Post-fire dynamics of woody vegetation in seasonally flooded forests (impucas) in the Cerrado-Amazonian Forest transition zone

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\textbf{A B S T R A C T}

Fire disturbance alters the structural complexity of forests, above-ground biomass stocks and patterns of growth, recruitment and mortality that determine temporal dynamics of communities. These changes may also alter forest species composition, richness, and diversity. We compared changes in plant recruitment, mortality, and turnover time over three years between burned and unburned sites of two seasonally flooded natural forest patches in a predominantly savanna landscape (regionally called ‘impucas’) in order to determine how fire alters forest dynamics and species composition. Within each impupa, 50 permanent plots (20 m × 10 m) were established and all individuals >5 cm diameter at breast height (DBH) identified and measured in two censuses, the first in 2007 and the second in 2010. Unplanned fires burned 30 plots in impupa 1 and 35 in impupa 2 after the first census, which enabled the comparison between burned and unburned sites. The highest mortality (8.0 and 24.3% year\textsuperscript{-1} for impupa 1 and 2) and turnover time (69 and 121.5 years) were observed in the burned sites, compared to 3.7 and 5.2% year\textsuperscript{-1} (mortality), and 28.4 and 40.9 years (turnover), respectively, for the unburned sites. Although these seasonally flooded impupa forests are embedded in a fire-adapted savanna landscape, the impucas vegetation appears to be sensitive to fire, with burned areas having higher mortality and turnover than unburned areas. This indicates that these forest islands are potentially at risk if regional fire frequency increases.

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Introduction

The increase in global demand for grain, livestock, and biofuels, driven also by the rising price of oil, combined with episodic drought and fire, have led to a rapid process of structural degradation and fragmentation of some Amazonian forests (Nepstad et al., 2008; Nogueira et al., 2008). Deforestation for the expansion of agriculture occurs mainly in the southern Amazonia “arc of deforestation”, where transitional areas between forest and savanna prevail (Nogueira et al., 2008). Over the last two decades these areas have experienced several intense droughts (Marengo et al., 2011). Deforestation and drought events not only induce tree mortality (Phillips et al., 2009), but also alter the forest microclimate – for example, by allowing sun-light to penetrate canopy openings and fragment edges, drying the forest floor, rendering it more flammable, and thereby favouring the spread and recurrence of fires (Nepstad et al., 2008; Davidson et al., 2012). In addition, frequent fires modify the structure, floristic composition and functioning of plant communities in the Amazon, favouring dry-forest and savanna species which are more adapted to the presence of fire (Nepstad et al., 2008). Fire is considered one of the major threats to Amazonian forest diversity (Cochrane and Schulze, 1999; Barlow and Peres, 2004, 2008). It is therefore important to understand the effects of fire on Amazonian forests, especially in vegetation types representing the rapidly shrinking forest-savanna transition zone, to understand how plant community structure and composition changes through time.

The structure and dynamics of forests may be strongly influenced by natural or man-made disturbance and fire (Cochrane et al.,...
especially due to the low resistance and resilience of forest species against such impacts (Hoffmann, 2000; Hoffmann et al., 2003) – which normally results in high mortality rates (Barlow and Peres, 2004, 2008; Balch et al., 2008). Small-scale disturbances, such as those originating from branch or tree fall, are responsible for an increase in forest structural and floristic complexity (Molino and Sabatier, 2001; Budke et al., 2010). On the other hand, large-scale disturbances such as selective logging, fragmentation and burning, may exert considerable effects on forest dynamics, causing a reduction in richness and diversity (Strasberg et al., 1995; Thonick et al., 2001). Seasonal flooding and the saturation of soils may also affect vegetation structure and composition (Jirkj et al., 2007). The effects of seasonal flooding (Guilherme et al., 2004) and fire (Nepstad et al., 2001; Balch et al., 2008) on tropical forest dynamics are known for some areas of Amazonia; however, there is currently a lack of information about how fire affects seasonally flooded forest located in the transition zone between the Amazon forest and the Cerrado biome. Moreover, the transitional forests between Cerrado and Amazon forest are very vulnerable to burning (Balch et al., 2008; Davidson et al., 2012), mainly when the occurrence of fire is related to episodes of severe droughts (Alencar et al., 2006; Balch et al., 2008; Aragão and Shimabukuro, 2010; Davidson et al., 2012).

