

Key species in the encroachment of forests over an Amazonian savanna

Espécies-chave na invasão da floresta sobre uma savana amazônica

Especies clave en la invasión del bosque en una sabana amazónica

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ABSTRACT

Structural stability and tree encroachment in savannas are affected by fire regimes, but the role of savanna and forest species in these processes in Amazonian savannas is unclear. We investigated whether fire retards tree encroachment, what species are responsible for tree encroachment, and whether facilitation process favors tree encroachment. The study was undertaken in an Amazonian savanna-forest mosaic. We classified tree species as either forest or savanna based on their abundances in savanna and forest. Grass cover surrounding young individuals was used to evaluate characteristics of establishment sites, and locations of recruitment to the tree layer were used to evaluate whether there were differences in species persistence between shrub thickets and grassy

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areas. Density of trees changed in 1,9 % during the period with regular burning, but tree cover, especially of forest species, increased in 113% the period without fires. Of the all species, 60% establish and recruit inside thicket but only 18% species establish and recruit over grass. During periods without frequent burning, *Tachigali vulgaris* acts as an ecosystem engineer in forest encroachment over savanna. Few species associated with the savanna to forest transition are more important in initial encroachment of forest over savanna than tree pioneer species typical of the Amazon forest.

Keywords: structural dynamics, permanent plots, fire, grass, thicket, tree.

RESUMO

A estabilidade estrutural e a invasão de árvores nas savanas são afetadas pelo regime de queimadas, mas o papel das espécies de savana e de floresta nesses processos é incerto em savanas amazônicas. Investigamos se o fogo retarda a invasão de árvores, quais espécies são responsáveis por essa invasão e se a entrada delas na savana é facilitada por moitas. O estudo foi realizado em um mosaico de floresta e savana amazônica. Classificamos espécies de árvores como típica da floresta ou da savana com base em suas abundâncias nos respectivos ecossistemas. A cobertura de capim ao redor dos jovens foi usada para avaliar características dos locais de estabelecimento. O local de recrutamento para o estrato arbóreo foi usado para avaliar se houve diferença na persistência das espécies entre moitas e capim. A densidade de árvores mudou 1,9% durante o período com queima regular, mas a cobertura arbórea, especialmente de espécies florestais, aumentou 113% no período sem queimadas. De todas as espécies, 60% se estabelecem e recrutam dentro das moitas, mas apenas 18% se estabelecem e recrutam em meio ao capim. Durante períodos sem queimadas frequentes, *Tachigali vulgaris* atua como um engenheiro de ecossistemas na invasão florestal sobre a savana. Poucas espécies associadas à transição de savana para floresta são mais importantes no início dessa invasão do que as espécies pioneiras típicas da floresta amazônica.

Palavras-chave: dinâmica estrutural, parcelas permanentes, fogo, capim, moita, árvore.

RESUMEN

La estabilidad estructural y la invasión arbórea en las sabanas se ven afectadas por los regímenes de incendios, pero el papel que desempeñan las especies de sabana y de bosque en estos procesos en las sabanas amazónicas no está claro. Investigamos si los incendios retrasan la invasión arbórea, qué especies son responsables de dicha invasión y si los procesos de facilitación favorecen la invasión arbórea. El estudio se llevó a cabo en un mosaico de sabana y bosque amazónicos. Clasificamos las especies arbóreas como forestales o de sabana en función de su abundancia en la sabana y el bosque. Se utilizó la cobertura de pastos que rodeaba a los individuos jóvenes para evaluar las características de los sitios de establecimiento, y se utilizaron las ubicaciones de reclutamiento en el estrato arbóreo para evaluar si existían diferencias en la persistencia de las especies entre los matorrales y las zonas de pastos. La densidad de árboles varió un 1,9 % durante el período con quemas regulares, pero la cobertura arbórea, especialmente de especies forestales, aumentó un 113 % en el período sin incendios. De todas las especies, el 60 % se establece y recluta dentro de matorrales, pero solo el 18 % de las especies se establece y recluta sobre pastizales. Durante los períodos sin quemas frecuentes, *Tachigali vulgaris* actúa como ingeniero del ecosistema en la invasión forestal sobre la sabana. Pocas especies asociadas a la transición de la sabana al bosque son más importantes en la invasión inicial del bosque sobre la sabana que las especies arbóreas pioneras típicas de la selva amazónica.

Palabras clave: dinámica estructural, parcelas permanentes, fuego, pastizal, matorral, árbol.

1 INTRODUCTION

Savanna landscapes are composed of an almost continuous layer of grass with scattered trees and bushes (Moustakas et al. 2010). However, as the number of trees increases, the savanna may grade into forest formations (Moreira 2000; Oliveira-Filho and Ratter 2002; Ribeiro and Tabarelli 2002). Therefore, any factor that limits tree productivity is important to drive the dynamic between savanna and forest physiognomies (Hoffmann et al. 2012). Climate, soil and fire regimes have been used to model alterations in the limits between savanna and forest (Favier et al. 2004b; Moustakas et al. 2010). However, models of vegetation structure indicate that the present climate and edaphic conditions acting alone would not exclude forests, which suggests that fire (Bond et al. 2005, Staver et al. 2011a,b) or other disturbances (Hirota et al. 2011; Lehman et al. 2011) are necessary for the maintenance of savannas.

Fire maintains savannas because limits establishment of trees, it kills small trees, prevents tree recruitment and it has little effect on larger trees (Hoffmann et al. 2012), therefore the tree cover in savannas is generally relatively stable (Russell-Smith et al. 2003; Bond 2008). Hoffmann et al. (2009) found low mortality rates in both forest and savanna species, suggesting resilience of the forest-savanna boundary under fire. Experiments of fire exclusion results in a large increase in the woody vegetation of savannas in regions with more than 750 mm of rainfall per year (Higgins et al. 2007; Bond and Keeley 2005). However, fires have not prevented increase in tree cover in some mesic savannas in the Congo (Favier et al. 2004a). What species contribute to increase tree cover in toward forest physiognomy either presence or absence of fire is unclear.

