

### Programa de Pós Graduação em Ecologia e Conservação

Centro de Ciências Biológicas e da Saúde Universidade Federal de Mato Grosso do Sul

## Environmental filters influence functional structure and growth of monodominant forest patches in the Pantanal floodplain

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# Filtros ambientais influenciam a estrutura funcional e o crescimento de manchas florestais monodominantes na planície de inundação do Pantanal

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### **General Abstract**

In the tropics, monodominant stands occurring interspersed with mixed forest or savanna formations with high species diversity is an issue that still challenges ecologists. Despite several studies on this topic, there is still no explanation for all aspects of this phenomenon. Some key factors have been pointed out, and two general approaches have been discussed. Firstly, the lack of disturbance, where better competitors stand out in most advanced stages of succession, and secondly, the presence of environmental filters, such as fire, flood and poor soils, which exclude less tolerant species. Environmental filters can influence strategies for nutrient uptake by plants, varying between acquisitive or conservative strategies. In this thesis, we show in three chapters how environmental filters influence the structure of the community and individual traits in monodominant stands of Leptobalanus parvifolius (Huber) Sothers & Prance (= Licania parvifolia Huber, recently synonymized, see Sothers et al. 2016) in the Pantanal floodplain, in central South America. In addition, given the importance of climate for tree growth, we analysed growth rings to verify if El Niño and rainfall events and flooding influence the establishment and growth of L. parvifolius individuals. We found that L. parvifolius dominance increases with higher flooding, greater soil fertility and higher livestock disturbance, or in less fertile and more flooded soils, but without livestock. A plausible explanation is that floods and livestock disturbances can prevent the establishment of other species in more fertile soils and, therefore, facilitate the *L. parvifolius* dominance. Trees in more flooded areas have conservative strategies (slower growth), while in less flooded areas, they resort to acquisitive strategies (faster growth). That result may represent higher productivity and nutrient cycling in less flooded areas. Thus, monodominant stands of L. parvifolius are niche structured along environmental gradients. This may be related to the plasticity of the dominant species, which may be a relevant factor for the monodominance of L. parvifolius and other species in the Pantanal. Flooding in the region seems not strong enough to affect the growth of L. parvifolius. The establishment of L. parvifolius individuals occurs mainly in years with flooding duration between 30 and 110 days. In turn, El Niño events have a significant negative influence on the growth of L. parvifolius. The expected climate changes and consequent increase in El Niño frequency and Intensity can drastically modify the hydrology and climate of the Pantanal, which can compromise the establishment and growth of monodominant species, causing drastic changes in the floodplain landscape.

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Keywords: Dendrochronology, *El Niño*, flood, functional traits, growth rings, *Leptobalanus parvifolius, Licania parvifolia*, monodominance, rainfall.

### **Resumo geral**

Nos trópicos, a ocorrência de stands monodominantes intercalados com formações florestais ou savânicas mistas, com alta diversidade de espécies, é uma questão que ainda desafia os ecólogos. Apesar de vários estudos voltados para esse tema, ainda não há explicação para todos os aspectos desse fenômeno. Alguns fatores chave têm sido apontados e duas abordagens gerais são: a falta de distúrbio, onde espécies que são melhores competidoras se sobressaem nos estágios mais avançados de sucessão, e a presença de filtros ambientais, como por exemplo fogo, inundação e solos pobres, que excluem as espécies menos tolerantes. Esses filtros ambientais podem influenciar nas estratégias de uso de nutrientes pelas plantas, variando entre estratégias aquisitivas ou conservativas. Nesta tese mostramos, em três capítulos, como os filtros ambientais influenciam na estrutura funcionalidade da comunidade e crescimento de indivíduos em formações monodominantes de Leptobalanus parvifolius (Huber) Sothers & Prance (= Licania parvifolia Huber, sinonimizado recentemente, ver Sothers et al. 2016) na planície de inundação do Pantanal no centro da América do Sul. Além disso, dada a importância do clima para o crescimento de árvores, analisamos anéis de crescimento para verificar se eventos de El Niño e precipitação, além de inundação, influenciam o estabelecimento e crescimento de indivíduos de L. parvifolius. Nossos principais resultados foram que a dominância de L. parvifolius aumenta com maior inundação, maior fertilidade nos solos e maior perturbação do gado, ou em solos menos férteis e mais inundados, mas sem gado. Uma explicação plausível é que inundações e distúrbios pelo gado podem impedir o estabelecimento de outras espécies em solos mais férteis e, portanto, podem facilitar o estabelecimento e aumentar a dominância de L. parvifolius. Indivíduos em áreas mais inundáveis possuem estratégias conservadoras (menor crescimento), enquanto que em áreas menos inundadas eles lançam mão de estratégias aquisitivas (crescimento mais rápido). Este resultado pode representar maior produtividade e ciclagem de nutrientes em áreas menos inundáveis. Assim, stands monodominantes de L. parvifolius são nichoestruturados ao longo dos gradientes ambientais. Isso pode estar relacionado à plasticidade da espécie dominante, o que pode ser um fator importante para a monodominância desta e de outras espécies no Pantanal. A inundação na região parece não ser suficientemente forte para realmente afetar o crescimento de L. parvifolius. O estabelecimento de indivíduos de L. parvifolius ocorre principalmente em anos com inundação entre 30 e 110 dias. Por sua vez, os eventos de *El Niño* têm uma influência negativa significativa no crescimento de *L. parvifolius*. As alterações climáticas esperadas e o consequente aumento na frequência e intensidade dos eventos *El Niño* podem modificar drasticamente a hidrologia e o clima do Pantanal, o que pode comprometer o estabelecimento e crescimento de espécies monodominantes, causando mudanças drásticas na paisagem.

Palavras-chave: Anéis de crescimento, dendrocronologia, *El Niño*, inundação, *Leptobalanus parvifolius, Licania parvifolia*, monodominância, precipitação, traços funcionais.

### **General introduction**

The dominance of species within communities and their consequences has been discussed for more than a century (Clements 1916; Mcnaughton & Wolf 1970). Ecological dominance is defined by the relative importance of a species to the functioning of ecosystems. This importance can be estimated through measures of relative abundance, cover or biomass. It can be explained by the mass ratio hypothesis (Grime 1998), which predicts that species with greater biomass are primarily responsible for the ecological and ecosystem processes in these communities (such as competitive relationships and facilitation, primary production, nutrient cycling, among others). More recent studies have shown the importance of dominant species on the stability of ecosystems (Sasaki & Lauenroth 2011), contradicting the well-established idea of a positive relationship between diversity and stability (Tilman 1999; Tilman et al. 2006).

Under certain conditions, the dominance can be spearheaded by a single species with more than half of the individuals in a community. This condition characterises the monodominance (Hart et al. 1989), which is defined as communities in which a species has  $\geq$  50% of the number of individuals (Connell & Lowman 1989), biomass or cover (Guo & Rundel 1997). Two main approaches can be considered to explain the phenomenon of monodominance. The first approach deals with dominance in tropical forest ecosystems using the lack of endogenous disturbances as a key factor for monodominance (Richards 1952; Connell & Lowman 1989; Hart et al. 1989; Hart 1990; Hart 1995). In this system, monodominance is achieved throughout succession through competitive exclusion (Bhaskar et al. 2014; Lohbeck et al. 2014). In addition, issues such as association with ectomycorrhiza (Connell & Lowman 1989; McGuire 2007; Corrales et al. 2018; Lambers et al. 2018), tolerance to shading and limited dispersion (Torti et al. 2001), among others are also important (Peh et al. 2011). On the other hand, monodominance can also be attributed to environments subjected to stressful environmental conditions. Here, dominance occurs mainly due to intolerable conditions for most species, such as seasonal fire events, floods and poor soils (Hart 1990). Despite the widely discussed importance of soil conditions, little evidence indicates the relationship between low soil nutrient content and monodominance (Hart 1990; Torti et al. 2001). In addition, some studies have shown that soil is not a determining factor for monodominance (Nascimento & Proctor 1997; Peh et al. 2011).

With a range of factors identified as critical to monodominance, it is difficult for species in different ecosystems to depend on just one factor to achieve monodominance. A more plausible condition is a set of endogenous and exogenous factors interacting to set monodominance.

In floodplains such as the Pantanal, the occurrence of monodominance is quite frequent (Pott et al. 2011; Damasceno-Junior et al. 2021). The Pantanal is a floodplain located in the centre of South America. The climate is Aw, tropical with dry winter and annual average temperature ranging between 24 and 26 °C (Alvares et al. 2013). The rainfall varies between 1000 and 1200 mm per year (Thielen et al. 2020). Soils vary according to the origin of the sediments and are influenced by the hydrological regime of each subregion. Sandy soils are predominant due to the sediments carried from the plateau. In the study subregion, the main soil types are Espodossolos and Vertisolos (Cunha 1981; Amaral 1987; Soares et al. 2006; Couto & Oliveira 2010).

The vegetation in the Pantanal aggregates elements common to several adjacent biomes, that is, Cerrado, Atlantic Forest, Amazonia, Caatinga and Chaco. The main influence comes from the Cerrado, which appears with greater expression in North, East and Southeast (Silva et al. 2000; Souza et al. In Press). In the study area is possible to observe vegetation mosaics with floodable shrub-herbaceous grasslands with native pastures intermingled with monodominant stands such as *Byrsonima cydoniifolia* ("Canjiqueiral"), *Couepia uiti* ("Pateiral") and *Leptobalanus parvifolius* ("Pimenteiral"), in addition to riparian forests and semideciduous seasonal forest islets on slightly elevated terrains (locally called "capões" and "cordilheiras").