This transition zone in Mato Grosso State in Brazil presents a wide range under physiognomic, structural, and floristic aspects, resulting from the presence of and influence from three important biomes, the cerrado, the Amazon forest and the Pantanal (Eiten, 1975, 1985; Ackerly et al., 1989; Alho, 2008). In present times, this region is highly threatened: almost 500,000 km² of original cerrado vegetation were converted into pasture through mid-2000, an area equivalent to the land surface of Spain (Klink and Machado, 2005); and, according to Latrubesse et al. (2009), “no other biome in the I.c. has been destroyed so quickly and thoroughly in human history” (I.c., p. 239).

In the Araguaia Plain, or Araguaia Pantanal, in the transition between Cerrado and Amazon forest, there are flooded forests regionally known as ‘impucas’ (Eiten, 1985; Marimon et al., 2008), occurring in natural depressions, which favour seasonal flooding for a longer period of time. On the plains, the Araguaia River forms a vast basin and maintains the most important wetlands of Central Brazil. Threats to the biodiversity of this area are enormous (Latrubesse et al., 2009), especially as a result of recurrent fires (Marimon et al., 2008). The few studies of impucas (or ‘ipucas’) found in the literature provide only general descriptions of the vegetation structure and are based on only one inventory (Barbosa et al., 2011; Brito et al., 2006, 2008; Marimon and Lima, 2001; Marimon et al., 2008; Martins et al., 2002). Seasonal flooding is a factor that restrains species richness and diversity in flooded forests in general (Ivanuskas et al., 1997) and also in impucas (Brito et al., 2008; Barbosa et al., 2011), since survival in flooded environments requires species having specific physiological and morphological adaptations (Joly and Crawford, 1982; Scarano et al., 1994; Toniato et al., 1998). In addition, flood-tolerance may present an important competitive advantage (Joly and Crawford, 1982; Parolin et al., 2004), with adapted species becoming very abundant. These flood-adapted species may also be exposed to fire, which enters from the surrounding grasslands and woody savanna. Despite the regional importance of fire, it is unclear how impucas vegetation responds to fire.

The aim of this study, therefore, was to analyse and compare the woody vegetation dynamics of burned and unburned sites of two seasonally flooded impucas in north-eastern State of Mato Grosso, Brazil. We tested the hypothesis that impucas are highly susceptible to fire, which significantly alters community dynamics and vegetation species composition in a relatively short period due to a strong increase in mortality rates and a decrease in basal area and recruitment rates.

Materials and methods

Study sites

The study was carried out in two seasonally flooded forests (impucas), in the Araguaia State Park (PEA), municipality of Novo Santo Antônio, eastern Mato Grosso State (Impuco 1: 12°09′4.2″ S and 50°49′37″ W; Impuco 2: 12°19′11.2″ S and 50°44′15.6″ W: Fig. 1). The PEA encompasses an area of 223,619 ha and is located in the flood plain formed by the confluence of the Rio das Mortes with the Rio Araguaia. It has a mean altitude of 200 m, and is part of the Sedimentary Plain of Bananal or, according to Marimon et al. (2008), in the Araguaia Pantanal. The topography of the PEA is generally flat, and waterlogged in the rainiest months. Soils are primarily composed of plinthosols and gleysols, both with drainage impediments and subject to seasonal flooding (Brasil, 1994). The regional climate is the Aw type (hot tropical continental), according to Köppen’s classification, characterised by a dry season between April and September, and a rainy season between October and March (Silva et al., 2008).

The Araguaia Plain, which extends across the States of Goiás, Tocantins and eastern Mato Grosso, within the area of the Rio das Mortes and Rio Araguaia, constitutes a region with high biodiversity (Marimon and Lima, 2001), as it occurs in the transition zone between the Cerrado and the Amazon Forest biomes (Ratter, 1987). This influences the floristic composition and creates a complex vegetation mosaic in the seasonally flooded wide plain (Barbosa et al., 2011; Marimon and Lima, 2001; Martins et al., 2008). The region has been classified by vegetation, animal and physical specialists as an area of “extremely high biological importance” (MMA, 1999; Marimon and Lima, 2001). However, during the dry season, anthropogenic fire is becoming increasingly frequent, caused by local inhabitants, who burn the vegetation to promote the sprouting of native grasses and feed cattle, since ranching is the main activity within the park (Marimon et al., 2008).

Fires of varying sizes, intensities and frequencies occur in the Araguaia State Park (PEA) (Marimon et al., 2008). Sometimes, fire burns the surrounding matrix of the impucas (wet grasslands), but does not reach the forest (Barbosa et al., 2011; Marimon et al., 2008). Nevertheless, under conditions of low humidity and with the presence of invasive species of the genus Scleria (Barbosa et al., 2011), flames do penetrate also into the impucas and cause high tree mortality. In some cases, the impucas do not burn completely because, even in the dry season, they can be partially flooded.