As forest species generally have thin bark, they are more vulnerable to fire than most savanna species, which have thick bark protecting their vascular cambium (Hoffmann and Moreira 2002; Hoffmann et al. 2009). The savanna species is fastest than forest species to reach a bark resistant to fire. It is therefore assumed that savanna species are responsible for increasing tree cover in the presence of intermittent fires around the world (Hoffmann et al. 2012). On the other hand, Bond and Midgley (2000) proposed that an increase in atmospheric CO₂ will lead to an increase in tree growth rates, thereby reducing the time needed for trees to reach a size where they become resistant to fire. Since forest species assimilate more CO₂ and grow faster than savanna species (Rossato et al. 2009; Hoffmann and Franco 2003), they may be more able to cause forest encroachment of savannas than savanna species in the absence of fire in the future.

There are conflicting opinions as to the role of forest species in the densification of woody vegetation in savannas of South America. The increase in tree vegetation after 25 years of fire exclusion in Venezuela (San José and Fariñas 1983 and 1991) and after 18 years without fires in Central Brazil (Moreira, 2000) has been attributed to savanna species. Both forest and savanna

species contributed to forest encroachment in savannas protected from fire for 13 years in central Brazil, but forest species contributed only 14% to the number of tree stems in the savanna (Geiger et al. 2011). In contrast, Durigan and Ratter (2006) reported that forest species dominated savanna areas that had been protected from fire for 38 years in São Paulo State. Although forest species are usually involved in encroachment tree over savanna is uncertain whether succession to forest is absolutely dependent them (Hoffmann et al. 2012).

Durigan and Ratter (2006) suggested that forest species establish in savanna after other vegetation forms an organic substrate, which reduces root contact with toxic aluminum. Increases in soil humidity and nutrients (Kellman 1979; Mordelet et al. 1993), and shade (Hoffmann 1996) may also facilitate colonization of savannas by forest species. Savanna species may act as facilitators for forest species in Africa and in Australia, but some forest species can establish directly in the savanna (Fenshan et al. 2003; Favier et al. 2004a; Russell-Smith et al. 2004). San José and Fariñas (1983) reported that establishment of tree seedlings was greater among grasses than under trees in a Venezuelan savanna. Favier et al. (2004a) defined three groups of pioneers that facilitate colonization of typical forest species over mesic savannas: forest edge pioneers (short-lived), shrub-nucleating pioneers (medium longevity), and pioneers from the first decades of the forest (long-lived). The ecological differences among types of pioneers can affect the speed and diversity of species involved in the process (Favier et al. 2004b; Geiger et al. 2011; Norden et al. 2011). The relative roles of these pioneers in South American savannas are poorly understood.

The inability of forest species to develop over savanna soils has been used to explain the occurrence of savanna patches within the Amazonian rainforest biome (Beard 1953; RADAMBRASIL 1976; Rizini 1997). Indeed, savanna patches in Alter do Chão region the soil texture under savanna differs from that under forest (Sanaiotti et al. 2002), and even there some savannas occur on soils with different textures (Franklin et al. 2004). Our team undertaken long-term study in Alter do Chão savanna-forest mosaic in permanent plots under different fire regimes of which dates enables answer the interesting questions for understanding savanna-forest dynamics in this region: (1) Does fire inhibit increase tree cover? (2) Is increase tree cover caused by savanna or forest species? (3) Is there facilitation process in encroachment of the trees?

2 MATERIAL AND METHODS

Study area

The study was conducted near the village of Alter do Chão (02° 31'41.91"S; 54° 57'15.28"W), Santarém Municipality, Pará State, in a mosaic of savannas and forests (Fig. 1). The savannas of Alter do Chão are classified as "campo cerrado" (Oliveira-Filho and Ratter 2002), and

are dominated by the grasses *Trachypogon plumosus* and *Paspalum carinatum* (Magnusson et al. 2008). The trees and shrub species found in the savannas are common in the Cerrado biome and other neotropical savannas, and these occur as isolated individuals or clumped within the landscape (Sanaïotti and Magnusson 1995).

The predominant soil in these savannas is composed of loose sand but some soils more compact and clayey (Franklin et al. 2004). The soils are infertile and classified as Distrophic Yellow Latosol; Distrophic Yellow Latosol, plinthic and clayey; and Distrophic Quartzous Sand, with flat to undulating terrain (RADAMBRASIL 1976). The climate is tropical humid, with average rainfall of 1,950 mm.year⁻¹, with monthly means varying between 49.7 and 386.4 mm, and mean temperature of 27.7 °C. The rainy season extends from December to July and the dry season from July to November (Miranda 1995).

Density and basal area of the tree layer in the 24-yr plot

Data were collected in seven years (1986, 1990, 1994, 1995, 1996, 2009 and 2010) within a 24 year period in a 100 m x 100 m 24-yr plot (Q₁) adjacent to a forest patch. The plot burned in 9 of the years between 1986 and 1996, and there were no fires between 1997 and 2010. Sanaïotti and Magnusson (1995), based on anecdotal evidence, reported that the area had not burned between 1981 and 1985.

All trees with trunk diameter ≥ 5 cm at 30 cm above ground in the plot were measured in each census. The individuals were tagged and plotted on a map to facilitate identification and location in the 24-yr plot. Density and basal area of each species were calculated according to Felfili and Rezende (2003). Trees that lost their aerial parts and reappeared in subsequent censuses were included as continually present. The data for standing dead individuals was included in analyses, but only in the first census that they were reported dead.

Nonmetric multidimensional scaling (NMDS) was used to produce an ordination of the species in relation to patterns of change in density and basal area among censuses in the 24-yr plot. Data for each species were transformed by division by the sum, and the Bray-Curtis distance used to describe dissimilarities among plots. Analyses were carried out in the vegan package of the R program (R Development Core Team 2008).

Classification as forest or savanna species

The average abundance of each species that was recorded in the 24-yr plot was estimated around four parallel 250 m lines in 40 plots in savannas and 34 plots in forest distributed throughout the region (Fig. 1). Each plot covered approximately 3.75 ha (250 x 150 m). Trees with trunk

diameter ≥ 5 cm at 30 cm above ground level were surveyed in 2002 in a strip 3 m wide around each transect in 40 savanna plots (Mokross 2004), and trees with diameter at breast height (DBH) ≥ 10 cm at 130 cm above ground were surveyed in a 3 m wide strip around transects in 34 forest plots (W.E. Magnusson and J.C. Costa, unpublished data). The average abundance per plot in savannas and forests was used to classify tree species as being forest or savanna.

