i>Platypodium elegans</i> Vogel	An	—	N	II
<i>Pouteria ramiflora</i> (Mart.) Radlk.	Z	+	N	II
<i>Pradosia brevipes</i> (Pierre) T.D. Penn.	Z	—	Y	P ^b
<i>Protium heptaphyllum</i> (Aubl.) Marchand	Z	+	N	II
<i>Prunus myrtifolia</i> (L.) Urb.	Z	+	N	C ^b
<i>Pseudolmedia laevigata</i> Trécul	Z	+	N	C
<i>Psidium australe</i> Cambess.	Z	—	Y	P ^b
<i>Psidium guineense</i> Sw.	Z	—	Y	C ^b
<i>Psidium pohlianum</i> O. Berg	Z	—	Y	P ^b
<i>Qualea cordata</i> (Mart.) Spreng.	An	—	Y	II
<i>Qualea grandiflora</i> Mart.	An	—	Y	II
<i>Qualea multiflora</i> Mart.	An	—	Y	P
<i>Rapanea umbellata</i> (Mart.) Mez	Z	+	N	II
<i>Roupala montana</i> Aubl.	An	+	N	II
<i>Schefflera vinosa</i> (Cham. and Schltdl.) Frodin and Fiaschi	Ø	+	Y	II
<i>Senna rugosa</i> (G. Don) H.S. Irwin and Barneby	At	—	Y	II
<i>Siparuna guianensis</i> Aubl.	Z	+	N	II
<i>Solanum mauritanium</i> Scop.	Z	—	N	P ^b
<i>Solanum paniculatum</i> L.	Z	—	N	P ^b
<i>Strychnos brasiliensis</i> (Spreng.) Mart.	Z	+	N	II
<i>Stryphnodendron obovatum</i> Benth.	At	—	Y	II
<i>Styrax camporum</i> Pohl	Z	—	Y	C ^b
<i>Styrax camporum</i> Pohl	Z	—	Y	P ^b
<i>Syagrus romanzoffiana</i> (Cham.) Glassman	Z	+	N	II
<i>Symplocos mosenii</i> Brand	Z	+	N	C
<i>Tabernaemontana catharinensis</i> A. DC.	Z	+	N	P
<i>Tachigali vulgaris</i> L.F. Gomes da Silva and H.C. Lima	An	—	Y	C ^b
<i>Tapirira guianensis</i> Aubl.	Z	+	N	II
<i>Terminalia glabrescens</i> Mart.	An	—	N	II
<i>Tibouchina stenocarpa</i> (DC.) Cogn.	An	—	N	II
<i>Tocoyena formosa</i> (Cham. and Schltdl.) K. Schum.	Z	—	Y	P
<i>Vochysia tucanorum</i> Mart.	An	—	Y	II
<i>Xylopia aromatica</i> (Lam.) Mart.	Z	—	Y	II
<i>Zanthoxylum rhoifolium</i> Lam.	Z	+	N	P ^b

Functional groups studied: (1) dispersal syndrome, Z = zoochory; An = anemochory; At = autocory, (2) tolerance to frost and (3) shade tolerance: (+) positive or (−) negative, (4) endemism in cerrado: S = endemic, N = non-endemic; P/C: environment in which the species were recorded: II = both, P = P understory planting P. elliottii, C = cerrado.

^a Exotic species.

^b Did not meet the inclusion criteria, occurred in only one place.

Hymenaea stigonocarpa, *Qualea multiflora* and *Tocoyena formosa*. Among these, *H. stigonocarpa* is classified as “near threatened” in the threatened species list in São Paulo state (Mamede et al., 2007), which gives the understory of the pine stands the capacity

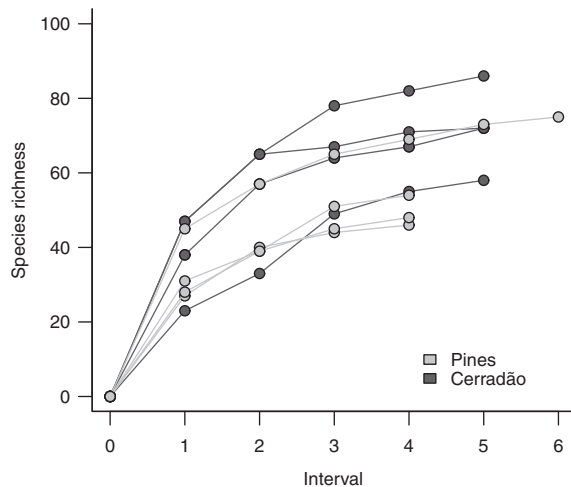


Fig. 1. Sampling effort showing the number of recorded species at each interval in the both studied areas; under pines and in cerrado. Recording was done during 15 min and stopped when a maximum of three species were observed in the last interval.