Vegetation inventory

In September 2007 we established five parallel transects in each impuco, 50 m apart. Each transect was subdivided into plots of 20 m × 10 m, with the length depending on the form and size of each impuco, and ranging from 50 to 120 m (Fig. 1). In each transect, all living individuals with diameter at breast height (DBH) ≥5 cm were tagged and identified, and their diameter measured (Barbosa et al., 2011). In 2010, all plots were re-surveyed, with all surviving and standing dead individuals re-measured. Individuals that reached 5 cm diameter were treated as recruits, tagged and identified. Species identifications were carried out through comparisons with the herbarium collections of the University of Mato Grosso State, Nova Xavantina Campus (Herbarium NX), the University of Brasilia (Herbarium UB), the Federal University of Mato Grosso (Herbarium UFMT), the Herbarium of Embrapa Amazonia Orien- tal (Herbarium IAN), and by consulting specialists. All herbarized specimens with flowers and/or fruits were incorporated into the collection of NX Herbarium.

After the first vegetation census two fires occurred at the PEA. The first occurred in September 2007 soon after installation of
the transects and reached 30 plots of impica \text{1} and the second in September 2008, reaching 35 plots of impica \text{2}. In order to analyse the effects of the fires, the subplots were designated as either burned or unburned.

**Data analysis**

Based on the data collected in the 2007 and 2010 inventories, we calculated basal area for the community and for individual species (Mueller-Dombois and Ellenberg, 1974), and from these values calculated several metrics to assess how dynamics and composition changed due to the fire impact. First, based on the basal area, we calculated the average annual mortality rates, MO (Eq. (1)),

\[
MO = \left\{ 1 - \left[ \frac{AB_0 - AB_m}{AB_0} \right]^{1/t} \right\} \times 100
\]

where \(AB_0\) is initial basal area, and \(AB_m\) is dead basal area, and \(t\) is the elapse of time in years.

Recruitment RE (Eq. (2)) was calculated (Sheil et al., 1995, 2000) as,

\[
RE = \left[ 1 - \left( 1 - \frac{AB_t}{AB_f} \right)^{1/t} \right] \times 100
\]

where \(AB_t\) is recruits basal area, \(AB_f\) is final basal area, and \(t\) is the elapse of time in years.

Loss, \(L\) (Eq. (3)) and gain, \(G\) (Eq. (4)) in basal area (Guimarães et al., 2008), in addition to the basal area turnover time, TUR (Eq. (5)), were calculated (Korning and Balslev, 1994) as,

\[
L = \left\{ 1 - \left[ \frac{(AB_0 - AB_m - AB_g)}{AB_0} \right]^{1/t} \right\} \times 100
\]

\[
G = \left\{ 1 - \left[ 1 - \frac{AB_t + AB_g}{AB_t} \right]^{1/t} \right\} \times 100
\]

\[
TUR = \frac{T_{1/2} + T_2}{2}
\]

where \(AB_0\) is initial basal area, \(AB_m\) is dead basal area, \(AB_g\) is basal area decrement, \(AB_t\) is recruits basal area, \(AB_f\) is basal area increment, \(AB_t\) is final basal area, \(t\) is the elapsed time in years, \(T_{1/2}\) is half-life time, and \(T_2\) is duplication time.

Based on the individuals occurring in both inventories, we calculated the average annual mortality rates, \(Mo\) (Eq. (6)) and recruitment rates, \(Re\) (Eq. (7)), following Sheil et al. (1995, 2000):

\[
Mo = \left\{ 1 - \left[ \frac{N_0 - N_m}{N_0} \right]^{1/t} \right\} \times 100
\]

\[
Re = \left[ 1 - \left( 1 - \frac{N_f}{N_t} \right)^{1/t} \right] \times 100
\]
Table 1

<table>
<thead>
<tr>
<th></th>
<th>Impuca 1</th>
<th></th>
<th>Impuca 2</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Unburned</td>
<td>Burned</td>
<td>Unburned</td>
<td>Burned</td>
</tr>
<tr>
<td></td>
<td>2007</td>
<td>2010</td>
<td>% Change</td>
<td>2007</td>
</tr>
<tr>
<td>Number of individuals</td>
<td>650</td>
<td>616</td>
<td>5.2</td>
<td>620</td>
</tr>
<tr>
<td>Basal area</td>
<td>10.08</td>
<td>9.8</td>
<td>2.8</td>
<td>15.1</td>
</tr>
<tr>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

where \( N_0 \) is the initial number of individuals, \( N_m \) is the number of dead individuals, \( N_r \) is the number of recruits, \( N_t \) is the final number of individuals, and \( t \) is the elapsed time in years.