Tree species cover in thirteen 10-yr savanna plots

Thirteen of the 40 savanna plots (Fig.1) were used to quantify fire frequency and change in tree cover over 10 years (1997-2007). Each year, the four 250 m transects in each plot were surveyed at the end of the wet season. The both burned and unburned areas were registered at two-meter intervals, and the extent of fire was estimated as the proportion of the 500 points with burned area. Cover of each species of tree in the thirteen 10-yr plots was estimated from the proportion of the 500 points that touch it. The difference in cover between the 1997 and 2007 surveys was used as an index of rate of change for each species. One of the thirteen 10-yr plots overlaid the 24-yr plot and we used for assessment the basal area was not measured in those plots. The strong linear relationship founded (Appendix A1) allowed to use tree cover in 10-yr plot as special replicas of the structural dynamics in 24-yr plot.

Establishment and recruitment sites

We developed this method to evaluate whether tree species establish over grass or inside thicket. We assumed that thicket is good represented in savanna by reduction in grass cover. Vegetation cover around the sites where small individuals (< 1 m in height) had established in the 24-yr plot was estimated in three 100x10 m transects, 50 m apart. Only individuals of the same species separated by at least 10 m were included in analyses to increase the independence among samples. The number of individuals used to calculate the median grass cover was 11 for *Anacardium occidentale* and *Copaifera martii*, 8 for *Byrsonima coccolobifolia* and *Vatairea macrocarpa*, 6 for *Miconia lepidota* and 10 for the remaining species. Too few individuals of *Lafoensia pacari*, *Alchornea shomburkii*, *Swartzia recurva*, and *Nictaginaceae* sp1. were encountered to include them in analyses. Two 1 m lines perpendicular to each other were centered on each individual and a 2 mm diameter rod placed vertically every 10 cm along the lines (20 points per plant). The proportion of points touching grasses or sedges was used as an index of the proportion of savanna cover around each individual.

Locations of individuals recruited to the tree layer that had trunk diameter ≥ 5 cm at 30 cm above ground level were mapped. All shrubs in the 24-yr plot were mapped in 1986 (Sanaiotti and

Magnusson 1995). This map was used to plot new individuals registered in the following surveys. The distance from the edge of the closest shrub thicket to the recruited individual was used to quantify tree recruitment inside and outside of the thicket. Distances from thicket edge to inside were given a negative sign, and distances from the thicket edge into the grassland were given positive signs. Ten individuals of each tree species recruited during the study were selected randomly, except that a minimum distance of 10 m between individuals of the same species was maintained to increase independence among samples. *Protium heptaphyllum* and *Tapirira guianensis* had only four recruits registered in the study, but were included in the analysis because they were frequent in the establishment phase.

3 RESULTS

The species registered in the 24-yr plot (Fig. 2) during the study tended to be either typically savanna species (close to the x-axis), or forest species (close to the y-axis) when quantified in other many savanna and forest plots. A few species, such as *Tachigali vulgaris*, *Xylopia aromatica* and *Copaifera martii* (see abbreviation in Table 1), were equally frequent in forest and savanna, but no species was common in both the savanna and forest (Fig. 2).

Ordination of the species based on their fluctuations in abundance in the 24-yr plot (Table 1) separated those typically from savannas (uppercase) from those typical of forest (lowercase), both in terms of density (Fig. 3a) and basal area (Fig. 3b). Of the species that greatly increased in abundance in the absence of fire (Table 1), *Tachigali vulgaris*, *Xylopia aromatica* and *Copaifera martii* occurred in both savannas and forest, although with low abundance, while *Miconia albicans* and *Miconia lepidota* were not found in any of the savanna or forest plots (Fig. 2).

Savanna species showed little variation in density or basal area during the interval with frequent fires. Furthermore, since most species showed similar fluctuations in abundance (Fig. 3). Results for density and basal area were similar and we present results only for density (Fig. 4). However, forest species, and those found in both savanna and forest, varied more in their dynamics, with *X. aromatica* and *T. vulgaris* being closest to savanna species, while the remaining species were located towards the extreme right of Fig. 3a and 3b. *Tachigali vulgaris* was the only forest species that was reasonably common during the period with fires (Table 1). It caused the greatest structural changes and it was not a typical savanna or forest species. Therefore, we present results for this species separately. Differences in density in the period with fire and the period without fire were significant for savanna species ($F_{1,5} = 338$, $P < 0.001$), forest species excluding *T. vulgaris* ($F_{1,5} = 12.5$, $P < 0.001$), and *T. vulgaris* ($F_{1,5} = 348$, $P < 0.001$).

Tree density and basal area increased by over 100% during the period without fire (Fig. 4), and almost all tree species benefited from the absence of fires (Table 1). Forest species contributed less than 10% to density and 15% to basal area during the period with fire, but represented 30% and 35% of these variables in the absence of fires, and were responsible for more than 50% of the structural change in the savanna in this period (Figure 4).

The five savanna species, which represented 75% of tree density and 80% of basal area at the beginning of the study, remained well represented, with 49% and 51% of density and basal area, respectively, at the end of the study. The forest species *T. vulgaris*, which initially represented only 7% of density and 2.7% of basal area, contributed 20% to density and 23% to basal area at the end of the study (Fig. 4), and had the highest density and basal area of any species at the end of the period without fire (Table 1).

Of the thirteen 10-yr plots, those that did not burn during the period showed the greatest positive change in tree cover, and forest species were the ones that changed most. Plots that burned generally showed reduction in tree cover, and savanna species showed the greatest changes, because forest species were not registered in five of the 11 burned plots (Figure 5). Two of the eleven burned plots increased in tree cover, but that increase was less than the increase in unburned plots (Figure 5).

There was no simple linear relationship (Fig. 6) between the frequency of establishment of species in grasses and sedges (Appendices Fig. A2) and their frequency of recruitment to the tree layer in thickets (Appendices Fig. A3). The species separated into three groups: species that establish and recruit in grasses; species that establish and recruit in shrubs; and species that establish in shrubs, but recruit in grasses. Of the all species, 60% establish and recruit inside thicket but only 18% species establish and recruit over grass. No species established in grass and recruited in shrubs.