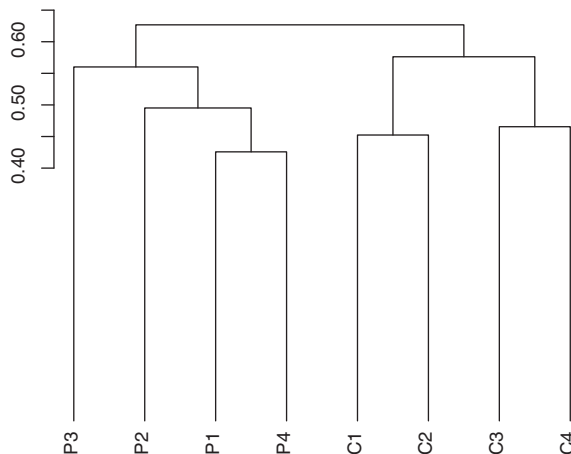


Fig. 2. Cluster Analysis (dissimilarity Jaccard's coefficient with groups average) the presence of native species in distinct environments: cerrado (C1 through C4) and under pine stands (P1–P4) in Assis, SP, Brazil.

to host species even at risk of extinction, as observed by Pawson et al. (2010) in New Zealand. The species composition of the two distinct vegetation types studied shows a tendency of floristic distinction between the environments of cerrado and pine understory (Fig. 2).

Although, *P. elliottii* is recognized as an aggressive invader over riparian and wet areas of cerrado (Zanchetta and Pinheiro, 2007; Almeida et al., 2010; Abreu and Durigan, 2011), in the eight studied areas, only a few young individuals of the exotic species were observed in regeneration either in the stands of pine or in the cerrado. In this way, further investigation about species invasiveness is needed since the presence of these young individuals can be seen as a sign of potential invasion itself, or the absence of a structured population can be seen as a sign of no invasion in these areas. As observed by Collautti and McIsaac (2004), no species is equally invasive on all environmental conditions.

Exploratory analysis of biotic and abiotic factors that could be acting as filters, based on functional traits of the species in each plant community, has shown that dispersal syndromes, soil humidity or air temperature and relative humidity, do not explain the differences between the floristic communities analyzed. The

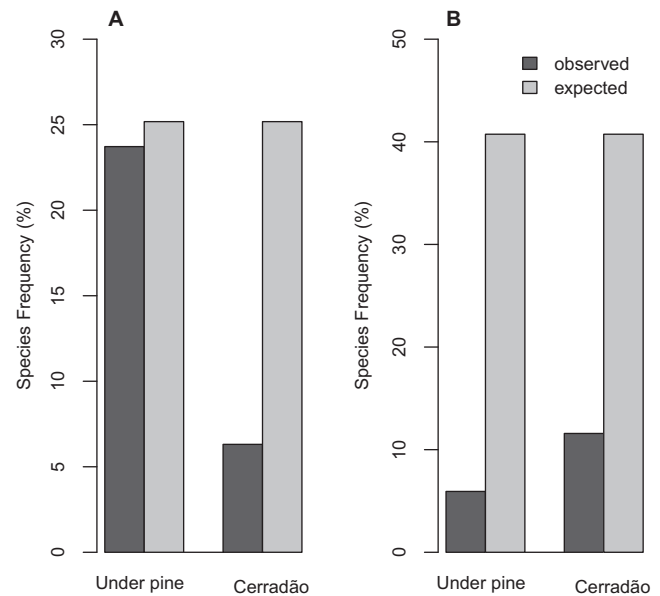


Fig. 3. (A) Frequency of endemic species of cerrado under pine stands and cerrado understory ($\chi^2 = 14.264$; $\chi^2_{0.001(1df)} = 10.828$) by the expected frequency (proportion of endemic species of the cerrado in the set of all species sampled), (B) Frequency of shade-tolerant species in pine stands and cerrado ($\chi^2 = 50.510$; $\chi^2_{0.001(1df)} = 10.828$) by the expected frequency (proportion of shade-tolerant species in the set of all species sampled).