Further, the half-life time, \( T_{1/2} \) was calculated (Eq. (8)), i.e., the time necessary for a given population to decrease by 50% of its individuals, based on its current mortality rate, the duplication time, \( T_2 \) (Eq. (9)), i.e., the time necessary for a given population to duplicate its individuals, based on its current recruitment rate (Lieberman et al., 1985).

\[
T_{1/2} = \frac{\ln(1/2)}{\ln(N_0 - N_m)} \left( \frac{N_0 - N_m}{N_0} \right)^{1/2} \tag{8}
\]

\[
T_2 = \frac{\ln(2)}{\ln(N_0 - N_r)} \left( \frac{N_0 - N_r}{N_0} \right)^{1/t} \tag{9}
\]

the stability, \( E, \) (Eq. (10)), with values nearest to zero indicating that the community would be more stable, and, also at community level, the turnover time (TUR) (Eq. (11)), i.e., how much higher will be the turnover rate, higher mortality rates and/or recruitment (Korning and Balslev, 1994).

\[
E = T_{1/2} - T_2 \tag{10}
\]

\[
TUR = \left[ \frac{T_{1/2} + T_2}{2} \right] \tag{11}
\]

where, \( \ln \) is the natural logarithm, \( N_0 \) is the initial number of individuals, \( N_m \) is the number of dead individuals, \( N_r \) is the number of recruits, \( t \) is the elapsed time in years, \( T_{1/2} \) is the half-life time, and \( T_2 \) is the duplication time.

In addition, for the ten main species in terms of importance value (VI sensu Curtis and McIntosh, 1950) measured in the 2007 inventory, we calculated the average annual mortality and recruitment rates, and the half-life and duplication times based on the number of individuals between 2007 and 2010. For the same period, and based on the individual basal area, we calculated the average annual rates of loss (Eq. (3)) and gain in basal area (Eq. (4)).

The average annual rates of mortality, recruitment, loss, gain and turnover (based on the number of individuals and the individual basal area), and the half-life and duplication times for each plot were used to compare the dynamics of burned and unburned sites within each impuca. For these comparisons, we used the non-parametric analysis of Mann–Whitney (Sokal and Rohlf, 1995). Histograms were plotted of individual and basal area distribution in diameter classes, where the equation for the calculation of the class intervals was based on Spiegel (1976). To compare the distributions of both inventories within the same sites of each impuca, we performed Kolmogorov–Smirnov tests. To determine the relationship between mortality (number of dead individuals and their basal area) and the diameter classes, we used simple linear regressions. All analyses were conducted using the R software statistical platform (R Development Core Team, 2011).

Results

Between 2007 and 2010, there was a reduction in basal area and absolute density of individuals in both the later burned and the continuously unburned sites of the impucas (Table 1). For the burned sites, there was little reduction in impuca 1 (2.8% on a basal area-basis), while in impuca 2 the reduction was 8%, for a basal area-basis. In the burned sites, the reduction in basal area was greater for both impuca 1 (10.1%, basal area-basis) and for impuca 2 (39.3%, for basal area-basis): Table 1. The higher basal area loss due to mortality compared to basal area gain due to recruitment resulted in an average net loss of basal area for all of the sites (Table 1).

As an effect of fire, there were high average annual mortality rates (8% year⁻¹ in impuca 1 and 24.3% in impuca 2) compared to recruitment in the burned sites (0.68% yr⁻¹ in impuca 1 and 0.66% in impuca 2), and also compared to mortality in the unburned sites of both impucas (Table 2). Due to the high mortality rates observed in the burned sites, there was a significant difference with respect to basal area loss between burned and unburned sites in both impucas (Table 2). For the gain rate of basal area, there was only a significant difference between the burned and unburned sites of impuca 1, with a greater gain for the unburned sites. In contrast, despite the burned sites of impuca 2 having higher gain rates of basal area than the unburned sites, their rate of loss of individuals was nearly four times higher, compared to unburned sites (Table 2). The recruitment rates of all sites (burned and unburned) were low (between 0.7% year⁻¹ in impuca 1 and 2% year⁻¹ in impuca 2): Table 2. Even the unburned sites had lower recruitment than mortality rates. The individual- and basal area-based mortality rates in the burned sites were higher than the rates observed in the unburned sites of both impucas. In contrast, the recruitment rates in the burned sites were higher than in the unburned sites of both impucas (Tables 1 and 2).