4 DISCUSSION

The structural stability of our 24-yr plot under a regime of frequent fires was due to the presence of savanna species. Controlled experiments with fire regimes have shown the resistance of the savanna tree vegetation to moderately frequent and intense fires (Russell-Smith et al. 2003; Smit et al. 2010). Nonetheless, since fire affects the woody vegetation and favors grasses, it creates a more open aspect in savannas (Moreira 2000; Silvério et al. 2013). The reduction in the woody vegetation is greater when fires occur at the end of the dry season (Russell-Smith et al. 2003; Smit et al. 2010), and when they occur annually or biannually (Moreira 2000; Davies et al. 2010). Frequent fires at the end of the dry season in Alter do Chão appear to be reducing the tree cover in many areas of the savanna, and potentially could eliminate species with reduced sprouting capacity

in the long term. Where saplings lack capacity of the sprout repeatedly those are eliminated under frequent fires (Fenshan et al. 2003).

The greatest increase tree cover in absence of burn indicates fire is main inhibitor of encroachment over savanna in Alter do Chão region. The results are according with many mesic savannas around the world (Higgins et al. 2007; Bond and Keeley 2005). The increase both savanna and forest species is explicated due the intervals without burns are opportunity for all tree species became safety to fire (Hoffmann et al. 2012). Nevertheless the major contribute to forests species in encroachment tree is probably due more growth rate them (Rossato et al. 2009; Hoffmann and Franco 2003).

Even though we separated two kind species in savanna and forest we found a small group of the five species classified neither savanna nor true forest species, but their frequency suggests that are true forest transition species. *Tachigali vulgaris*, *M. albicans*, *C. martii*, *X. aromatica* and *M. lepidota* apparently represented the initial stage of savanna-forest succession in Alter do Chão, and can be considered colonizing species because they were rare or absent in open savannas and forests. Geiger et al. (2011) studied expansion of riparian forest into a savanna in Central Brazil and concluded that species invading the savanna belong to a small group of forest and edge species. That five are ephemeral species that occupy an opportunist niche in savannas in intervals without fire, especially *Tachigali vulgaris*. Although *T. vulgaris* is usually considered forest pioneer the role of it in forest regeneration after fire seem is slight (Balch et al. 2013) but it quickly comes to dominate savanna near forest in the absence of regular fires. This it indicates that *T. vulgaris* is specialized in savanna to forest transition.

Tachigali vulgaris, previously considered to be *Sclerolobium paniculatum* (da Silva and de Lima 2007; van der Werff 2008), has been indicated as responsible for forest encroachment in other Brazilian savannas (Aquino et al. 2007; Líbano and Felfili 2007) but was considered savanna species (Moreira 2000, Geiger et al 2011). *Tachigali vulgaris* is well adapted to invade open savannas during short periods without fire. It is grows quickly in full sun (Felfili et al. 1999) and respond positively the presence of charcoal in soil (Souchie et al. 2011), as well as shown in this study, establishes among grasses, where it reaches high annual growth rates (Aquino et al. 2007; Roitman et al. 2008; Reis et al. 2015) both in the rainy and dry seasons (Palhares et al. 2010). Líbano and Felfili (2007) registered a continuous increase in the importance value of *T. vulgaris* under fire intervals of five years, as well as an increase in basal area, even though there was a reduction in density over the 18 years of monitoring. Models suggest that recruitment from saplings to adults varies depending on the amount of grass in the system (Staver et al. 2011b), and the presence of pioneer species capable of colonizing grass increases tree densities in savanna (Favier et al. 2004b,

Marcilio Silva et al. 2015). In our study, *T. vulgaris* was one of the few tree species and single forest species capable of establishing among grass.

Tachigalli vulgaris play important role as a key species in the succession from savannas to forests. The species exerts a bottom-up control over forest advancement. When the top-down control caused by fires (Bond and Keeley 2005) is eliminated, the savanna becomes vulnerable to the establishment of *T. vulgaris* seedlings in grassy areas, where, they quickly reach large sizes, and become resistant to fire (Reis et al. 2015). *T. vulgaris* acts as an ecosystems engineer (Jones et al. 1994), since it excludes grasses and forms an area protected from fire under its crown. In that sense, it eliminates two major inhibitors of tree establishment in the savanna (Bond 2008, Lehmann et al. 2011, Staver et al. 2011a), and exerts a bottom-up control for the establishment of new tree species. Our results according to ecological thresholds model (Hoffmann et al. 2012) and indicate *T. vulgaris* as a key species to reach fire-suppression threshold and quickly promotes encroachment forest over savanna on poor soils.

Thicket forming shrub species can develop in the *T. vulgaris* litter because even though *T. vulgaris* starts growth in grass, all large individuals in our study area were nucleating shrub thickets. Thicket-nucleating species create conditions for colonization by other forest species (Favier et al. 2004a). *Xylopia aromatica*, *M. albicans* and *C. martii* are formers thickets because establish in intermediate grass cover but recruits abundantly within thickets. *Simarouba amara*, *P. heptaphyllum* and *T. guianensis*, which are abundant in Alter do Chão forests and common in forest patches in the Cerrado biome, constitute the second stage of forest encroachment because only a few individuals recruited to the tree layer during the study. However, their seedlings were common in thickets. These species are zoochorous, and, once they reach the canopy, have greater longevity than initial species. However, they depend on shrub thickets to colonize this savanna. Favier et al. (2004a) proposed that the arrival of these large sized secondary species represents the conversion to a forest formation. They overlap the thicket-nucleating species and facilitate the entry of species typical of forests.

Except for *M. lepidota*, we found no pioneer species typical of Amazonian forests, such as *Cecropia palmata*, in the initial stage of savanna encroachment. Although *Cecropia palmata* and other species typical of Amazonian secondary-forests (De Oliveira and Mota 2010) are abundant in forest surrounding savanna at Alter do Chão (W.E. Magnusson and J.C. Costa, unpublished data), we have never recorded them in savanna.

Almost half of the savanna species analyzed recruited in shrub thickets, even though they can be found as isolated individuals among grass in the study area. They therefore persist long into the tree encroachment stage, and should a severe fire eliminate forest competitors, they could quickly return to being the dominant trees in the area. Fires may not limit only forest species. Of the

savanna species, only *Byrsonima crassifolia* and *Salvertia convallariodora* were common in open areas, and they are the most abundant tree species in Alter do Chão savannas (Mokross 2004; Magnusson et al. 2008), which tend to have low tree cover (Magnusson et al. 2002). The high frequency of fires in the region (Magnusson et al. 2010) may be inhibiting the formation of shrubs and the regeneration of other savanna species.