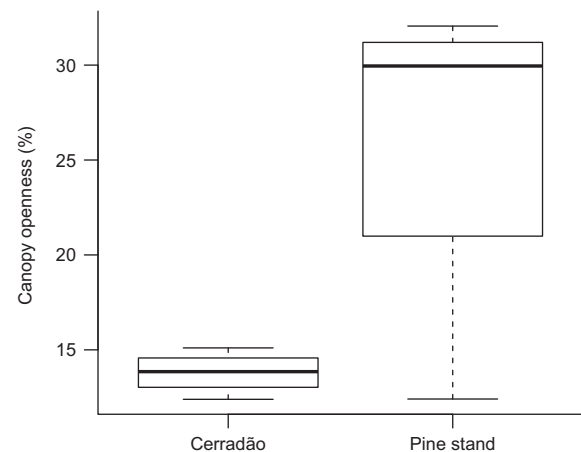


Fig. 4. Boxplot (mean \pm quartiles) comparing the canopy openness (%) of the cerrado and stands of *Pinus elliottii* in the Ecological Station of Assis, Brazil in 2010.

only variable that differed between the two environments studied was the canopy openness, which in this case represents the amount of light available to plants occurring in the understory. Since the species respond differently to the light intensities received (Souza and Valio, 2001; Valio, 2003), the light availability seems to be the ecological filter to determine the flora of each vegetation type. Considering that typical endemic Cerrado species are on the most heliophytic (Eiten, 1972; Goodland and Ferri, 1979; Franco, 2005), the shading becomes a limiting factor for the development of these species (Larcher, 2000; Lemos Filho et al., 2010). Therefore, the closed canopy of the cerrado retains much of the light, which is prevented from reaching the strata closer to the ground (Coutinho, 1990; Ribeiro and Walter, 2008). Thus, the 78 species that were common to both environments appear to have greater plasticity related to the condition of light availability and thus tolerate environments from sunny to shady. On the other hand, the more open canopy of long term managed pine stands al-



Fig. 5. Hemispherical photographs in cerrado vegetation canopy (top) and pine stand (bottom) in Assis, SP, Brazil. The white areas are open canopy that allow sunlight entrance.

lows the occurrence of typical cerrado species, which disappear from the *cerradão*. Additionally, the high resilience of cerrado vegetation must be considered. Even after decades of pine cultivation, some of the 18 cerrado endemic species occurring under pine are likely survivors from the previous native vegetation, which presents a very high capacity of sprouting many times from roots and stems after disturbances (Hoffmann, 1998; Saha, 2001; Viani, 2005).

In the Cerrado as well as in other savanna types in the world, the protection against disturbances such as fire and grazing implies a progressive increase in woody vegetation (Rawitscher, 1950; Archer et al., 1988; Bowman et al., 2001; Henriques and Hay, 2002; Hoffmann and Moreira, 2002). Thus, the open physiognomies of savanna, if protected, tend to evolve towards more closed vegetation, in places where soil conditions allow these changes (Goodland and Ferri, 1979; Ratter et al., 1988; Ratter, 1992; Felfili et al., 2000; Durigan and Ratter, 2006). In a recent study on the cerrado of Assis Ecological Station, Durigan and Pinheiro (2009) analyzed changes in vegetation over 44 years after full protection demonstrating gradual thickening, with all the open vegetation types (*clean field*, *dirty field*, *closed field* and *cerrado sensu stricto*) evolving into cer-

radão. This thickening of vegetation may explain the low occurrence of heliophytic species in the *cerradão* and the presence of these species under the pine stands. Rossato et al. (2008) consider that the disappearance of grasslands and savannic physiognomies, replaced by forest vegetation types, can lead to local extinction of many heliophytic plant species. The main consequences of this process would be physiognomic changes in the local flora, by the arrival of species most adapted to the new condition (Franco, 2005).

The current structure of the old pine stands, which allows for the new growth or colonization by heliophytic species typical of open forms of savanna, is the result of a series of management practices that include regular pruning and cleaning of understory for resin and timber exploitation. In Brazil, suppressing the native understory is also a way of ensuring the harvest licensing by environmental inspection (Viani et al., 2010), since the clearcutting can be prohibited when there is a high density of native plants in regeneration. Thus, these management practices that affect the understory are applied at intervals shorter than necessary, as a simple cleaning operation, which hinder the natural regeneration and increase the costs of production (Viani et al., 2010). Such practices cause great impacts on the understory and sometimes exclude completely the aerial parts of the native plants in regeneration. This practice results in low species richness in stands under management.