For all studied sites (burned and unburned), the values of half-life time were lower than the duplication time, on both an individual- and a basal area-basis (Table 2). The values of turnover time, on both an individual– and a basal area–basis, were higher for the burned than for the unburned sites in both impucas (Table 2). There was a reduction in the number of individuals in most of the diameter classes after fire occurrence, and changes within and between the diameter classes occurred (Fig. 2). The distribution of individuals among diameter classes did not differ between inventories for unburned sites (KS, \( x^2 = 0.0319, P = 0.05 \) ) and burned sites (KS, \( x^2 = 0.0537, P > 0.05 \) for impuca 1 and \( x^2 = 0.0301, P > 0.05 \) for impuca 2) (KS, \( x^2 = 0.0301, P > 0.05 \) ). There was only a reduction in the frequency of individuals of burned sites in impuca 2 (KS, \( x^2 = 0.1818, P < 0.001 \) ).

For mortality, on an individual-basis, there was a negative relationship with increasing diameter class for the burned sites of both impuca 1 (\( R^2 = 0.79, F = 27.42, P = 0.002 \) ) and impuca 2 (\( R^2 = 0.90, F = 66.76, P = 0.001 \)): Fig. 4A and B. Mortality on a basal area-basis was negatively related with the diameter class only for the burned sites of impuca 2 (\( R^2 = 0.60, F = 11.54, P = 0.01 \)), but with no significant relationship in impuca 1 (\( R^2 = 0.17, F = 2.43, P = 0.16 \)): Fig. 4C and D. Even with most of the dead individuals concentrated in the
Table 2
Parameters of the woody vegetation dynamics of burned and unburned sites of two seasonally flooded forests (impucas).

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Impuca 1</th>
<th></th>
<th>Impuca 2</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Average annual mortality rates (individual-basis, % year⁻¹)</td>
<td>3.7</td>
<td>8.0</td>
<td>149.00</td>
<td>5.2</td>
</tr>
<tr>
<td>Average annual recruitment rates (individual-basis, % year⁻¹)</td>
<td>2.0</td>
<td>0.7</td>
<td>431.50*</td>
<td>1.2</td>
</tr>
<tr>
<td>Average annual rates of gain (basal area-basis, % year⁻¹)</td>
<td>0.6</td>
<td>0.2</td>
<td>398.00</td>
<td>1.9</td>
</tr>
<tr>
<td>Average annual rates of loss (basal area-basis, % year⁻¹)</td>
<td>3.9</td>
<td>4.9</td>
<td>181.00</td>
<td>4.3</td>
</tr>
<tr>
<td>Average annual mortality rates (basal area-basis, % year⁻¹)</td>
<td>1.4</td>
<td>3.6</td>
<td>170.00</td>
<td>2.9</td>
</tr>
<tr>
<td>Average annual recruitment rates (basal area-basis, % year⁻¹)</td>
<td>0.4</td>
<td>0.1</td>
<td>333.00</td>
<td>13.0</td>
</tr>
<tr>
<td>Half-life time (individual-basis, years)</td>
<td>18.3</td>
<td>6.8</td>
<td>121.5</td>
<td>17.1</td>
</tr>
<tr>
<td>Duplication time (individual-basis, years)</td>
<td>38.6</td>
<td>13.1</td>
<td>469.50**</td>
<td>68.9</td>
</tr>
<tr>
<td>Turnover rate (individual-basis, years)</td>
<td>28.4</td>
<td>69.0</td>
<td>424.50**</td>
<td>40.9</td>
</tr>
<tr>
<td>Turnover rate (basal area-basis, years)</td>
<td>91.2</td>
<td>428.2</td>
<td>390.00</td>
<td>203.8</td>
</tr>
<tr>
<td>Half-life time (basal area-basis, years)</td>
<td>17.3</td>
<td>14.2</td>
<td>373.6</td>
<td>373.6</td>
</tr>
<tr>
<td>Duplication time (basal area-basis, years)</td>
<td>165.0</td>
<td>842.1</td>
<td>390.6</td>
<td>1285.6</td>
</tr>
<tr>
<td>Stability (individual-basis, years)</td>
<td>20.3</td>
<td>124.3</td>
<td>55.9</td>
<td>238.0</td>
</tr>
<tr>
<td>Stability (basal area-basis, years)</td>
<td>147.6</td>
<td>827.9</td>
<td>373.6</td>
<td>1281.5</td>
</tr>
<tr>
<td>Recruits basal area (m² ha⁻¹)</td>
<td>0.13</td>
<td>0.04</td>
<td>0.07</td>
<td>0.04</td>
</tr>
<tr>
<td>Dead basal area</td>
<td>1.14</td>
<td>2.05</td>
<td>1.45</td>
<td>9.02</td>
</tr>
</tbody>
</table>

W = test of Mann–Whitney.