5 CONCLUSION

Fire appears to be the main agent maintaining the savannas of Alter do Chão. The few species responsible for rapid changes in tree cover in the absence of fire are not typical either of savannas or mature forests. They are associated with the interface between savanna and forest in most parts of tropical America, and are not associated with forest regeneration in non-savanna areas. One of the species, *T. vulgaris*, can be considered an ecosystem engineer, given that it is the only large-sized tree species capable of rapidly colonizing savanna grasslands. There is also evidence that, after reaching large size, it can inhibit fire spread and favor the establishment of other non-savanna tree species. That species can play important role in regeneration forest project in grass dominate areas. Without this species, succession from this Amazonian savanna to forest probably would me much slower.

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Table1 Absolute density and absolute basal area of species in census undertaken in 24-yr plot. Family was based in Angiosperm Phylogeny Group II. Abbreviations - savanna species: A-P / forest species: a-n. Periods - fire: 1986-1997, without fire: 1998-2010.

Species (family)	Abbrev.	Density (indv.ha ⁻¹)							Basal area (m ² .ha ⁻¹)						
		1986	1990	1994	1995	1996	2009	2010	1986	1990	1994	1995	1996	2009	2010
<i>Byrsonima crassifolia</i> (Malpighiaceae)	A	99	79	74	69	68	97	97	0.2733	0.2267	0.2067	0.2088	0.2045	0.3628	0.2366
<i>Salvertia convallariodora</i> (Vochysiaceae)	B	85	86	91	86	88	142	134	0.4716	0.4784	0.4692	0.4843	0.4556	0.6836	0.5799
<i>Qualea grandiflora</i> (Vochysiaceae)	C	98	111	112	110	113	159	151	0.5729	0.518	0.5439	0.5387	0.4909	0.6935	0.6219
<i>Lafoensia pacari</i> (Lythraceae)	D	65	69	76	73	73	101	95	0.2255	0.2089	0.2536	0.2211	0.2007	0.3565	0.2697
<i>Pouteria ramiflora</i> (Sapotaceae)	E	42	44	40	41	42	79	79	0.2941	0.2953	0.3092	0.2421	0.2708	0.3893	0.3608
<i>Byrsonima coccolobifolia</i> (Malpighiaceae)	F	20	20	24	24	25	36	34	0.0565	0.0565	0.0623	0.0587	0.0630	0.0765	0.0704
<i>Vatairea macrocarpa</i> (Fabaceae)	G	18	21	26	23	23	40	38	0.0919	0.0925	0.1009	0.0752	0.0880	0.1125	0.1073
<i>Bowdichia virgilioides</i> (Fabaceae)	H	12	12	12	12	13	12	12	0.0923	0.1142	0.1215	0.0819	0.1334	0.1434	0.1317
<i>Anacardium occidentale</i> (Anacardiaceae)	I	6	13	16	15	15	19	19	0.0149	0.0411	0.0521	0.0303	0.0350	0.0973	0.0962
<i>Tabebuia ochracea</i> (Bignoniaceae)	J	6	8	9	7	8	8	7	0.0360	0.0382	0.0455	0.0464	0.0430	0.0424	0.0455
<i>Tocoyena formosa</i> (Rubiaceae)	K	6	8	13	9	9	11	9	0.0047	0.0048	0.0121	0.0154	0.0054	0.0152	0.0111
<i>Roupala montana</i> (Proteaceae)	L	1	1	1	1	1	0	0	0.0110	0.0041	0.0053	0.0058	0.0060	0.0000	0.0000
<i>Plathymenia reticulata</i> (Fabaceae)	M	2	2	2	2	2	0	0	0.0113	0.0100	0.0106	0.0107	0.0100	0.0000	0.0000
<i>Myrcia obtusa</i> (Myrtaceae)	N	2	2	3	1	1	2	2	0.0061	0.0086	0.0026	0.0000	0.0102	0.0039	0.0035
<i>Cybistax antisyphilitica</i> (Bignoniaceae)	O	1	1	0	0	0	0	0	0.0087	0.0071	0.0058	0.0000	0.0000	0.0000	0.0000
<i>Himatanthus fallax</i> (Apocynaceae)	P	9	11	16	16	17	56	57	0.0561	0.0343	0.0417	0.0420	0.0493	0.1991	0.1992
<i>Tachigali vulgaris</i> (Fabaceae)	a	37	35	36	25	28	236	226	0.0632	0.2017	0.3495	0.3900	0.4066	10.345	0.9443
<i>Xylopia aromatica</i> (Annonaceae)	b	10	8	8	5	3	64	66	0.0170	0.0147	0.0160	0.0234	0.0078	0.0850	0.1878
<i>Protium heptaphyllum</i> (Burseraceae)	c	0	0	1	1	1	4	4	0.0000	0.0000	0.0013	0.0000	0.0020	0.0051	0.0058
<i>Simarouba amara</i> (Simaroubaceae)	d	1	1	0	0	0	13	14	0.0007	0.0029	0.0000	0.0000	0.0000	0.0221	0.0265
<i>Miconia albicans</i> (Melastomataceae)	e	0	0	0	0	0	21	24	0.0000	0.0000	0.0000	0.0000	0.0000	0.0385	0.0400
<i>Copaifera martii</i> (Fabaceae)	f	0	0	0	0	0	25	29	0.0000	0.0000	0.0000	0.0000	0.0000	0.0378	0.0429
<i>Miconia lepidota</i> (Melastomataceae)	g	0	0	0	0	0	19	26	0.0000	0.0000	0.0000	0.0000	0.0000	0.0187	0.0256
<i>Tapirira guianensis</i> (Anacardiaceae)	h	0	0	0	0	0	4	4	0.0000	0.0000	0.0000	0.0000	0.0000	0.0094	0.0134
<i>Swartzia recurva</i> (Fabaceae)	i	0	0	0	0	0	1	1	0.0000	0.0000	0.0000	0.0000	0.0000	0.0016	0.0017
<i>Heisteria densifrons</i> (Olacaceae)	j	0	0	0	0	0	1	1	0.0000	0.0000	0.0000	0.0000	0.0000	0.0061	0.0061
<i>Alchornea shomburkii</i> (Euphorbiaceae)	l	0	0	0	0	0	2	2	0.0000	0.0000	0.0000	0.0000	0.0000	0.0032	0.0033
<i>Nyctaginaceae</i> sp1. (Nyctaginaceae)	m	0	0	0	0	0	1	1	0.0000	0.0000	0.0000	0.0000	0.0000	0.0008	0.0010
<i>Casearia sylvestris</i> (Salicaceae)	n	1	1	1	1	1	0	0	0.0007	0.0007	0.0007	0.0006	0.0004	0.0000	0.0000
Total		521	533	561	521	531	1153	1132	23.085	2.368	26.105	24.754	24.826	44.378	40.322