The primary environmental filter for vegetation in the Pantanal is flooding, which causes a reduction in the availability of oxygen and an increase in CO<sub>2</sub>, which leads to reduction in plant physiological activities (Dalmagro et al. 2016). Despite the restrictions, several species tolerate flooding with different time course, with species composition varying along the flood gradient (Nunes da Cunha & Junk 2001; Damasceno-Junior et al. 2005; Oliveira et al. 2014). In general, tree community in the Pantanal has a significant reduction in photosynthetic capacity during the flood due to the decrease in the potential for soil oxidation-reduction potential. However, this reduction is species-specific, with some species presenting similar photosynthetic performances similar to the terrestrial phase (Dalmagro et al. 2016).

Like flooding, extensive livestock activity has a strong influence on the Pantanal landscapes. The cattle can reduce herbaceous vegetation and thus favour fast-growing tree-shrub pioneers. Trampling and grazing can also exclude non-sprouting woody species and favour those prone-sprouting (Bovey 2001; ter Steege et al. 2019; Scogings & Sankaran 2020).

Such specific environmental conditions, such as flood, drought, fire and pioneering behaviour, allow some species to form monodominant stands (Torti et al. 2001; Nunes da Cunha & Junk 2004; Nunes da Cunha et al. 2007; Gris et al. 2020; Manrique-Pineda et al. 2021). These stands can exhibit varied patterns along environmental gradients, considering both species within these formations and the dominant species (Bueno et al. 2014). Among the monodominant species in the Pantanal, *L. parvifolius* is one of the most widely distributed in the plain, with monodominance concentrated in the southern part of the plain (Damasceno-Junior et al. In Press).

*Leptobalanus parvifolius* is a tree species of wide distribution in North, Midwest and Northeast Brazilian regions, usually associated with riparian forest. It has trunks generally branched at the base that seem to sprout from underground around the others stems (Chapter 3, Fig. 2). The trees usually range from 3 to 7 m tall (Pott & Pott 1994). Flowering occurs between May and June and less frequently, until November or February, with fruiting usually between October and December (Appendix 1). In Pantanal floodplain, its monodominant stands occur throughout the plain in seasonally floodable areas flooded between six and eight months, with a common presence in riparian forest and sandy and silty soils with low fertility (Nunes da Cunha & Junk 2009; Arieira et al. 2016).

In the studied area, the monodominant stands of *L. parvifolius* were found mainly bordering intermittent water bodies (locally called "corixos") and on the edge of slightly elevated terrains with semideciduous forest patches ("capões" and "cordilheiras"). It occurs almost always accompanied by patches or isolated individuals of *Couepia uiti* (same family), another typical monodominant species in the region (see Appendix 3). *Leptobalanus parvifolius* is considered a pasture invader, therefore, being undesired by ranchers. Due to great vigour and sprout capacity, the spreading of these monodominant stands is difficult to be controlled (Santos et al. 2006). It can grow relatively faster than other typical species of the region, which can be problematic in native pasture farms (Nunes da Cunha & Junk 2004).

All these conditions make the monodominant stands of *L. parvifolius* in the Pantanal a favourable environment to study the determinant processes that structure monodominant stands. Thus, in this thesis, we dedicate ourselves to elucidate, in three

chapters, the effects of different environmental filters potentially structuring these monodominant formations.

In the first chapter, we tested the hypotheses that flooding reduces richness, basal area and height, favouring the dominance of *L. parvifolius*, and that soil fertility has a positive relationship with abundance, height and basal area, and negative with richness. In turn, soil acidity has negative relation with richness; Cattle act preventing the establishment of several species, reducing richness, basal area and height probably due to the effects of trampling and browsing, which can benefit the dominance of *L. parvifolius* because it is a sprouting-prone species.

In addition to the responses of the species present in these monodominant stands, individual functional characteristics can reveal the plant strategies more accurately. Therefore, in the second chapter, we checked whether flooding and soil nutrients influence the functional diversity of the community and whether the strategies for nutrient use by individuals within the monodominant formations of *L. parvifolius* vary across environmental gradients. We tested whether soil nutrients, flood and livestock disturbance influence the individual functional traits of these monodominant patches. We expected that resource-conservative strategies are related to more flooding, while in less floodable areas, plants adopt acquisitive strategies. In addition, we expected that the influence of flooding on strategies will vary according to the availability of nutrients in the soil and that richer soils will provide greater functional diversity while increasing flooding will decrease functional diversity.

Bearing in mind that knowing the relationship between climatic conditions and the growth of trees and how changes in the hydrological cycle can affect the monodominant landscapes in the Pantanal is of paramount importance for developing management strategies in these areas. Therefore, in the third chapter, we used growth ring analyses to understand how *El Niño* events, flood and rainfall influence the establishment and growth of *L. parvifolius* individuals. We hypothesise that *El Niño* and inundation negatively influence and that rainfall positively influences the growth of *L. parvifolius*.

### **Chapter 1**

# Flood, soil and livestock influence the structure of monodominant forests patches

### Abstract

Classical monodominance appeals to lack of disturbance as a key factor for some tree monodominance. However, this may not be true in floodplains. To clarify the mechanisms that underpin the structure of monodominant forests in floodplains, we tested the influence of soil (fertility and acidity), cattle disturbance and flooding and also the interactions between them on the species richness, dominance, abundance, basal area, height and persistence (proxied by basal ramification) in floodable monodominant stands of Leptobalanus parvifolius (Huber) Sothers & Prance. We set 47 plots with  $5 \times 30$  m into patches of L. parvifolius monodominant stands distributed in an area of approximately 97 km<sup>2</sup>. We used the relative basal area (%) of L. parvifolius as the dominance of this species. We measured the watermark of the last flood on the trunks and used it as a flood measurement. For macronutrient analyses, we collected five soil portions from 0-20 cm depth and mixed then to obtain on composed sample per plot. We found that the dominance of L. parvifolius increases with combination of (i) more flooding, more fertile soils and more cattle disturbance, or (ii) more flooding, less fertile soils and less cattle disturbance. Richness was lower in more flooding and more fertile soils. Communities with cattle disturbances have a higher basal area and number of branches. Basal area and abundance were positively related to soil fertility, but abundance was negatively related to soil acidity. In conclusion, in less fertile soils, L. parvifolius can take advantage if more flooding is associated with less cattle disturbance. A parallel explanation for its monodominance is that flood along with cattle disturbance may hinder the establishment of non-sprouting species in higher fertile soils, thus, it can facilitate the establishment and increase the dominance of L. parvifolius.

Keywords: Environmental filters, Cattle, Leptobalanus parvifolius, Licania parvifolia, monodominance.

### Resumo

A monodominância clássica apela à ausência de perturbação como um fator-chave para a monodominância de algumas árvores. No entanto, isso pode não ser verdade nas planícies inundáveis. Para esclarecer os mecanismos que sustentam a estrutura das florestas monodominantes em planícies de inundação, testamos a influência do solo (fertilidade e acidez), distúrbios do gado e inundações e também as interações entre eles sobre a riqueza de espécies, dominância, abundância, área basal, altura e persistência (representada pela ramificação basal) em formações monodominantes de Leptobalanus parvifolius (Huber) Sothers & Prance. Instalamos 47 parcelas de  $5 \times 30$  m em manchas monodominantes de L. parvifolius distribuídos em uma área de aproximadamente 97 km<sup>2</sup>. Usamos a área basal relativa (%) de L. parvifolius como a dominância desta espécie. Medimos a marca d'água da última inundação nos troncos e a usamos como uma medida de enchente. Para análises de macronutrientes do solo, coletamos cinco porções de solo de 0-20 cm de profundidade e misturamos para obter uma amostra composta por parcela. A dominância de L. parvifolius aumenta com a combinação de (i) maior inundação, solos mais férteis e maior distúrbio pelo gado, ou (ii) maior inundação, solos menos férteis e menor distúrbio pelo gado. A riqueza foi menor em áreas mais inundáveis e solos mais férteis. Áreas com maior distúrbio pelo gado apresentam maior área basal e maior número de ramos. A área basal e a abundância foram positivamente relacionadas à fertilidade do solo, e a abundância foi negativamente relacionada à acidez do solo. Em conclusão, em solos menos férteis, L. parvifolius pode ter vantagem se maior inundação estiver associada com menor perturbação pelo gado. Uma explicação paralela para a monodominância de L. parvifolius é que a inundação juntamente com a perturbação do gado e solos mais férteis podem dificultar o estabelecimento de espécies com menor capacidade de brotamento em solos mais férteis, podendo assim, facilitar o estabelecimento e aumentar a dominância de L. parvifolius.

Keywords: Filtros ambientais, gado, Leptobalanus parvifolius, Licania parvifolia, monodominância.

### Introduction

Flood is the main factor determining structure diversity and distribution of forests in floodplains (Damasceno-Junior et al. 2005; Wittmann et al. 2006; Parolin & Wittmann 2010; Arruda et al. 2016). Flooding can reduce tree species richness gradually (Amador et al. 2012). However, in the |Pantanal highest species richness tends to occur in slightly flooded terrains (Nunes da Cunha & Junk 2001), which can support both flood- and drought-tolerant species, and also generalist ones (Nunes da Cunha & Junk 2001; Damasceno-Junior et al. 2004). Flooding can affect metabolism and, therefore, growth of several species, decreasing the individual basal area (Arruda et al. 2016). Changes in metabolism due to flooding are mainly caused by depleting O<sub>2</sub>, photosynthesis rate decrease and accumulation of CO<sub>2</sub>. The absorption of macronutrients (markedly N, P, and K) is typically reduced in flood-intolerant plants (Kozlowski 1997). Due to these drastic changes in physiological conditions under flood, many species cannot withstand flooding, which leads to a reduction in richness (Duivenvoorden 1996; Ferreira & Stohlgren 1999). It can be an relevant factor for establishing monodominant tree stands in the tropics (Nascimento et al. 2017).