* P<0.05.
** P<0.01.
*** P<0.001.
ns. = not significant.

smaller diameter classes (Fig. 4), the highest mortality rates were observed for the larger diameter classes for the unburned sites of impuca 1 (>35–40 cm) and impuca 2 (>30–35 cm). Fig. 2A and C, while for the burned sites of these impucas, the highest mortality rates were observed in the diameter class 5–10 cm (Fig. 2A and C). The highest recruitment rates, on both an individual- and a basal area-basis, were found in the smallest diameter classes of the burned and unburned sites of both impucas (Fig. 2B and D).

Fig. 2. Structural changes and dynamics of the woody vegetation between the years 2007 and 2010 by diameter classes of the burned and unburned sites of a seasonally flooded forest (impucas 1 and 2). A and C = Average annual rate of loss in basal area and average annual rate of mortality; B and D = Average annual rate of gain in basal area and average annual rate of recruitment; UN = unburned site and BU = burned site.
Considering both individual- and basal area-basis, the rates of change were negative for most of the classes of all the burned and unburned sites, except for the larger diameter classes (Fig. 4).

For the ten main species in terms of importance value in all sites, seven had higher mortality than recruitment rates. Only three species in the unburned sites of impuca 1 had recruitment rates equal or higher than mortality rates (Licania apetala, Ormosia excelsa and Diospyros poepigiana): Table 3. For the basal area in the burned sites, all species had higher rates of loss than gain. However, in the unburned sites, the rates of basal area gain were higher than basal area loss for six species of impuca 1 (Licania apetala, Mabea paniculata, Ormosia excelsa, Calophyllum brasiliense, Diospyros tetrandra, and D. poepigiana) and three species of impuca 2 (Ternstroemia candolleana, Symmeria paniculata, and Roupala montana) (Table 3).

**Discussion**

The results of this study, the first of our knowledge examining the response of impucas to fire, indicate that these seasonally flooded forests are generally not fire-resistant. Mortality rates and basal area loss were high, while recruitment was outpaced by mortality. Some species have adaptations to fire, e.g. a thick bark (Calophyllum brasiliense, Licania apetala, Roupala montana and Vochysia divergens). This unique vegetation type in the Cerrado-Amazon forest transition appears to be highly dynamic (both unburned and burned plots), responding to the dual stress of seasonally water-saturated soil environment of the roots and infrequent, but over the years increasing fire events.

**Community-level patterns**

Mortality rates from the unburned impucas of our study were higher than those in an experimental study in a burned Amazonian transition forest (4.8% per year; Balch et al., 2008). Furthermore, annual mortality rates in the burned impucas of our study were two to six times this rate. Mortality rates commonly reported for protected tropical forests are approximately 1–2% per year (Condit et al., 1995; Stephenson and van Mantgem, 2005), much lower than the rates observed for the burned and unburned impucas sites. This suggests that the unburned impucas may also be affected by additional factors with negative influence (e.g. drought). On the other hand, the high mortality rates measured in the burned sites of our study show that fire clearly has a negative effect on the impuca vegetation and, that areas that are seasonally inundated are still susceptible to fire intrusion despite long periods of the seasons with water-saturated soil and likely proximity of the water table to the surface (Brito et al., 2008).

A high number of dead individuals and reduced basal area in burned compared to unburned sites is consistent with our hypothesis that the impucas are highly susceptible to fire. However, since a
The reduction in individual density and in basal area was also measured in the unburned forest, it is also possible that the 2010 drought – which reduced rainfall in this region compared to the long-term average (Marengo et al., 2011) – may have been a factor influencing negatively all the sites. The reduction in individuals in the unburned sites in our study may also be a result of a time-lag in mortality from previous fires, since some *impucas* in the region may already have previously burned (Barbosa et al., 2011). It is also important to emphasise that the losses due to fire may go beyond the direct effects observed immediately after the burning, since fire increases the probability and susceptibility to future burning (Cochrane et al., 1999).