Figure captions

Fig. 1 24-yr plot Q₁ (black circle), left arrow. Distribution of 40 plots in savanna (black squares) and 40 plots in forests (black triangles) used to distinguish savanna and forest species. Data on cover were collected in 13 of the savanna plots (black squares rounded). Savanna is white, forests dark gray, water light gray, urban areas hatched; adapted from Guizoni Jr et al. (2005)

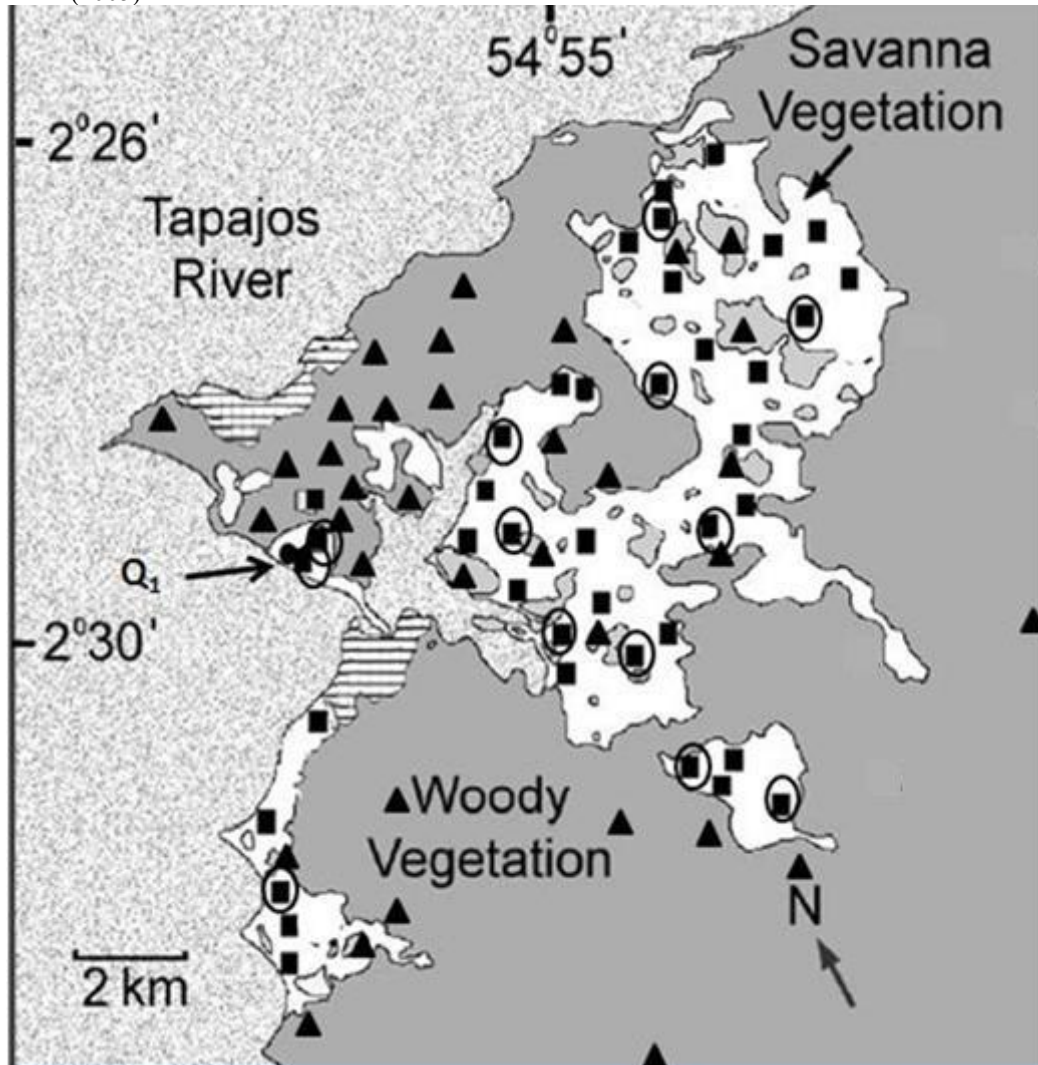


Fig. 2 Mean number of individuals per plot of species in savanna ($n = 40$) and forest ($n = 34$) plots. Abbreviation of species in Table 1