Monodominance is characterized when more than half of the individuals in a community belong to the same species (Hart et al. 1989). However, in the tropics, very likely flooding is not the only important factor in structuring the community and establishing monodominance. It has been argued that conditions such as soil drainage (Degagne et al. 2009; Nascimento et al. 2017), low soil fertility with extreme aridity and low levels of cation exchange (Draper et al. 2018), and ectomycorrhizal associations, which allow better exploration of soil decomposed organic matter (Henkel 2003; Corrales et al. 2016), acquisition efficiency and use of nutrients (Hall et al. 2020) are determinants as well.

On the contrary, depending on the geographic scale, high fertile soils are generally associated with lower species richness (Huston 1980; Enright et al. 1994; Harpole & Tilman 2007; Slik et al. 2010), which can facilitate establishing monodominance. Soils with high water availability and high nutrients levels allow faster growth, with more biomass allocation and a higher number of individuals, which can cause competitive exclusion resulting in lower diversity (Enright et al. 1994). Besides fertility, high soil acidity also can be related to lower species richness (Dupré et al. 2002; Ewald 2003; Schuster & Diekmann 2003). Although some studies shows a negative relationship

between species richness and soil fertility and acidity, depending on the type of vegetation, geographic scale and range of soil conditions, this relationship can be unimodal and hump-shaped, or even positive (Dupré et al. 2002). Another soil characteristic associated with monodominance can be the lower decomposition rate than mixed forest (Torti et al. 2001; Peh et al. 2011).

One of the main lines of investigation has attributed the monodominance to lack of disturbance and environmental filters, called classical monodominance, characterized as low diversity where high diversity is expected (Peh et al. 2011). Meanwhile, other studies indicate that, as soil features, the disturbance is a relevant condition for increasing dominance (ter Steege et al. 2019). In floodable grasslands of the Pantanal, livestock is the mean human activity (Seidl et al. 2001). Cattle disturbance can cause physical and chemical alterations in soil characteristics (Kurz et al. 2006), which can affect the response of the plants (Whitehead 2000). However, the cattle cause disturbances through trampling and grazing, that can directly affect vegetation, such as facilitating the growth of some woody species, mainly pioneers due to reducing the competition with grasses (LaMalfa et al. 2019). Woody plants adapted to environments with frequent disturbances have sprouting as the primary means of propagation and maintenance in the environment (Kennard et al. 2002; Bond & Midgley 2003). Although little explored, sprouting is an important factor for monodominance in the Amazon forest (ter Steege et al. 2019).

Therefore, in addition to flooding, it is known that several factors, like soil properties (Damasceno-Junior et al. 2021), can act together in the structuring and establishment of monodominant forests (Peh et al. 2011; Manrique-Pineda et al. 2021). Despite this, studies have focused on factors individually without systematic approaches to the interactions between them. It is essential to understand the interactions between flood, soil and disturbance because: a) cattle can affect vegetation both directly by grazing and trampling and indirectly by changing the chemical and physical characteristics of the soil (Kurz et al. 2006); b) similarly, flooding can affect vegetation differently depending on the availability of nutrients in the soil (Kozlowski 1997). Thus, understanding the interaction between factors, that is, how the effect of one factor on the community structure varies combined with another factor, allows for a better understanding of the effects of all factors. That allows for more accurate predictions of anthropogenic environmental disturbances, which can facilitate management and conservation strategies.

The Pantanal is a vast floodplain in the centre of South America, flooded by the Paraguay River and its tributaries (Hamilton et al. 1996). The vegetation types are very diverse, highlighting the monodominant communities such as *Copernicia alba* Morong. ("carandazal") and *Attalea phalerata* Mart. ex Spreng. ("acurizal") palm lands, *Tabebuia aurea* (Silva Manso) Benth. & Hook.f. ex S.Moore ("paratudal"), *Vochysia divergens* Pohl ("cambarazal") and *L. parvifolius* (pimenteiral) woodlands, among others (Damasceno-Junior et al. In Press; Pott et al. 2011; Damasceno-Junior et al. 2021). Due to these characteristics, the Pantanal floodplain offers an excellent opportunity to study monodominant communities.

Thereby, in this study, we verified the influence of soil fertility and acidity, cattle disturbance and flooding on the species richness, abundance, basal area, height and sprouting capability in monodominant stands of *L. parvifolius*. We also tested the effect of interactions between soil and cattle disturbance and between soil and flood on the same response variables. We expected that: a) flood affects wood community decreasing abundance, richness, basal area and height; due to this scenario, *L. parvifolius* can increase its dominance in more flooded areas; b) soil fertility influences abundance, height and basal area positively and richness negatively, and soil acidity positively affect richness and; c) cattle grazing and trampling cause damage to sprouts and regeneration woody vegetation decreasing richness, abundance basal area and height. However, due to cattle disturbance being a potential trigger to sprout (Busby et al. 2010), sprouting species like *L. parvifolius* benefit from cattle disturbance for increasing the number of ramification and basal area. That would lead to an increased dominance of *L. parvifolius* in areas with high cattle disturbance.

### Methods

### Study area

The study was carried out in monodominant stands of *L. parvifolius* in the Pantanal floodplain in Abobral and Nhecolândia sub-regions (Fig. 1). The climate of the region is tropical with dry winter (Aw), with rainfall between 1000 - 1200 (Thielen et al. 2020) and an annual average temperature between 24 and 26 °C (Alvares et al. 2013). The Pantanal soils of each region are influenced by the different hydrologic regimes (Cunha 1981; Soares et al. 2006; Couto & Oliveira 2010). In the study region, the main soil types are Spodosols and Vertisols (INPE 2010). The vegetation is a mosaic with riparian forest, semideciduous seasonal forest islets on slightly elevated (c.a 1 m) terrains (locally called "capões") and other monodominant stands intermingled with floodable shrub-herbaceous natural grasslands (Allem & Valls 1987).



Fig. 1. Location of study area and plots in *Leptobalanus parvifolius* formations in the Pantanal floodplain.

Leptobalanus parvifolius is a tree about 7 m in height, with a trunk usually branched at the base (Fig. 2), with wide distribution in the tropical forest from Colombia and Venezuela to the Brazilian Pantanal and Amazon. The monodominant stands of *L. parvifolius* occur in riparian forests and areas with intermittent water systems, flooded usually between six and eight months per year. Some species associated are *Inga vera* Willd, *Calophyllum brasiliense* Cambess., *Erythroxylum anguifugum* Mart. and *Alchornea discolor* Poepp. (Nunes da Cunha et al. 2007; Pott et al. 2011). In our study area, the stands were located mainly through intermittent watercourses and sometimes alongside paleodykes (locally called "cordilheiras").

#### Data collection

In an area with 97 km<sup>2</sup> approximately, we settled 47 plots with  $5 \times 30$  m into patches dominated by *L. parvifolius* (Fig.1). The plots were separated by at least 30 m. Each plot was placed to have a minimal variation of the terrain level inside the plot to avoid confusion in flood effects. We allocated 21 plots in areas isolated from cattle activity (non-disturbance), 16 in areas with low disturbance, and 10 with high cattle disturbance. Areas with low and high cattle disturbance were determined by the number of hoof prints and dung pads within plots. Therefore, we allocated ten 1-m<sup>2</sup> plots 2-meters apart from each other in the centre of the  $5 \times 30$  m plots and counted the number of 1-m<sup>2</sup> subplots with cattle signs. We considered low disturbance when up to half of the plots had cattle marks and high disturbance when more than half had cattle marks, and non-disturbance without cattle mark within plots.

We measured the circumference of the tree trunks (> 10 cm) at 50 cm high from the soil level. We also counted the number of basal ramifications (from soil level up to 50 cm height). We calculate the basal area for each ramification and sum them to obtain the individual basal area. We used the relative basal area (%) of *L. parvifolius* as dominance measurement of this species. We measured the watermark of the last flood on all the trunks (Fig. 2) and calculated the average of this watermarks as a flood measurement per plot. We also counted the number of basal ramifications (from soil level up to 50 cm height).



Fig. 2. Watermark from the last flood (2018) on a trunk of *Leptobalanus parvifolius* in a monodominant forest patch in the Pantanal floodplain. Note the basal ramification. Photo: Evaldo B. Souza.

To take soil samples, we set a 30 m line in the centre of each plot and collected five soil subsamples 7.5 m apart from each other, from 0-20 cm depth by using a soil auger with 6 cm in diameter. Then, we joined the five soil subsamples to obtain one mixed sample per plot. The analysed chemical components were: Phosphorus (P), Organic Matter (OM), Hydrogenionic potential (pH), Potential acidity (H+Al), Magnesium (Mg), Potassium (K), Calcium (Ca) and Nitrogen (N). Chemical soil analyses were performed according to EMBRAPA protocols (Nogueira & Souza 2005) at the Soils Lab of the Universidade Federal de São Carlos. P and K were extracted by ion exchange resin, and P was evaluated by spectrometry. OM content was evaluated by the addition of potassium dichromate and determined by colourimetry and K by a flame photometer. Ca and Mg were extracted with 1.0 mol L–1 KCl and measured by atomic absorption spectrophotometry. The pH was measured by calcium chloride 0.01 M and potential acidity (H + Al) using Shoemaker, McLean, and Pratt (SMP) buffer solution.