However, the high resilience of savanna by re-growth from underground structures remaining (Durigan 2003; Hoffmann, 1999) contributes to high species richness, after the cessation of impact, as observed in stands of pine trees about 15 years after the suspension of management practices. Connell (1978), in proposing the intermediate disturbance hypothesis, stated that the species diversity remains high when species composition changes continually and greater diversity is achieved when the disturbances are intermediate in frequency and intensity scales. The ecological succession immediately after the disturbance would only bring propagules of species from the vicinity and, if the frequency and intensity of disturbance were high, it would only allow the colonization by these species, resulting in low diversity. However, if the interval between disturbances is expanded, ecological succession progresses and the diversity of species increase. This seems to happen in the pine stands, which have periodically been managed at long intervals. Connell (1978) also reports that after a long period without disturbance, ecological succession stabilizes and diversity decreases due to the dominance of some species, which seems to happen with the *cerradão*, where shade tolerant trees become superior competitors, replacing heliophytic shrub species. Thus, the management of pine stands would be equivalent to an unusual disturbance, but of great intensity, capable of bursting the early stages of ecological succession (Connell, 1978). In areas occupied by *cerradão*, the occurrence of heliophytic species is likely to be restricted to the edges of the fragments (Max et al., 2007), where light is abundant.

On replying to the research question that motivated the study, the high native species richness observed under the pine stands shows that the impact on the cerrado vegetation caused by forestry practices over nearly five decades, was not enough to derail the passive restoration.

5. Conclusions

Contrary to expectations, the flora of shrubs and trees native to the cerrado under pine commercial stands in the study areas is richer than the flora of the adjacent undisturbed natural vegetation. The canopy of *cerradão* creates an environment of low light availability, acting therefore as an ecological filter, to inhibit the occurrence of shade intolerant species and encouraging the entry and

persistence of shade-tolerant species, which also occur in the Atlantic forest in the same region.

Although the flora cannot be considered different between the two environments, since a great number of species occur in both, canopy closure by native vegetation as a result of fire suppression is leading to a distortion of the local flora, with a tendency towards the disappearance of species endemic to the Cerrado biome. On the other hand, pine stands, managed in a long cycle, have maintained a reasonable pool of cerrado endemic species in the understory. Thus, planting operations in order to introduce new species are not necessary to restore the diversity of the native vegetation, all that is needed is to eliminate the cultivated exotic trees. Finally, we believe that after suppression of the pine trees, the same trend of vegetation canopy-closure and decrease in richness will succeed if disturbance (management practices, prescribed fires, grazing, etc.) will be definitely excluded from the system.

Acknowledgements

The authors thank EA Honda for collection and processing the soil samples, JM Torezan for lending fisheye equipment used in data collection and MS Suganuma for drawing graphical abstract, the Instituto Florestal for research permission, the Conselho Nacional de Desenvolvimento Científico e Tecnológico – CNPq, for support (Process 475286/2007-3) and research grants to RCR Abreu, G Durigan, and also the Fundação de Amparo à Pesquisa do Estado de São Paulo – FAPESP for MSc grant to GB Assis.