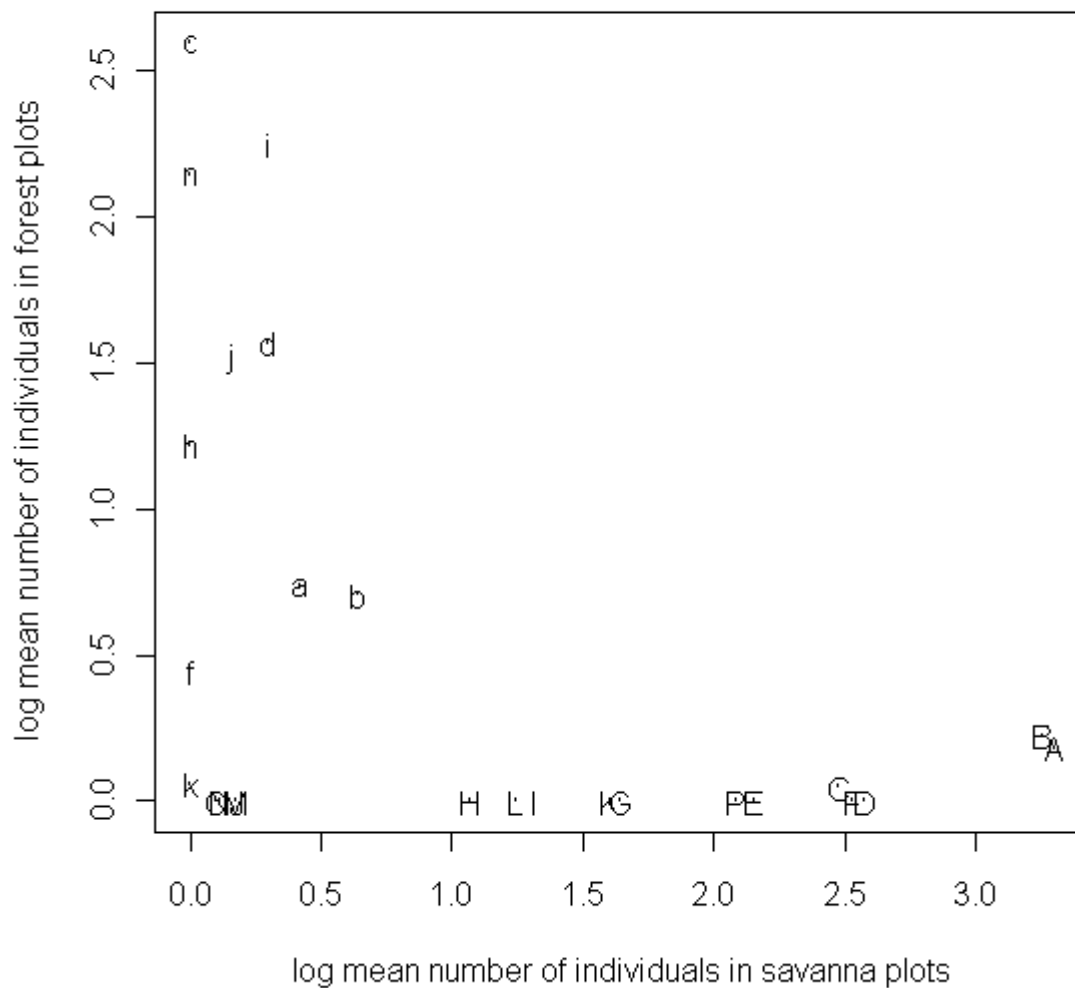


Fig. 3 Ordination of species based on patterns of change in (a) density and (b) basal area during the study period in 24-yr plot

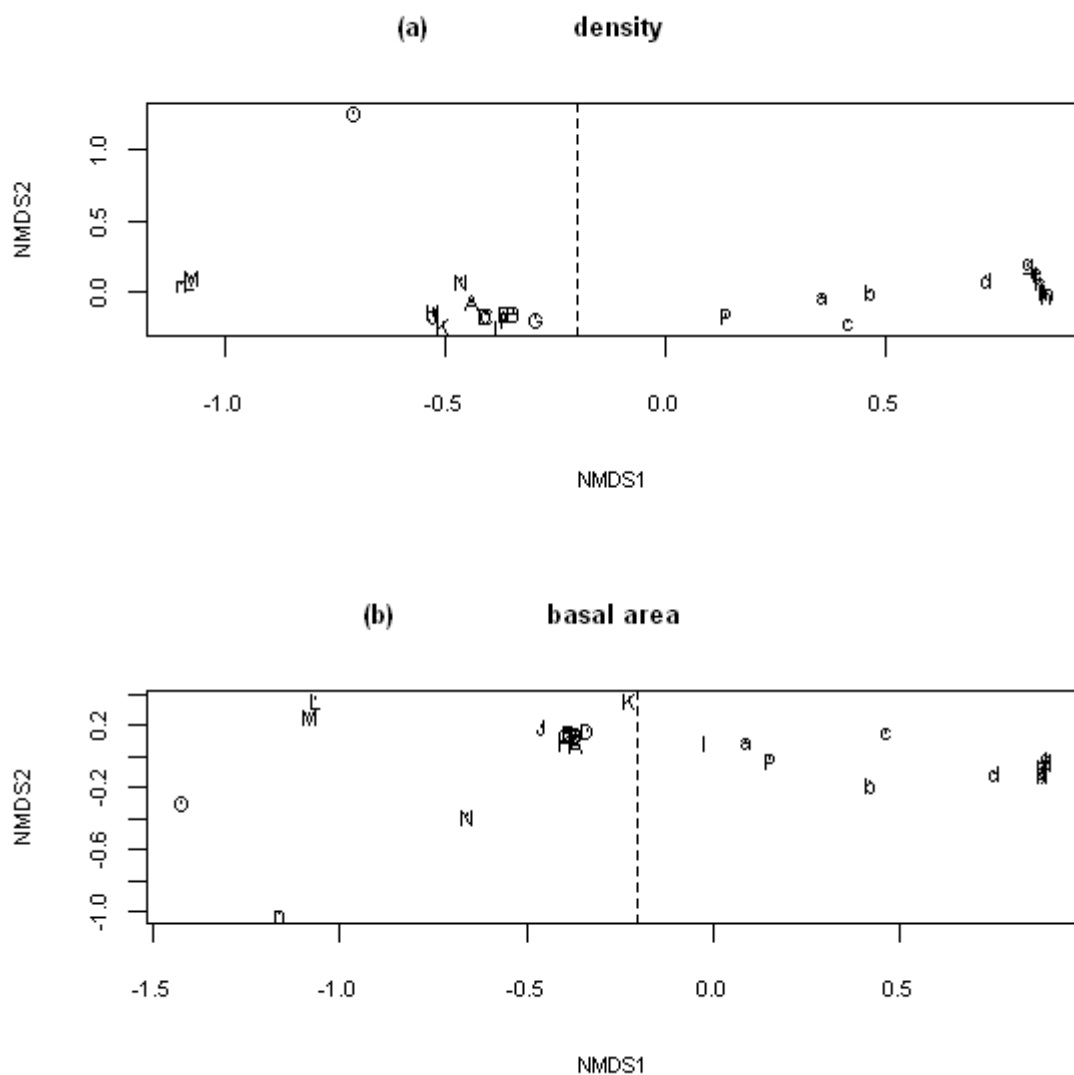


Fig. 4 Structural dynamics of the trees in 24-yr plot based on number of individuals. Savanna species (white), *T. vulgaris*, (checkered), other forest species without *T. vulgaris* (black). Plot burned frequently before 1996, and did not burn thereafter