### Data analyses

To reduce the dimensions and verify the main patterns in soil data, we ran a principal component analysis (PCA) and use the first and second axes as predictors (Fig. 1). For basal area and number of branches, we used the average value per plot, that is, the total basal area and the total number of branches in the plot divided by the abundance. In this way, the basal area represents the average area occupied by each individual, and the number of branches represents the average number of branches per individual per plot. Thus, these two variables are not affected by abundance. However, we also tested for the total basal area of plots since it is a proxy of the total biomass produced and can be influenced by both size and number of individuals.

We analysed the influence of environmental variables (flooding and edaphic) and interactions on the community structure (dominance, basal area, richness, abundance, number of branches and height) by using generalised linear models (GLMs) in the R environment (R Core Team 2020). We used Gaussian distribution for the basal area and the average number of branches and Poisson distribution for abundance and species richness. Since *L. parvifolius* dominance are proportional values (relative basal area), we used a quasi-binomial distribution (Consul 1990).

To select the best set of predictor variables, we used the backward stepwise selection method. For that, we ran the full model and removed, step-by-step, the non-significant (p < 0.05) and less important variables (with largest *p*-values). The procedure

ends when removing a variable does not ameliorate or even reduce the model fit (Farawey 2015). We used the adjusted  $D^2$  (proportion of adjusted deviance explained by a GLM) as the fit measure of the model (Guisan & Zimmermann 2000), accessed by the function Dsquared in the package modEvA (Barbosa et al. 2013). To access the variable significances in the final models, we used a type III ANOVA test for models with interaction terms and type II ANOVA for models without interaction terms. When cattle disturbance was significant, we ran a multiple comparison post-test (Least-square means) with the function emmeans of the package emmeans (Lenth 2020).

### Results

We found 31 tree species. After *L. parvifolius*, the others more abundant were *Couepia uiti*, *Erythroxylum anguifugum* and *Andira inermis* (Appendix 4). The *L. parvifolius* dominance varied from 36 to 100% per plot and the richness from 1 to 9 species. The abundance of individuals varied from 4 to 30 per plot.

In the chemical soil analyses, the first PCA axis contained 35.9% of the variation, and the second comprised 18.1%. The variables that contributed most to the variation and had the highest positive correlation with the first axis were Ca, N, Mg and OM (Fig. 3a, b, c). Thus, the first axis in the PCA of the soil data represented a fertility gradient, which the positive coordinates comprise the most fertile soils. H+Al and pH explained 81.4% of the variation in the second axis and presented a gradient between high pH values (negative coordinates in PCA) and high H+Al values (positive coordinates in PCA) (Fig. 3a). Therefore, we consider the second PCA axis as a soil acidity gradient. The less important variable in the PCA was P, producing variation only in the third axis (Fig. 3b, c). The average basal area had the highest explained variance and was explained by the highest number of predictors (Tab. 1).



Fig. 3. Principal component analysis (PCA) from soil data (a). Contribution of the soil variables to the variances of first, second and third PCA dimensions (b), and Pearson correlations between variables and the first, second and third PCA dimensions (c).

Tab. 1. ANOVA table from selected GLMs. AIC = Akaike information criterion, and  $adjD^2$  = Proportion of adjusted deviance explained by GLM (Guisan & Zimmermann 2000) for full and final models; LR = Likelihood-ratio Chi-square test; na = not available; PC = principal coordinates. Significant predictor variables in bold.

Response	Model fit	Full	Final	Preditors (final model)	LR	р
L. parvifolius dominance	AIC	na	na	Flood	17.90	<0.01
	adjD <sup>2</sup>	0.26	0.30	Cattle	2.85	0.24
				Soil acidity (PC2)	0.04	0.85
				Soil fertility (PC1):Cattle	11.84	<0.01
Richness	AIC	192.56	181.83	Flood	5.18	0.02
	adjD <sup>2</sup>	0.08	0.18	Soil fertility (PC1)	2.64	0.10
				Soil fertility (PC1):Flood	4.02	0.04
Abundance	AIC	274 03	262.88	Cattle	2 88	0.24
Abundance	adiD <sup>2</sup>	274.03	0.12	Calle	2.00	0.24 <0.01
	aujD-	0.05	0.15	Son actuary (PC2)	1.37	<0.01
Average basal area	AIC	-201.83	-206.68	Flood	4.98	0.03
	adjD <sup>2</sup>	0.35	0.38	Cattle	10.96	<0.01
				Soil fertility (PC1)	12.58	<0.01
				Soil acidity (PC2)	2.06	0.15
				Soil acidity (PC2):Cattle	8.01	0.02
			0.44			
Total basal area	AIC	7.65	0.46	Flood	2.39	0.12
	adjD <sup>2</sup>	0.17	0.25	Cattle	2.73	0.25
				Soil fertility (PC1)	14.09	<0.01
				Soil acidity (PC2):Flood	5.75	0.02
				Soil acidity (PC2):Cattle	7.28	0.03
Number of branches	AIC	186.29	181.41	Cattle	8.41	0.01
	adjD <sup>2</sup>	0.09	0.11			

The soil fertility was positively related to *L. parvifolius* dominance in areas with high cattle disturbance (red line in Fig. 4a) and negatively in areas without cattle disturbance (blue line in Fig. 4a), which means that cattle disturbance and greater soil fertility together favour the *L. parvifolius* dominance. On the other hand, the lack of disturbance and high fertility are unfavourable for *L. parvifolius* dominance (Fig. 4a). However, neither soil fertility nor cattle disturbance individually explained the *L. parvifolius* dominance.

Flooding positively influenced the *L. parvifolius* dominance (Fig. 4b) and negatively the species richness. However, the influence of flooding on the richness varies according to soil fertility levels, being negative only in more fertile soils (blue and green lines in Fig. 4c) and null in less fertile soils (red line in Fig. 4c).



Fig. 4. Variation of *L. parvifolius* dominance in relation of interaction between soil fertility and cattle disturbance (a) and flood (b); and variation of species richness in relation to interaction between flood and soil fertility on species richness (c) in monodominant stands of *Leptobalanus parvifolius* in Pantanal floodplain. LR = Likelihood ratio test. The break values of soil fertility (PC1) in panel (c) are the 10th, 50th, and 90th quantiles.

The soil acidity (PC2) influenced total abundance negatively (Fig. 5a). On the contrary to our expectations, when we consider only the cattle disturbance it did not increased the abundance of *L. parvifolius*. However, the number of branches was higher in areas with high cattle disturbance (Fig. 5b).



Fig. 5. Relation of abundance with Soil acidity (PC2) (a), and number of branches with cattle disturbance (b) in monodominant stands of *Leptobalanus parvifolius* in Pantanal floodplain. LR = Likelihood ratio test. Different letters in b indicates significant differences (p<0.05) according to Least-square means.

The variation of average basal area along soil acidity gradient was negative in conditions of high disturbance and positive in low and zero disturbance (Fig. 6a), meaning that when there are no cattle, the increase in soil acidity acidity favors this tree growth. We also observed that the isolated relation of cattle disturbance with the average basal area was positive (Table 1), which means that the average basal area was higher in conditions of high cattle disturbance. However, this relation only occurs in soils with low acidity. The average basal area was negatively related to flood (Fig. 6b), that is, individuals are, on average, smaller in more flooded areas. Soil fertility had a positive effect on the average basal area (Fig. 6c).



Fig. 6. Variation of average basal area in relation to the interaction between soil acidity (PC2) and cattle disturbance (a), flood (b) and soil fertility (PC1) (c) in monodominant stands of *Leptobalanus parvifolius* in the Pantanal floodplain. LR = Likelihood ratio test.

As the average basal area, the total basal area was negatively related to soil acidity in high cattle disturbance conditions and positively in the absence of cattle disturbance (Fig. 7a). However, cattle disturbance had no isolated relation with the total basal area.

The relation of the total basal area with flooding varied between soil acidity levels. The total basal area was negatively affected by flood in high acid soils and positively in low acid soils (Fig. 7b). The total basal area was large in low flooding and acid soil, indicating a greater biomass accumulation. When acidity was low, flooding had little influence. There was no isolated influence of acidity on the basal area.

Fertility was related to total basal area positively (Fig. 7c). That is, both abundance and total biomass increased in more fertile soil. Stand height was not explained by any of the predictors variables.


Fig. 7. Variation of total basal area in relation to interaction between soil acidity (PC2) and cattle disturbance (a), between soil acidity (PC2) and flood (b) and to soil fertility (PC1) (c) on total basal area in monodominant stands of *Leptobalanus parvifolius* in Pantanal floodplain. LR = Likelihood ratio test. The values of soil acidity (PC2) in panel (b) are the 10th, 50th, and 90th quantiles.

### Discussion

Our work showed two potential scenarios for *L. parvifolius* dominance. The first is related with more flooding, fertile soils and cattle disturbance. The second reasonable scenario has less fertile sois in more flooded areas, but without cattle. Fertile soils and cattle disturbance was related to *L. parvifolius* dominance. On the other hand (second scenario), infertile soils and the absence of cattle were associated with higher *L. parvifolius* dominance.

In both first and second *L. parvifolius* dominance scenarios, flooding may be the most prevalent factor because neither cattle disturbance nor soil fertility individually explained dominance. However, there is evidence that monodominance depends on both endogenous characteristics of the species (e.g. functional traits) and the environmental filters. The interaction between these endogenous and exogenous factors allows several mechanisms for a given species to attain monodominance (Parolin et al. 2002; Peh et al. 2011).