References

- Almeida, R.S.de, Cielo-Filho, R., de Souza, S.C.P.M., de Aguiar, O.T., Baitello, J.B., Pastore, J.A., Kanashiro, M.M., Mattos, I.F.A., Franco, G.A.D.C., Lima de, C.R., 2010. Campo Sujo Úmido: fisionomia de Cerrado ameaçada pela contaminação de *Pinus elliottii* Engelm. na Estação Ecológica de Itapeva, Estado de São Paulo. *Rev. Inst. Florest.* 22, 71–91.
- Archer, S., Scifres, C., Basshan, C.R., 1988. Autogenic succession in a subtropical Savanna: conversion of grassland to thorn woodland. *Ecol. Monogr.* 58, 111–127.
- Assis, A.C.C., Coelho, R.M., Pinheiro, E.S., Durigan, G., 2011. Water availability determines physiognomic gradient in an area of low-fertility soils under Cerrado vegetation. *Plant Ecol.* 212, online first.
- Barbosa, C.E.A., Benato, T., Cavalheiro, A.L., Torezan, J.M.D., 2009. Diversity of Regenerating Plants in Reforestations with *Araucaria angustifolia* (Bertol) O. Kuntze of 12, 22, 35, and 43 Years of Age in Paraná State, Brazil. *Restor. Ecol.* 17, 60–67.
- Batalha, M.A., Aragaki, S., Mantovani, W., 1997. Florística do cerrado em Emas, Pirassununga, SP. *Bol. Bot. Univ. São Paulo* 16, 49–64.
- Bone, R., Lawrence, M., Magombo, Z., 1997. The effect of a *Eucalyptus camaldulensis* (Dehn) plantation on native woodland recovery on Ulumba Mountain, southern Malawi. *For. Ecol. Manage.* 99, 83–99.
- Bowman, D.M.J.S., Walsh, A., Milne, D.J., 2001. Forest expansion and grassland contraction within a *Eucalyptus* savanna matrix between 1941 and 1994 at Litchfield National Park in the Australian monsoon tropics. *Glob. Ecol. Biogeogr.* 10, 535–548.
- Brewer, J.S., 1998. Patterns of plant species richness in a wet slash-pine (*Pinus elliottii*) savanna. *J. Torrey Bot. Soc.* 125, 216–224.
- Camus, J.M., Parrotta, J., Brockerhoff, E., Arbez, M., Jactel, H., Kremer, A., Lamb, D., O'Hara, K., Walters, B., 2006. Planted forests and biodiversity. *J. For.* 104, 65–77.
- Catani, R.A., Romano Gallo, J., Gargantini, H., 1955. Amostragem de solo, métodos de análise interpretação e indicações gerais para fins de fertilidade. *Boletim número 69. Secretaria da agricultura do estado de São Paulo. Instituto Agrônomo. Campinas.*, 29.
- Connel, J.H., 1978. Diversity in tropical rain forests and coral reefs. *Science* 199, 1302–1310.
- Coulatti, R.I., MacIsaac, H.J., 2004. A neutral terminology to define 'invasive' species. *Divers. Distrib.* 10, 135–141.
- Coutinho, L.M., 1990. Springer, Verlag, Berlin, pp. 82–105.
- Abreu, R.C.R.de, Durigan, G., (2011). Changes in the plant community of the Brazilian grassland savanna after 22 years of invasion by *Pinus elliottii* Engelm. *Plant Ecol. Divers.* online first. doi:10.1080/17550874.2011.594101.
- Durigan, G., 2003. Bases e Diretrizes para restauração da vegetação do cerrado. In: Kageyama, P.Y., Oliveira, R.E., Moraes, L.F.D., Mendes, F.B.G., Engel, V.L., Gandara, F.B. (Eds.), *Restauração Ecológica de Ecossistemas Naturais*. Botucatu: FEPAF, Botucatu, pp. 166–185.