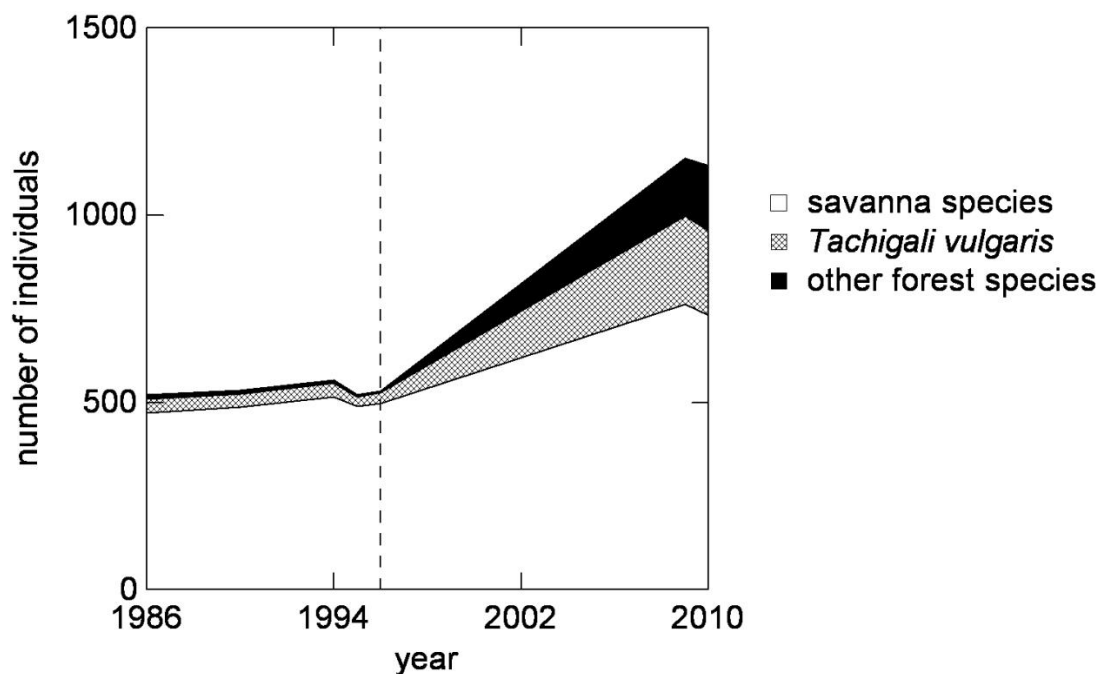


Fig. 5 Changes in tree cover in a ten-year period, for forest and savanna species in 13 plots in savanna under different fire regimes. Burned plots represented by open circles ($n = 11$), Unburned plots by black triangles ($n = 2$). The same 13 plots are shown for savanna and forest species

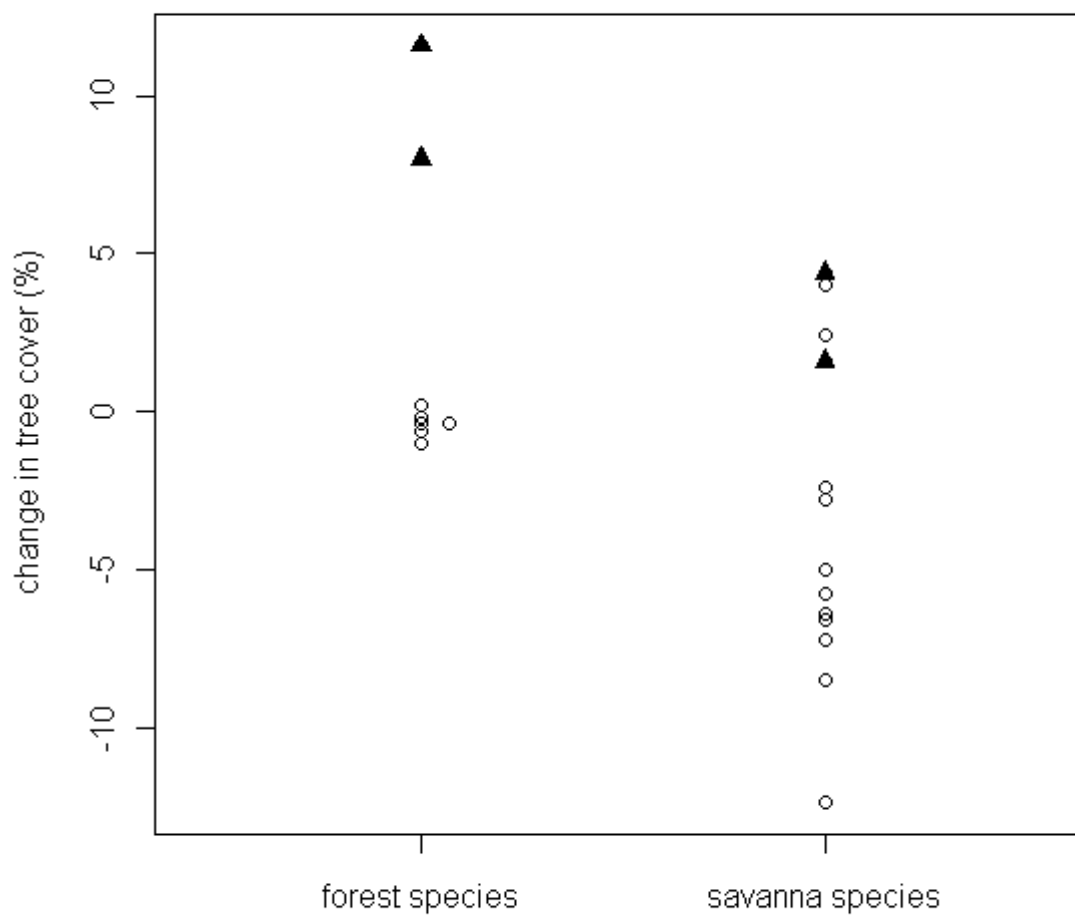


Fig. 6 Median cover of grasses and sedges in establishment sites for small individuals of each species recorded in the 24-yr plot during the study period (x-axis), and mean distance from the shrub-grass boundary of sites where individuals recruited to the tree layer for each species (y-axis). Negative values on the y axis indicate that the species recruits to the tree layer within thickets and positive values indicate that the species recruits to the tree layer among grasses. The number of individuals used to calculate the medium grass cover was 11 (species I, e and f), 8 (species F and G), 6 (species g), and 10 for the remaining species. The number of individuals used to calculate the medium recruitment distance from the shrub-grass boundary was 4 (species c and i), and 10 for the remaining species. Abbreviation of species in Table 1. Distances for each species and species names are given in Appendices Fig. A2 and Fig. A3