According to Peh et al. (2011), one of the main drivers leading a species to attain monodominance (in a classical view) is the lack of exogenous disturbance for a long time, favouring better competitors under such condition. However, the establishment of monodominance without disturbance seems true only for late-successional species (Hart et al. 1989; Hart 1990). Pioneer species can become established and dominate large areas after disturbances or colonize hostile environments with high seasonal variability (Parolin et al. 2002). A sequence of several years with extreme floods in the Pantanal, for example, could enlarge populations of pioneer monodominant trees like Vochysia divergens (Nunes da Cunha & Junk 2004). Also, the annual regularity of flood and pluriannual stochasticity of fire can keep the vegetation in an initial succession stage, which pioneer plants would be benefitted (Ribeiro & Brown 2002; Manrique-Pineda et al. 2021). In the same way, cattle disturbance could reduce the competition by keeping plant density and richness lower, benefiting pioneer species (Lohbeck et al. 2014). Thus, in the Pantanal floodplain, competition cannot be the most determinant factor impelling monodominance. Considering that L. parvifolius is a pioneer, fast-growing and flood-tolerant species (Santos et al. 2006; Pott et al. 2011; Junk & Nunes da Cunha 2012), it could certainly have more advantages than some other species in seasonally flooded areas.

The clear positive relation of flood with *L. parvifolius* dominance can be related to its higher flood tolerance than other non-dominant species in the region (Dalmagro et

al. 2016). The flood regime seems to shape many plant monodominant communities in the Pantanal. Several species are flood-tolerant and have dominance characteristics (Pott et al. 2011; Damasceno-Junior et al. In Press). For example, the palm *Copernicia alba* has its germination ameliorated by flood and fire (João Roberto Fabri, unpublish data), setting vast populations throughout the floodplain, near the Paraguay river. Species such as *T. aurea* seem not to tolerate floods in early-growth phases. Because of this, it usually start to grow on earthmounds flooded only by above-average floods (Ribeiro & Brown 2002; Manrique-Pineda et al. 2021).

Differently, L. parvifolius colonizes open grasslands during recurrent years with above-average flooding (Pott & Pott 1994; Nunes da Cunha & Junk 2004). Episodic evidence is L. parvifolius present in the roadside drainage ditches along almost the whole Parque road in Pantanal. A similar condition is recognized in Couepia uiti (Santos et al. 2006) in our study area, usually growing near with L. parvifolius, but in slightly more flooded terrains. Though forming monodominant stands in floodable areas, L. parvifolius has not demonstrated higher physiological advantages under varying hydrological conditions than other non-super-dominant species in the Pantanal. However, one difference concerning non-monodominant species, such as Alchornea discolor, Duroia duckei Huber and Tocoyena formosa (Cham. & Schltdl.) K.Schum., is that L. parvifolius has no significant photosynthetic rate variation between flooded and dry seasons (Dalmagro et al. 2016). Considering that changes in photosynthetic capacity may affect biomass production (von Caemmerer & Evans 2010). L. parvifolius could occur as a codominant species with V. divergens, the main monodominant species in the northern Pantanal (Machado et al. 2015). It indicates that flood tolerance can be similar for both species. In addition to these characteristics, flood-tolerant species, like L. parvifolius, tend to absorb more macronutrients than flood-intolerant ones (Kozlowski 1984a).

Contrary to *L. parvifolius* dominance, and as expected, flooding was negatively related to richness in more fertile soils but not in less fertile soils, indicating that the richness tends to be lower in more fertile and flooded soils. Flooding is the primary habitat filter for the establishing of woody species in the Pantanal floodplain (Nunes da Cunha & Junk 2001; Damasceno-Junior et al. 2005; Arruda et al. 2016). That can be noticed when, in regions with long and intense floods, dry forest species are found in areas with long and intense floods but restricted to the elevations in the terrain such as paleodykes ("cordilheiras") and earthmounds ("capões") and at the edge of road embankments in the Pantanal (Prance & Schaller 1982). The tree species richness varies according to flooding

gradient, with more richness in slightly flooded terrains (Nunes da Cunha & Junk 2001; Amador et al. 2012). For example, in the highest parts of riparian forests, tree mortality is higher; thus, fewer tree species are found after extreme flooding (Damasceno-Junior et al. 2004). Nevertheless, tree richness in mixed flooded forests sometimes can be higher than in upland forests (Vourlitis et al. 2017).

Like the flood, the greater availability of nutrients is generally related to lower species richness and a higher number of individuals (Huston 1980; Enright et al. 1994; Harpole & Tilman 2007; Slik et al. 2010). A higher nutrient availability allows faster growth with more biomass accumulation and more individuals, which can trigger exclusive competition leading to reduced species richness (Enright et al. 1994). Dispite the negative relationship between species richness and soil fertility in large part of the studies, soil fertility can positively or negatively affect richness and dominance (Dupré et al. 2002). Ribeiro and Brown (2002) reported a higher fertility level in soils of *Tabebuia aurea* monodominant formation ("paratudal") in the Pantanal wetland, than in the Cerrado biome, where this species is not dominant. Contrarily, Torti *et al.* (2001) found a relationship between low nutrient availability and monodominant forests. They showed that soils beneath the monodominant *Gilbertiodendron dewevrei* (De Wild.) J.Léonard forest had a lower supply rate of ammonium and nitrate in the soils of the monodominant forest was lower than in those of the mixed forest (Torti et al. 2001).

In general, researches has shown that soil proprieties do not determine monodominance in the tropical forest. For example, Peh et al. (2011) showed that the soil is not an essential factor for the monodominance of *G. dewerei* in Central Africa. Also, there is no evidence that the soil determines the boundaries between *Peltogyne gracilipes* Ducke-dominated forest and the adjacent high-diversity forest in Maracá Island, Brazil (Nascimento & Proctor 1997). Likewise, monodominant forests of *Celaenodendron mexicanum* Standl. have similar soil properties to adjacent high-diversity forest in Mexico (Martijena 1998). however, soil can be an important factor for monodominance floodplains as the Pantanal (Damasceno-Junior et al. 2021)

*Leptobalanus parvifolius* may occur in sandy and silty soils with low fertility (Arieira et al. 2016). This type of soil occurs at paleo-alluvial sediments (Assine et al. 2015) and is related to low clay activity, elevated acidity and high concentrations of toxic elements such as  $Fe^{2+}$  and  $Mn^{2+}$ . Such a situation can indicate that species living at this place can uptake soil nutrients better than others (Ponnamperuma 1972; Cunha 1981).

The relation of the basal area with soil acidity was negative in high cattle disturbance and positive in low and zero cattle disturbance. Such results show that the presence of cattle can change the relationship between acidity and basal area. In this way, acidity can reduce the ability of water to carry through the roots and inhibit nutrients absorption (Caspary 1991), reducing the growth rate, and therefore the basal area. Thus, an increased number of branches and potentially greater basal area due to cattle, as shown in our result, and less acidic soils can be a positive scenario for increasing basal area.

Furthermore, as well as observed in other monodominant species (Nunes da Cunha & Junk 2004), L. parvifolius produces abundant seeds during the rainy season, before the flood season (Pott & Pott 1994; Lorenzi 2009). It can be a suitable dispersal strategy to colonize new areas and settling monodominant stands. Leptobalanus *parvifolius* is a heliophilous species, and thus, a shade-intolerant, needing open areas to hold establishment and dominance (Nunes da Cunha & Junk 2004). Probably, for that reason, we very rarely find seedlings or saplings in its understory, characteristic that differs from some monodominant tropical forests like Dicymbe altsonii Sandwith, in Guiana (Isaacs et al. 1996) and other classical monodominant forests like G. dewevrei in Africa (Hart 1995; Torti et al. 2001), and Brosimum rubescens in Cerrado-Amazonia transition (Marimon & Felfili 2006; Marimon et al. 2020). However, the absence of seedlings may also occur due to the lack of a longer period with adequate conditions for germination and establishment (Parolin et al. 2002; Parolin et al. 2010; Parolin & Wittmann 2010). There is evidence that individuals of L. parvifolius settle exclusively in years of flooding (see chapter 3), which may be related to its requirements for germination. Similar to L. parvifolius, the low occurrence of seedlings and saplings in the understory was also observed for Licania kunthiana Hook. f. (Chrysobalanaceae) in the Amazon forest (Nascimento 1994). Licania kunthiana is not a monodominant species but is one of the most abundant tree in some areas dominated by P. gracilipes and its population is declining due to competition with the *P. gracilipes* (Nascimento 1994).

*Leptobalanus parvifolius* is considered an invader and undesired plant due to its encroacher characteristic (Allem & Valls 1987). Encroacher woody plants can hinder herbaceous and shrub forage species (Silva et al. 2016). With less space for forage herbs, the pasture carrying capacity is reduced. Such as scenario leads to more introduction of exotic forage species because they produce more in less space and increase stocking rate (Nunes da Cunha & Junk 2004; Santos et al. 2006). Woody encroachment generates an intensification of localized environmental disturbance due to the overuse of some areas (Silva et al. 2016).

Sometimes it is challenging to control woody encroachment in grasslands because of their vigour and long-life span. The primary causes of these difficulties are vegetative propagation due to sprout capacity (Bovey 2001). Attempts to control the advance of these plants over the native pastures can be tiresome and frustrating due mainly to their ability to sprout (Santos et al. 2006). It is worth remembering that, in the Pantanal, a large part of the species with these characteristics also propagate very well through seeds (Pott & Pott 1994; Santos et al. 2006).