**Effects of tree size**

We found contrasting patterns of tree mortality by diameter class, with the larger classes having the highest mortality rates in unburned plots, but the smallest classes having the highest mortality rates in burned plots. Losses from the smaller size-classes may affect future regeneration, while losses from the larger diameter classes result in a large reduction in basal area and may affect seed sources. Also, irradiance below the tree canopies becomes increased. In forests, the highest numbers of dead individuals are commonly measured in the smaller diameter classes. This pattern could be attributed to the low capacity of smaller individuals to compete with canopy trees (Felitti, 1995), and to their higher vulnerability to disturbances, such as fire. In the present study, this pattern was observed in both the burned and unburned sites. It is probable that the higher mortality in the smaller size classes is related to the higher proportion of individuals in these smaller size classes (Fig. 2), and their low tolerance to fire (Hoffmann and Solbrig, 2003; Medeiros and Miranda, 2005). Barlow et al. (2003) reported significant loss of individuals in the Amazon Forest after fire disturbance, and observed that even large trees, which initially seemed to be fire resistant, died nearly three years after fire occurrence. In the unburned sites of the *impucas* of our study, the high mortality rates observed in the larger diameter classes may be related to the presence of older, senescent individuals or a delayed response to fires that occurred before 2007 (Herson Lima, PEA Administrator, pers. communication). However, the low number of individuals in the larger classes could result in an overestimation of the mortality rates, because of the high stochasticity in the data due to small sample sizes. Sampling and evaluation of the plot data for a longer period will give a still more realistic picture of the effects of fire on individuals with different diameters.

Fire also appears to have exerted a strong effect on the smaller individuals in the burned sites and did reduce recruitment. Generally, recruitment rates exhibited by the vegetation in the *impuca* forests were low, when compared to other forest studies – where values ranged from 3.5 to 4.5% year⁻¹ (Gomes et al., 2003; Paiva et al., 2007; Silva and Araújo, 2009). It is important to note that even the unburned sites had on average lower recruitment rates than those reported for other forests.

**Populations**

Species that had higher recruitment and gain rates than mortality and basal area loss, such as *Calophyllum brasiliense* and *Symmeria*...
Table 3
Parameters for vegetation dynamics of the 10 highest IV species (importance value) in 2007 for the burned and unburned sites of two seasonally flooded forests (impucas). The species are ordered according to the IV in 2007.

<table>
<thead>
<tr>
<th>Species</th>
<th>M (m)</th>
<th>R (m)</th>
<th>RBA (m)</th>
<th>IBA</th>
<th>DBA (m)</th>
<th>GBA (m)</th>
<th>LBA (m)</th>
</tr>
</thead>
<tbody>
<tr>
<td>IMPUCA 1 – unburned</td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ochthocosmus multiflorus Ducke (Ixonanthaceae)</td>
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<td>2.0</td>
<td>0.02</td>
<td>0.07</td>
<td>0.03</td>
<td>1.4</td>
<td>2.1</td>
</tr>
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<td>0.01</td>
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<td>15.5</td>
</tr>
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<td>1.1</td>
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<td>0.03</td>
<td>0.02</td>
<td>1.2</td>
<td>1.0</td>
</tr>
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<td>0.01</td>
<td>4.6</td>
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</tr>
<tr>
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<td>0</td>
<td>3.0</td>
<td>0</td>
</tr>
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<td>1.8</td>
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<td>0.01</td>
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IMPUCA 1 – burned

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<th>DBA (m)</th>
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<td>0.03</td>
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<td>0.01</td>
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<td>2.8</td>
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<td>0.02</td>
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<td>1.1</td>
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<td>0.08</td>
<td>0.02</td>
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<td>4.1</td>
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<tr>
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IMPUCA 2 – unburned

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<td>0.01</td>
<td>0.01</td>
<td>1.1</td>
<td>1.9</td>
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<tr>
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<td>0.02</td>
<td>0.01</td>
<td>1.6</td>
<td>1.4</td>
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<td>0.01</td>
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IMPUCA 2 – burned

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<th>DBA (m)</th>
<th>GBA (m)</th>
<th>LBA (m)</th>
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<td>0.01</td>
<td>3.9</td>
<td>10.1</td>
</tr>
</tbody>
</table>

M: mortality (% year\(^{-1}\)); R: recruitment (% year\(^{-1}\)); t\(_{1/2}\): half-life time (years); t\(_{1}\): duplication time (years); RBA: recruits basal area (m\(^2\) ha\(^{-1}\)); IBA: basal area increment (m\(^2\) ha\(^{-1}\)); DBA: decrrement in basal area (m\(^2\) ha\(^{-1}\)); GBA: gain in basal area (% year\(^{-1}\)); LBA: loss in basal area (% year\(^{-1}\)).

**Root system**

The soils of the forests of our study have a thick layer of organic matter and densely interspersed by a mesh of fine roots (Barbosa et al., 2011). During the month when the burnings occurred (September), the litter layer and the mesh of roots that covered the soil became dry and susceptible to fire. After fire had entered the forests, root systems of several trees were completely burned, resulting in the trunks of some large trees remaining suspended in the air, supported by their canopies locked into those of neighbouring trees. This observation reinforces other studies.
indicating that creeping fires on the forest floor causes major impacts in Amazonian forests, and in the case of our study, higher mortality rates.