- Durigan, G., Ratter, J.A., 2006. Successional changes in cerradão and cerrado/forest ecotonal vegetation in western São Paulo State, Brazil, 1962–2000. *Edinb. J. Bot.* 63, 119–130.
- Durigan, G., Siqueira, M.F., Franco, G.A.D.C., Contieri, W.A., 2004. A Flora Arbustivo-Arbórea do Médio Paranapanema: Base para a Restauração dos Ecossistemas Naturais. In: Vilas Bôas, O., Durigan, G. (Eds.), *Pesquisas em conservação e recuperação ambiental no Oeste Paulista: resultados da cooperação Brasil/Japão*. 1ª ed. São Paulo: Páginas & Letras, pp. 199–239.
- Eiten, G., 1972. The cerrado vegetation of Brazil. *Bot. Rev.* 38, 201–241.
- Eiten, G., 1994. Vegetação do Cerrado. In: M.N. Pinto (Org.), *Cerrado: Caracterização, Ocupação e Perspectivas*. Editora Universidade de Brasília, Brasília, pp. 17–73.
- EMBRAPA – Empresa Brasileira de Pesquisas Agropecuárias, 1997. Manual de métodos de análise de solo. Centro Nacional de Pesquisa de solos. 2ª ed., Rio de Janeiro.
- Felfili, J.M., Rezende, A.V., Silva Junior, M.C., Silva, M.A., 2000. Changes in the floristic composition of cerrado sensu stricto in Brazil over a 9 year period. *J. Trop. Ecol.* 16, 570–590.
- Filgueiras, T.S., Nogueira, P.E., Brochado, A.L., Guala, G.F., 1994. Caminhamento: um método expedito para levantamentos florísticos qualitativos. *Cad. Geocienc.* 12, 39–43.
- Franco, A., 2005. Biodiversidade de forma e função: implicações ecofisiológicas das estratégias de utilização de água e luz em plantas lenhosas do Cerrado. In: *Cerrado: ecologia, biodiversidade e conservação*. Scariot, A., Souza-Silva, J.C., Felfili, J.M., (Eds.), Ministério do Meio Ambiente, Brasília, pp. 179–196.
- Frazer, G.W., Canham, C.D., Lertzman, K.P., 1999. Gap Light Analyzer (GLA): imaging software to extract canopy structure and gap light transmission indices from true-colour fisheye photographs, users manual and program documentation. Copyright© 1999: Simon Fraser University, Burnaby, British Columbia, and the Institute of Ecosystem Studies, Millbrook, New York.
- Furley, P.A., Ratter, J.A., 1988. Soil resources and plant communities of the central Brazilian cerrado and their development. *J. Biogeogr.* 15, 96–108.
- Geldenhuys, C.J., 1997. Native forest regeneration in pine and eucalypt plantations in Northern Province, South Africa. *For. Ecol. Manage.* 99, 101–115.
- Gênova, K.B., Honda, E.A., Durigan, G., 2007. Processos hidrológicos em diferentes modelos de plantio de restauração de mata ciliar em região de cerrado. *Rev. Inst. Florest.* 19, 189–200.
- Goodland, R., Ferri, M.G., 1979. *Ecologia do cerrado*. EDUSP/Livraria Itatiaia Editora LTDA, São Paulo.
- Henriques, R.P.B., 2005. Influência da história, solo e fogo na distribuição e dinâmica das fitofisionomias no bioma do Cerrado. In: *Cerrado: ecologia, biodiversidade e conservação*. Scariot, A., Souza-Silva, J.C., Felfili, J.M. (Eds.), Ministério do Meio Ambiente, Brasília, pp. 73–92.