When encroacher species are established in grasslands, the cattle influence on these plants can be negative or positive. In some cases, cattle exclusion allows the growth of the woody plants, as *Vochysia divergen, Combretum laxum, Byrsonima Cydoniifolia* and *L. parvifolius*, (Nunes da Cunha & Junk 2004). However, overgrazing of herbaceous plants can favour woody plants due to more available space (Angassa 2014). Besides, injury caused by animals may stimulate the sprout from buds or rhizomes and produce new shoots (Bovey 2001). In the Pantanal, cattle are the main herbivores. Thus, as shown by our results, cattle disturbance can cause damage to woody plants and induce sprouting of new branches (Spatz & Mueller-Dombois 1972; Bowles 1983). A similar result of sprouting stimulation by feral pig trampling was found by Busby *et al.* (2010). The increasing of the branches number can indirectly increase basal area. Those interpretations are corroborated by our study that showed more branched individuals (individual average) and, consequently, more average and total basal area in areas under cattle disturbance. At the same time, non-sprouting plants can be killed by cattle browsing and trampling, giving an advantage to sprouters like *L. parvifolius*.

Therefore, cattle browsing and tramping can hinder the growth of those nonsprouting species leading to the dominance of prone sprouting (Bovey 2001; ter Steege et al. 2019; Scogings & Sankaran 2020) and flood-tolerant species such as *L. parvifolius*. Soil fertility can positively influence *L. parvifolius* dominance only in areas with cattle disturbance, indicating that cattle may hinder the establishment of other species in areas with high fertility. Cattle disturbance is also positively related to ramification and basal area increasing of *L. parvifolius*. Consequently, the removal of vegetation for pasture implantation may, potentially, favour the establishment or maintenance of *L. parvifolius* dominance. In summary, the monodominance of *L. parvifolius* may be linked mainly to flooding that, together with cattle disturbance might hinder the establishment of other species. That shows that disturbances and strong seasonal fluctuation, such as periods of drought and flooding in the Pantanal, are primary factors for tree species to achieve monodominance. Thus, the mechanisms responsible for the monodominance of trees in floodplains differ from those required for classic monodominance that occurs under low endogenous and exogenous disturbance.

# **Chapter 2**

Functional traits reveal trade-offs between resource acquisition and conservation strategies regulated by environmental filters in floodable monodominant forests

#### Abstract

The response of individual functional traits to environmental filters and their interaction can give us new perspectives on the trade-offs of plant conservative and acquisitive plant strategies and ecosystems functioning. This study verifies the relationships between functional traits and soil nutrients, flooding and disturbance by livestock in Leptobalanus parvifolius (Huber) Sothers & Prance in monodominant forest patches in the Pantanal floodplain, in the centre of South America. We sampled 43 plots with  $5 \times 30$  m in an area of 97 km<sup>2</sup>. We measure the tree trunk circumference at 0.5 m height and calculated the basal area. As functional traits, we measured specific leaf area (SLA), leaf thickness (LT), leaf dry mass content (LDMC), bark thickness (BT), bark dry mass content (BDMC), relative bark thickness (RBT) and plant height (H). We collected five soil sample at 0-20 cm depth in each plot by using a soil auger with 6 cm in diameter and mixed them to obtain one composed sample per plot. Our results show that functional traits values depend on the interaction between flood and soil nutrients and that functional diversity is not related to flood gradient. Plants in more floodable areas have conservative strategies, whereas plants in less flooded areas have acquisitive strategies, which means faster growth. This trend may represent greater productivity and nutrient cycling in lees flooded areas. Thus, although the monodominant stands of L. parvifolius seeming a homogeneous physiognomy, they are niche-structured along with environmental gradients, by the variation between the traits of the individuals, that is, by the plasticity of the dominant species. It can be an essential factor in the monodominance of this species in the Pantanal. Keywords: Community weighted means, functional diversity, monodominance, Pantanal.

## Resumo

A resposta de traços funcionais individuais a diferentes filtros ambientais, bem como suas interações podem nos dar novas perspectivas sobre as vantagens e desvantagens das estratégias conservativas e aquisitivas das plantas e do funcionamento dos ecossistemas. Neste estudo, verificamos as relações entre características funcionais e nutrientes do solo, inundação e perturbação pelo gado em manchas de floresta monodominante de Leptobalanus parvifolius (Huber) Sothers & Prance na planície de inundação do Pantanal. Amostramos 43 parcelas de  $5 \times 30$  m em uma área de 97 km2. medimos a circunferência do tronco dos indivíduos a 0,5 m de altura e calculamos a área basal. Como características funcionais, medimos a área foliar específica (SLA), espessura foliar (LT), conteúdo de massa seca da folha (LDMC), espessura da casca (BT), conteúdo de massa seca da casca (BDMC), espessura relativa da casca (RBT) e altura da planta (H). Em cada parcela coletamos uma amostra (composta de 5) de solo com 0-20 cm de profundidade em cada parcela, usando um trado de solo de 6 cm de diâmetro. As cinco amostras foram misturadas para obter uma amostra composta por parcela. Nossos resultados mostraram que os valores dos traços funcionais dependem da interação entre a inundação e os nutrientes do solo, e que, a diversidade funcional não está relacionada com o gradiente de inundação. Plantas em áreas mais inundáveis possuem estratégias conservadoras, enquanto plantas em áreas menos inundadas possuem estratégias aquisitivas, ou seja, crescimento mais rápido. Esta tendência pode representar maior produtividade e ciclagem de nutrientes em áreas menos inundadas. Assim, apesar dos agrupamentos monodominantes de L. parvifolius parecerem uma fisionomia homogênea, eles são estruturados em nichos ao longo dos gradientes ambientais. Isso é demonstrado pela variação dos traços dos indivíduos, ou seja, pela plasticidade da espécie dominante. Esse pode ser um fator importante para a monodominância dessa espécie no Pantanal.

Palavras chave: diversidade funcional, média ponderada da comunidade, monodominância, Pantanal.

## Introduction

The measurement of functional traits is currently one of the main indirect means of estimating patterns and processes in community ecology (Keddy 1992; Violle et al. 2007; Mokany et al. 2008; De Bello et al. 2011; Lavorel et al. 2011; Lavorel 2013; Cadotte et al. 2015; Iida & Swenson 2020). Functional traits allow testing hypotheses about community assembly, competition dynamics, coexistence, limiting similarity, species invasion (Fukami et al. 2005; Pillar et al. 2009; Cleland et al. 2011; Lohbeck et al. 2015; Malysz et al. 2019) and response to disturbances (Mouillot et al. 2013). Nowadays, large amounts of data on plant traits are available worldwide (Kattge et al. 2020). Thereby, it is possible to predict local patterns of response of plants to environmental filters (Souza et al. 2019) and to estimate the amplitude of the species' niche within communities (Pellissier et al. 2018; Carvalho & Cardoso 2020), as well as to predict the influence of climate change on vegetation cover and the health of ecosystems (Lavorel & Garnier 2002; Gong & Gao 2019; Worthy & Swenson 2019).

Functional traits can indicate which strategies are used by plants for growth, reproduction and survival (Violle et al. 2007; Reich 2014). There is much evidence that plants modulate trade-offs between growth and survival strategies across environmental gradients (Wright et al. 2004; Reich 2014; Rosell et al. 2014; Pan et al. 2019; Verbeeck et al. 2019; Pan et al. 2020). These different strategies can be represented by the plant economic spectrum (Y.T. Zhao et al. 2017), mainly focused on leaf traits, characterizing the leaf economic spectrum (Wright et al. 2004; Wright et al. 2005; Pan et al. 2020).

One end of the spectrum represents resource conservation strategies, i.e., limited and high-cost investment with little return on growth. Thus, plants at this extreme have a low growth rate. Therefore, they can handle resource scarcity better than fast-growing plants. At the other end of the spectrum are plants that invest in strategies for acquiring and using resources, which assures a high return for growth and reproduction (Reich 2014; Y.T. Zhao et al. 2017). This economic spectrum can explain the distribution of species along environmental gradients on both local and global scales. In this way, as functional traits are responses to environmental filters, they can help to predict which species can colonize and survive in a specific area. Consequently, the economic spectrum allows forecasts of the nutritional needs of plants and the environmental suitability of the habitats wherein are found (Lohbeck et al. 2015; Souza et al. 2019; Pan et al. 2020). For example, in nutrient-rich and water-supplied environments, plants tend to have higher specific leaf area (SLA) values and lower leaf dry matter content (LDMC) values (Ordoñez et al. 2009; Poorter et al. 2009). In addition, greater availability of resources can increase functional diversity (Van Ruijven & Berendse 2005; Zhu et al. 2016). Nevertheless, stress conditions, such as flooding, can restrict the variability in strategies in the community resulting in a convergence of functional traits and reduction in functional diversity (Cleland et al. 2011; Fu et al. 2014). In other words, with greater availability of resources, plants resort to nutrient acquisition and acquisitive strategies, reflecting faster growth (Wright et al. 2004), in addition to allowing greater functional diversity in the community (Zhu et al. 2016). In environments with stressful factors such as scarcity of soil nutrients or water deficit, plants tend to use resource conservation (or economy) strategies, as reduced the concentration of leaf N, thicker leaves with higher dry matter content (Oddershede et al. 2018; Souza et al. 2019), and thicker bark that allows more water stock (Rosell et al. 2014).

In floodplains, flooding is the primary stressor for most species, given that it tends to hinder nutrient absorption. In addition, flooding affects the acidity and availability of nutrients in the soil, which makes complex the relationship between flooding, soil nutrients and roots absorption by plants (Ponnamperuma 1972; Kozlowski 1997). The presence of large herbivores can also be relevant in modulating the trade-offs between growth or survival. Herbivory, and tramping, can trigger protection strategies and change the way plants absorb, distribute and use nutrients, interfering with the growth and variability of functional traits (Rahmanian et al. 2019; Scogings & Sankaran 2020).