**Factors causing instability in Amazonian transition forests**

Disturbances such as flooding, burning, droughts, and human activity may cause forest instability. Alencar et al. (2004) emphasized that the Amazonian transition forests, besides suffering strong deforestation pressure (Nogueira et al., 2008), have been suffering major damage caused by fire. This is partially a result of having a more open canopy structure compared to the dense forests of central Amazonia, making transitional forests more prone to drying, and increasing their vulnerability to fire. Moreover, several studies have reported disequilibrium between mortality and recruitment in seasonal forests (Appolinário et al., 2005; Enquist and Enquist, 2011) and gallery forests (Braga and Rezende, 2007; Miguel et al., 2011). Additionally, the ground fires are passing rather quickly a certain location so that extreme temperatures are measured there only for few minutes (e.g. Northern Conifer Forests). By contrast, crown-fires remain for a longer period of time at a particular site, thus increasing the extreme temperature situation and making inefficient all plant adaptations against quickly passing fire fronts, as observed in the *impuca*. Although in the current study it appears that fire and/or drought may be the main causative agent of this disequilibrium, natural flooding, or changes in the flood regime must in future studies also be evaluated as a potential driver of community turnover, since some studies have reported that the flood period is one of the most important factors that influence growth, distribution and richness of species in flooded forests in the Amazon (Wittmann et al., 2002, 2004).

**Turnover**

The high turnover time, duplication time, as well as the low half-life time observed in the burned sites reinforce that effects of fire on the *impuca* communities are quite deleterious, as they reduce the number of individuals by half within a short period of time (<7 years), so that it would take substantial time (>130 years) to duplicate the number of individuals, if the high rates of mortality and low rates of recruitment found in this study continued. For some forests not subjected to seasonal flooding, there is a reported pattern of balance between half-life and duplication times (Oliveira-Filho et al., 1997; Paiva et al., 2007; Silva and Araújo, 2009). The disequilibrium between such parameters reported in our study may be attributed to the imbalance between the mortality and recruitment rates. In the burned sites, fire may have been the key-factor for this increase in disequilibrium, since in these sites we observed low recruitment and high mortality of individuals. In order to be balanced, a forest community requires some stability in the parameters mortality, recruitment, half-life and duplication times (Korning and Balslev, 1994). The obvious lack of stability in these rates raises concerns about the maintenance of these forests in the short and medium term.

The values of half-life time of the unburned sites were similar to the 17.2 and 16.9 years in a semi-deciduous forest of Minas Gerais State, Brazil, reported by Paiva et al. (2007) and Silva and Araújo (2009). In a disturbed forest in the Peruvian Amazon, Nebel et al. (2001) reported higher half-life times (between 22 and 32 years) and lower duplication times (between 16 and 24 years). Other studies in Amazonia reported higher half-life times (between 24 and 99 years) and lower duplication times (between 25 and 86 years), e.g. Uhl et al. (1988); Rankin-de-Mérona et al. (1990); Gentry and Terborgh (1990); Phillips et al. (1994); Phillips and Gentry (1994), compared to those observed in the burned *impuca* sites. This underlines the high amount of disturbance observed in both forests of our study. The turnover times of our study were high when compared with those of non-seasonally flooded forests (Oliveira-Filho et al., 1997; Paiva et al., 2007; Silva and Araújo, 2009), indicating that *impuca*, both burned and unburned, are extremely dynamic compared to other forests.

**Conclusions**

Here we provided new information on the impacts of fire on seasonally flooded forests of the Cerrado–Amazon Forest transition areas. However, due to spatial and temporal limitations of our study, care should be taken when extrapolating our findings to other regions of Amazonia. Future studies should increase the number of sampling units, the monitoring period, and extend sampling to other physiognomies in the Amazon transitional zone. In summary, our results support the hypothesis that greater structural changes occurred in the burned sites of both forests. The high rates of mortality and loss in basal area and the relatively low rates of recruitment and gain in basal area observed in the burned sites may be attributed to the fire effects upon these forests. However, the high level of dynamism observed also for the unburned sites indicates that these forests must be affected also by other stress factors, in addition to fire. Humans have been responsible for the increased frequency of fire in *impuca*, and if these forests are to remain, it may be necessary to adopt fire prevention measures. Long-term studies that also examine the effects of flooding and drought on forest dynamics and productivity of such *impuca* will help to separate the effect of fire from climatic drivers of productivity in this unique vegetation community of the Amazon Forest–Cerrado Biome transition range.

**Acknowledgements**

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**References**