- Henriques, R.P.B., Hay, J.D., 2002. Patterns and dynamics of plant populations. In: Hoffmann, W.A., Moreira, A. (Eds.), *The role of fire in population dynamics of woody plants*. In: Oliveira, P.S., Marquis, R.S. (Eds.), *Ecology and Natural History of a Neotropical savanna: The cerrados of Brazil*. The University of Columbia Press, New York, pp. 159–177.
- Hoffmann, W.A., 1998. Post-burn reproduction of woody plants in a Neotropical savanna: the relative importance of sexual and vegetative reproduction. *J. Appl. Ecol.* 35, 422–433.
- Hoffmann, W.A., 1999. Fire and population dynamics of woody plants in a neotropical savanna: matrix model projections. *Ecology* 80, 1354–1369.
- Hoffmann, W.A., Franco, A.C., 2003. Comparative growth analysis of tropical forest and savanna woody plants using phylogenetically-independent contrasts. *J. Ecol.* 91, 475–484.
- Hoffmann, W.A., Moreira, A., 2002. The role of fire in population dynamics of woody plants. In: Oliveira, P.S., Marquis, R.S. (Eds.), *Ecology and Natural History of a Neotropical Savanna: The cerrados of Brazil*. The University of Columbia Press, New York, pp. 159–177.
- Juhász, C.E.P., Cursi, P.R., Cooper, M., Oliveira, T.C., Rodrigues, R.R., 2006. Dinâmica físico-hídrica de uma topossequência de solos sob savana florestada (Cerradão) em Assis, SP. *Rev. Bras. Cienc. Solo* 30, 401–412.
- Klink, A.C., Machado, R.B., 2005. A Conservação do Cerrado. *Megadiversidade* 1, 147–155.
- Kronka, F.J.N., Bertolani, F., Ponce, R.H., 2005. *A Cultura do Pinus no Brasil*. Sociedade Brasileira de Silvicultura, São Paulo.
- Larcher, W., 2000. *Ecofisiologia vegetal*. RiMa, São Carlos, SP, pp. 41–53.
- Lemenih, M., Teketay, D., 2005. Effect of prior land use on the recolonization of native woody species under plantation forests in the highlands of Ethiopia. *For. Ecol. Manage.* 218, 60–73.
- Lemos Filho, J.P., Barros, C.F.A., Dantas, G.P.M., Dias, L.G., Mendes, R.S., 2010. Spatial and temporal variability of canopy cover and understory light in a Cerrado of Southern Brazil. *Braz. J. Biol.* 70, 19–24.
- Lima, W.P., 1996. *Impacto ambiental do eucalipto*. 2 ed. São Paulo: EDUSP, p. 301.
- Mamede, M.C.H., Souza, V.C., Prado, J., Barros, F., Wanderley, M.G.L., Rando, J.G., 2007. *Livro Vermelho das espécies vegetais ameaçadas do Estado de São Paulo*. Instituto de Botânica, São Paulo, p. 165.
- Max, J.C.M., Melo, A.C.G., Honda, E.A., Durigan, G., Malícia, L.C., Souza, M.B.M., Cardoso, M.M., Bôas, O.V., Ramos, V.S., Contieri, W.A., 2007. Plano de Manejo da Floresta Estadual de Assis. IF Ser. Regist. 30, 1–80.
- Mendonça, R.C., Felfili, J.M., Walter, B.M.T., da Silva Jr., M.C., Rezende, A.V., Filgueiras, T.S., Nogueira, P.E., 1998. Flora vascular do Cerrado. In: Sano, S.M., de Almeida, S.P. (Eds.), *Cerrado: Ambiente e Flora*. Empresa Brasileira de Pesquisa Agropecuária, Planaltina, pp. 289–556.
- Modna, D., Durigan, G., Vital, M.V.C., 2010. *Pinus elliottii* Engelm como facilitadora da regeneração natural da mata ciliar em região de Cerrado, Assis, SP, Brasil. *Sci. For.* 85, 73–83.