Functional traits measurements, in general, are made at at the species level (Lohbeck et al. 2015). That is, the functions performed by these traits are considered adaptations through natural selection. In this approach, functional diversity in a community is established as the variation of the average of a functional trait between species and often weighted by the abundance of species in the community (Garnier et al. 2004; Lavorel et al. 2008; Laliberté & Legendre 2010). This method has been very useful in describing the functional structure, response of communities to environmental conditions, and ecosystem processes (Díaz et al. 2007; Cadotte et al. 2011; Cadotte et al. 2015; Faucon et al. 2017; Xu et al. 2018; Verbeeck et al. 2019).

However, a relevant component in communities is the trait variation between individuals (De Bello et al. 2011; Bolnick et al. 2011; Albert 2015; Des Roches et al. 2018; Palacio et al. 2019; Raffard et al. 2019). The variation between individuals can

promote diversity in local populations and have consequences for responses to environmental filters, population growth and dynamics of interspecific competition and coexistence (Hulshof et al. 2013; Jordani et al. 2019; Struckman et al. 2019). Just short over a decade, researchers have been concerned with addressing individual variations in community ecology (Cianciaruso et al. 2009; Raffard et al. 2019).

Thus, in addition to interspecific variations, individual functional traits can help elucidate intraspecific variations, estimate the species niches amplitude, and predict population growth or decline (Struckman et al. 2019). For example, the same species can vary morpho-physio-phenologically (the three primary sources of functional indicators) (Violle et al. 2007) along a gradient of suitability (Niinemets 2015). In other words, the economic spectrum can vary between individuals within the same species, allowing flexibility to deal with environmental filters such as resource availability, herbivory, temperature, fire frequency and flood. Consequently, individual trait values (rather than species) can describe the influence of environmental factors on the community more accurately (Liu et al. 2017).

The influence of factors such as nutrient availability, flooding and livestock browsing on functional traits has recently been addressed (Mason et al. 2012; Jager et al. 2015; Oddershede et al. 2018; Gong & Gao 2019; Rahmanian et al. 2019). Knowing that flooding can interfere both with the availability of nutrients in the soil and their absorption by plants (Kozlowski 1984b) and that browsing by cattle can act to reduce biomass (Chen et al. 2007; Staver et al. 2009; Giday et al. 2018), it is coherent to think that these factors can act simultaneously as a hierarchy of environmental filters (Lenssen et al. 2003). However, there is no study on how these factors affect plant functional traits together. The relationship of functional traits with soil nutrients, flooding and disturbance by livestock, as well as their interaction can give us new perspectives on the functioning of ecosystems.

In the Pantanal floodplain, the flood is the leading determinant of the structure and composition of species. Monodominant forest patches in the floodplain are mainly related to flood levels, but also to other factors such as soil pH, fire frequency and herbivory (Nunes da Cunha & Junk 2004; Ribeiro & Brown 2006; Arieira & Nunes Da Cunha 2012; Bueno et al. 2014; Manrique-Pineda et al. 2021). However, we do not know how the functional structure of floodplain monodominant forest responds to gradients of flooding, soil nutrients and livestock.

Therefore, in this study, we evaluated the response of functional traits to soil, flood and disturbance by livestock in monodominant forest patches in the Pantanal floodplain. Considering that the monodominant stands in the Pantanal have low species richness and that the other species (non-monodominant) are relatively rare in these patches (Arieira & Nunes Da Cunha 2012; Bueno et al. 2014; Manrique-Pineda et al. 2021), it would be challenging to determine what is the relationship of these plants to the environmental filters using species composition or functional groups, or even species trait means (which only considers interspecific variations of functional traits). Therefore, we opted for an approach of variation between individuals, that take into account interspecific and intraspecific variations together. This approach can better quantify functional diversity in communities (Violle et al. 2012; Albert 2015; Raffard et al. 2019)

Knowing that the flooding stress tends to hinder the absorption of nutrients (Kozlowski 1997), we expect that the greater the flooding, the plants will adopt conservative instead of acquisitive strategies. Therefore, with increasing flooding, we expect H1) a reduction in specific leaf area (SLA) and an increase in leaf dry matter content (LDMC), leaf thickness (LT) (Hernández-Vargas et al. 2019), bark thickness (BT) and relative bark thickness (RBT). We also expect that H2) the relationship of acquisitive and conservative strategies with flooding varies according to the soil nutrient levels in the soil. In turn, soil nutrients cattle disturbance and flooding can act in an integrated way in the variability of functional traits (Cleland et al. 2011). Hence, we expect that: H3) the availability of nutrients in the soil has a positive relationship with functional diversity and that this relationship is mediated by flooding. We also expect H4) a negative relationship between flooding and functional diversity.

## Methods

#### *Study area*

We conducted this study in monodominant patches of *L. parvifolius* in the Pantanal floodplain. The climate of the region is tropical with dry winter (AW), with rainfall between 1000-1200 mm (Thielen et al. 2020), and annual average temperature varies between 24 and 26 °C (Alvares et al. 2013). The Pantanal presented different types of soils influenced by the different hydrologic regimes (Cunha 1981; Soares et al. 2006; Couto & Oliveira 2010). In the study region, the main soil types are Spodosols and Vertisols (INPE 2010). The vegetation of the Pantanal is a mosaic with influences from adjacent vegetational domains (Pott et al. 2011).

Leptobalanus parvifolius is a tree of about 7 m in height, trunk usually branched at the base, widely distributed in the Amazonian rainforest and Pantanal (Pott & Pott 1994). The monodominant stands of *L. parvifolius* usually occur in riparian forests and areas with intermittent water systems until eight months flooded. Some companion species in these stands are *Alchornea discolor* Poepp., *Calophyllum brasiliense* Cambess, *Erythroxylum anguifugum* Mart., and *Inga vera* Willd (Pott & Pott 1994; Nunes da Cunha et al. 2007). In our study area, the stands were located mainly along intermittent watercourses, and sometimes alongside of paleodykes (locally called "cordilheiras").

#### Data collection

We settled 43 plots with  $5 \times 30$  m into patches dominated by *L. parvifolius*, distributed in an area with about 97 km<sup>2</sup>. The plots were separated by at least 30 meters from each other. We allocated 19 plots in areas isolated from cattle activity (without disturbance), 15 in areas occasionally accessed by cattle (low disturbance), and nine with frequent cattle access (high disturbance). Areas with occasional and frequent cattle access were specified by the hoof prints and dung pads into the plots. We allocated ten 1 m<sup>2</sup>-plots, 2 meters apart from each other, in the centre of the  $5 \times 30$  m plots and counted the number of 1 m<sup>2</sup>-plots with cattle signs. We considered low disturbance plots when up to five plots had cattle marks, and high disturbance plots when more than five plots had cattle marks.

We measured the watermark of the last flood on the trunks and used it as a flood index. We set a 30 m line in the centre of each plot and collected five soil samples distant 7.5 m each other with 0-20 cm depth by using a soil auger with 6 cm in diameter. Then, we homogenised the five soil cores in order to obtain a mixed sample per plot. The

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samples were stored in plastic bags and taken to the laboratory for chemical analyses. The soil analysed chemical components were: Phosphorus (P), Organic Matter (OM), Hydrogenionic potential (pH), Potential acidity (H+Al), Magnesium (Mg), Potassium (K), Calcium (Ca) and Nitrogen (N).

We sampled 218 individuals with  $\geq 10$  cm in trunk circumference (0.3 m height) from 15 species, and measured seven functional traits related to the response to disturbances, availability of nutrients, photosynthetic capacity and competition (Tab 1). We collected eight leaves only from individuals who had mature, healthy leaves (with no signs of senescence and disease) and exposed to full sun. Then, the leaves were taken to the laboratory and kept 04h00 in a water tank until saturation. We measured the leaf thickness (LT), leaf dry mass content (LDMC) and specific leaf area (SLA). LT was based on three measurements from each leaf (avoiding the mid-rib), for LDMC (ratio between dry and fresh weights), the leaves were weighed, dried in paper bags for 42h00 in oven at 60 °C and weighed again. To determine the SLA (fresh leaf area/dry mass), we scan the images of the fresh leaves using a flat scanner and calculate leaf area using the LeafArea package (Katabuchi 2015) in an R environment (R Core Team 2020). We also estimated the height of all individuals.

We collected a bark sample, including inner and outer bark at 0.5 m height of trunk from each trunk and measured the bark thickness (BT) in six points to determine an average value. We also calculate the bark dry mass content (BDMC). For BDMC, after measurements, the barks were weighed and oven-dried for 72 hours in an oven at 60 °C, and weighed again to calculate the bark dry mass content (BDMC), as the ratio between dry and fresh weights. We also calculated relative bark thickness (RBT), as the ratio between bark thickness and trunk radius.

Functional trait (units)	Functions
Specific leaf area (mm <sup>2</sup> /mg)	Nutrient residence time, lignin content, Foliar longevity, foliar defence against herbivory, potential relative growth rate and photosynthetic rate.
Leaf dry matter content (mg)	Leaf tissue density, water content, flammability, nutrient residence time, lignin content, leaf longevity, potential relative growth rate, and photosynthetic rate.
Leaf thickness (mm)	Leaf longevity, energy balance, respiration costs, protection against physical damage, and resource storage.
Bark thickness (mm)	Water storage, protection of tissues, meristem and buds, transport and uptake of oxygen and water.
Bark dry matter content (mg)	Carbohydrate transference, water storage and movement, plant vitality, protection of tissues.
Relative bark thickness (mm)	Bark investment, defence against fire, avoidance and repair of stem damage, resistance of drought stress, protection, storage mechanics, resistance to flooding.
Plant height (m)	Competitive strength, fertility and interval between disturbances.