- Mueller-Dombois, D., Ellenberg, H., 1974. Aims and methods in vegetation ecology. John Wiley & Sons, New York, NY.
- Myers, N., Mittermeier, R.A., Mittermeier, C.G., Fonseca, G.A., Kent, J., 2000. Biodiversity hotspots for conservation priorities. *Nature* 403, 853–858.
- Nobis, M., 2005. SideLook 1.1 – Imaging software for the analysis of vegetation structure with true-colour photographs. Available at: <http://www.appleco.ch>.
- Oksanen, J.F., Blanchet, G., Kindt, R., Legendre, P., O'Hara, R.B., Simpson, G.L., Solymos, P., Henry, M., Stevens, H., Wagner, H., 2010. *vegan*: Community Ecology Package. R package version 1.17-4. <http://CRAN.R-project.org/package=vegan>.
- Oliveira-Filho, A.T., Ratter, J.A., 2002. Vegetation Physiognomies and Woody Flora of the Cerrado Biome. In: Oliveira, P.S., Marquis, R.J. (Eds.), *The Cerrados of Brazil Ecology and Natural History of a Neotropical Savanna*. pp. 91–120.
- Pawson, S.M., Ecroyd, C.E., Seaton, R., Shaw, W.B., Brockerhoff, E.G., 2010. New Zealand's exotic plantation forests as habitats for threatened indigenous species. *NZ J. Ecol.* 34, 342–355.
- Pinheiro, E., Durigan, G., 2009. Spatial and temporal dynamics (1962–2006) of Cerrado vegetation types in a protected area, southeastern Brazil. *Rev. Bras. Bot.* 32, 441–454.
- R Development Core Team, 2009. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. Available from: <http://www.r-project.org/>.
- Ratter, J.A., 1992. Transitions between cerrado and Forest vegetation in Brazil. In: Furley, P.A., Proctor, J., Ratter, J.A. (Eds.), *Nature and dynamics of Forest – Savanna boundaries*, Chapman & Hall, London, pp. 417–430.
- Ratter, J.A., Leitão-Filho, H.F., Agent, G., Gibbs, P.E., Semir, J., Shepherd, G.J., Tamashiro, J., 1988. Floristic composition and community structure of a southern cerrado area in Brazil. *Notes R Bot. Gard. Edinb.* 45, 137–151.
- Ratter, J.A., Bridgewater, S., Ribeiro, J.F., 2001. Espécies lenhosas da fitofisionomia cerrado sentido amplo de 170 localidades do Bioma Cerrado. *B Herb Ezechias Paulo Heringer* 7, 5–112.
- Ratter, J.A., Bridgewater, S., Ribeiro, J.F., 2003. Analysis of the floristic composition of the Brazilian Cerrado vegetation. III: comparison of the woody vegetation of 376 areas. *Edinb. J. Bot.* 60, 57–109.
- Rawitscher, F., 1950. O problema das savanas brasileiras e das savanas em geral. *Anu. Bras. Econ. Florest.* 3, 32–38.
- Ribeiro, J.F., Walter, B.M., 1998. Fitofisionomias do bioma Cerrado. In: Sano, S.M., Almeida, S.P. (Eds.), *Cerrado: ambiente flora*. Embrapa-Cepac, Planaltina, pp. 87–166.
- Ribeiro, J.F., Walter, B.M.T., 2008. As principais fitofisionomias do bioma Cerrado. In: Sano, S.M., Almeida, S.P., Ribeiro, J.F. (Eds.), *Cerrado: ecologia e flora*. Embrapa Informação Tecnológica: Planaltina, DF: Embrapa Cerrados, Brasília, pp. 151–212.
- Richardson, D.M., Williams, P.A., Hobbs, R.J., 1994. Pine Invasions in the Southern Hemisphere: determinants of spread and invadability. *J. Biogeogr.* 21, 511–527.
- Rossato, D.R., Toniato, M.T.Z., Durigan, G., 2008. Flora fanerogâmica não-arbórea do cerrado na Estação Ecológica de Assis, Estado de São Paulo. *Rev. Bras. Bot.* 31, 409–424.
- Saha, S., 2001. Vegetation composition and structure of *Tectona grandis* (teak family Verbenaceae) plantations and dry deciduous forests in central India. *For. Ecol. Manage.* 148, 159–167.
- Sano, E.E., Rosa, R., Brito, J.L.S., Ferreira, L.G., 2009. Land cover mapping of the tropical savanna region in Brazil. *Environ. Monit. Assess.* 1, 1–12.
- Souza, R.P., Valio, I.F.M., 2001. Seed size, seed germination and seedling survival of Brazilian tropical tree species differing in successional status. *Biotropica* 33, 447–457.
- Tannus, J.L.S., Assis, A.M., Morellato, L.P.P.C., 2006. Fenologia reprodutiva em campo sujo e campo úmido numa área de cerrado no sudeste do Brasil. *Biota. Neotrop.* 6, 1–23.
- Valio, I.F.M., 2003. Seedling growth of understory species of a southeast Brazilian tropical forest. *Braz. Arch. Biol. Technol.* 46, 697–703.
- Viani, R.A.G., 2005. O uso da regeneração natural (Floresta Estacional Semidecidual e talhões de Eucalyptus) como estratégia de produção de mudas e resgate da diversidade vegetal na restauração florestal. 188 f. Dissertação (Mestrado em Biologia Vegetal), Universidade Estadual de Campinas, Campinas, SP.
- Viani, R.A.G., Durigan, G., Melo, A.C.G., 2010. A regeneração natural sob plantações florestais: desertos verdes ou redutos de biodiversidade? *Cienc Florest* 20, 533–552.
- Walter, B.M.T., Guarino, E.S.G., 2006. Comparação do método de parcelas com o “levantamento rápido” para amostragem da vegetação arbórea do Cerrado sentido restrito. *Acta Bot. Bras.* 20, 285–297.
- Weiser, V.L., Godoy, S.A.P., 2001. Florística em um hectare de cerrado stricto sensu na ARIE – cerrado Pé-de-Gigante, Santa Rita do Passa Quatro, SP. *Acta Bot. Bras.* 15, 201–212.
- Yirdaw, E., Lukkanen, O., 2003. Indigenous woody species diversity in *Eucalyptus globulus* Labill. plantations in the Ethiopian highlands. *Biodivers. Conserv.* 12, 567–582.
- Zalba, S.M., Villamil, C.B., 2002. Woody plant invasion in relictual grasslands. *Biol. Inv.* 4, 55–72.
- Zanchetta, D., Pinheiro, L.S., 2007. Análise biofísica dos processos envolvidos na invasão biológica de sementes de *Pinus elliottii* na Estação Ecológica de Itirapina, SP e alternativas de manejo. *Climatol. Estud. Paisag.* 2, 72–90.