Tab. 1 Functional traits and their functions (Gall et al. 2002; Lavorel & Garnier 2002; Pérez-Harguindeguy et al. 2013; Poorter et al. 2014; Rosell et al. 2014).

We calculated the community weight means (CWM) for each of the traits in each plot by using the basal area of the individuals as weight by using the formula:

$$CWM_{p} = \frac{\sum (BA_{ip} \times T_{ip})}{\sum BA_{ip}}$$

in which,  $CWM_p = Community$  weighted mean for plot p;  $BA_{ip} = basal$  area of the individual i in the plot p;  $T_{ip} = trait$  value of the individual i in the plot p. We weighted the CWM by using the individual basal area due to the low species richness in several plots (21 of them with only the dominant species), which makes weighing by species impossible. That approach is viable considering that the size of the individuals can represent the amount and type of resource that each one uses in the environment. Larger individuals can explore more area both above the ground to capture light and under the ground to absorb nutrients (Hikosaka & Hirose 2001).

#### Data analyses

To verify the influence of environmental variables on functional diversity, we use the ndimensional hypervolume approach by using the Hypervolume package (Blonder & Harris 2019). To build hypervolumes, we reduced the number of traits, eliminating those who presented collinearity. This procedure was necessary to meet the prerequisites about the maximum number of traits adequate to the number of samples, in which the number of dimensions must be at most equal to the log of the number of samples (Blonder et al. 2018). In this way, overfitting in the delimitation of hypervolumes is avoided. The excluded traits were height, bark thickness and LDMC, as these showed the highest relationships with other variables (see appendix 5). We build a hypervolume for each plot. Then, we calculated the kernel alpha diversity (KAD) for each plot using the kernel.alpha function, and considered it as the functional diversity. The KAD is represented by the total volume of the n-dimensional hypervolume (Mammola & Cardoso 2020).

To test the relationships between environmental variables (soil, flood and livestock disturbance), the CWM of the traits and the KAD, we use generalised linear models (GLMs). We used the fitdistrplus package (Delignette-Muller & Dutang 2015) to check the distribution that best fits each response variable. We use log-normal distribution for plant height, RBT, LT, LDMC and KAD; normal distribution for SLA and BT; and Gamma distribution for BDMC. We used stepwise backward models to verify which set of predictor variables best explained the variation of each trait. To verify the significance of each variable and the interactions in the model, we calculated a type III ANOVA using

the Anova function of the car package (Fox & Weisberg 2019). We also calculated the relative sum of squares to find the percentage of variance explained by each variable in the models.

## Results

All evaluated leaf traits were related with flood and its interaction with some edaphic variables (Fig. 1a, b). For flood, this relation occurred especially in higher pH levels. In turn, pH had a positive relation with SLA in low flood levels (Fig. 1b). pH was the best predictor for SLA, with 17.9% of explained variance (Tab.2). Contrarily to SLA, the flood had a positive relation with LDMC (Fig. 1c), which is expected since SLA is negatively correlated with LDMC ( $r^2 = -0.84$ ) (Appendix 5). In interaction with other variables, flooding had a positive relationship with LDMC at high levels of K and Mg (Fig. 1d, e) and in areas without livestock disturbance (Fig. 1f). Leaf thickness had a negative relation with flooding in lower Ca levels (Fig. 1g). Flood also had a negative relationship with tree height but only in plots without livestock disturbance and restricted up to 70 cm of flooding because, in all areas with over 70 cm of flooding, had no cattle activities (Fig. 1h). Plant height was also correlated with K (Fig. 1i) and Mg (Fig 1j).



Fig. 1. Relationship between environmental variables and leaf traits measurements and plant height of *Leptobalanus parvifolius* monodominant forests in the Pantanal. Models with significant variables (p<0.05). pH= potential of Hydrogen, K=Potassium (mmol<sub>c</sub>/dm<sup>3</sup>), Ca=Calcium (mmol<sub>c</sub>/dm<sup>3</sup>).

All bark traits were somehow correlated with flood and soil. The trait with the highest number of relationships with environmental variables was BT, with negative relationships with H+Al and positive with pH and N (Fig. 2a, b, c, respectively, and Tab. 2). Interactions between flood and P, OM, K and disturbance, were also related to BT (Fig. 2d, e, f, g). The flooding relationship with BT was negative at high P levels and positive at low levels of P (Fig. 2d). On the contrary, where there was little OM and K, the relationship between BT and flooding was negative (Fig. 2e, f). Flooding also had a negative relationship with BT, under high where livestock disturbance was high (Fig. 2g). The relative bark thickness was negatively influenced by K and by disturbance (Fig. 2h, i). BDMC was related only to the food-pH interaction, with a positive relationship with flooding at low pH levels (Fig. 2j).





Fig. 2. Relationship between environmental variables and measurements of plant height and the bark traits of *Leptobalanus parvifolius* monodominant stands in the Pantanal. Models selected by stepwise. Significant variables in bold (p<0.05). H+Al= potential acidity (mmolc/dm3), pH= potential of Hydrogen, N=Nitrogen (mg/kg), P=Phosphorus (mg/dm3), OM=organic matter (g/dm3), K=Potassium (mg/dm3).

Tab. 2 Percentage of explained variance and significance of each variable and they interactions in the selected models. SLA = specific leaf area; LDMC = leaf dry matter content; LT = leaf thickness; BT = bark thickness; RBT = relative bark thickness; BDMC = bark dry matter content; H = height; WM = water mark; P = phosphorus; pH = potential of hydrogen; CD = cattle disturbance; K = potassium; OM = organic matter; Mg = magnesium; HA1 = potential acidity; adjD2 = Proportion of adjusted deviance explained by a GLM (Guisan & Zimmermann 2000).

Trait	adjD <sup>2</sup>	Selected variable (Percentage of explained variance) <sup>Significance</sup>
SLA	0.36	WM $(8.9)^* + P (1.36)^{ns} + pH (17.9)^{***} + K (8.8)^* + CD (7.6)^{ns} + WM:P (3.0)^{ns} + WM:pH + (6.2)^* + WM:K (4.4)^{ns} + WM:CD (5.8)^{ns}; Residuals (35.9)$
LDMC	0.39	WM $(4.8)^*$ + OM $(3.0)^{ns}$ + pH $(6.9)^*$ + K $(11.9)^{**}$ + Mg $(1.9)^{ns}$ + HAl $(2.6)^{ns}$ + CD $(12)^{**}$ + WM:pH $(7.17)^*$ + WM:Mg $(4.4)^*$ + WM:HAL $(1.9)^{ns}$ + WM:CD $(9.82)^*$ ; Residuals (25.8)
LT	0.39	WM $(0.06)^{ns} + P (1.7)^{ns} + OM (1.6)^{ns} + Ca (1.9)^{ns} + Mg (4.6)^{ns} + HAl (5.2)^{ns} + CD (7.87)^{ns} + WM:P (4.81)^{ns} + WM:OM (3.7)^{ns} + WM:Ca (13.3)^* + WM:CD (7.6)^{ns};$ Residuals (47.5)
BT	0.52	WM $(0.18)^{ns}$ + P $(16.2)^{***}$ + OM $(0.8)^{ns}$ + pH $(5.8)^{**}$ + K $(10.3)^{***}$ + Mg $(2.2)^{ns}$ + HAl $(2.9)^{*}$ + N $(4.4)^{*}$ + CD $(4.3)^{*}$ + WM:P $(18.4)^{***}$ + WM:OM $(2.7)^{*}$ + WM:K $(12.1)^{***}$ + WM:CD $(4.7)^{*}$ ; Residuals (14.9)
RBT	0.28	WM $(4.5)^{ns}$ + P $(3.2)^{ns}$ + OM $(3.2)^{ns}$ + K $(13.8)^{**}$ + Mg $(4.2)^{ns}$ + CD $(14.5)^{*}$ + WM:CD $(8.21)^{ns}$ ; Residuals (48)
BDMC	0.002	WM $(9.6)^* + P (3.8)^{ns} + OM (3.51)^{ns} + pH (11.8)^* + Ca (3.4)^{ns} + Mg (1.2)^{ns} + WM:P$ $(4.0)^{ns} + WM:pH (10.3)^* + WM:Ca (3.3)^{ns} + WM:Mg (3.4)^{ns};$ Residuals (46.3).
Н	0.23	WM $(6.66)^*$ + K $(9.94)^*$ + Ca $(4.82)^{ns}$ + Mg $(7.11)^*$ + CD $(10.35)^*$ + WM:CD $(16.1)^{**}$ ; Residuals (45)

 $p^* < 0.05$ ;  $p^* < 0.01$ ;  $p^* < 0.01$ ;  $p^* < 0.001$ ;  $p^* = 0.001$ ;  $p^* = 0.05$ ; The Percentage of explained variance is the relative sum of square.

The functional diversity (kernel alpha diversity - KAD) was related to flood-Ca and flood-OM interactions. The amount of OM and Ca positively correlated with KAD in lower flood levels (Fig. 3). There was no isolated relationship between KAD and flood.



Fig. 3. influence of organic matter (a) and calcium (b) and their interaction with flood on kernel alpha diversity. Ca = calcium, WM = water mark (cm).

## Discussion

Our results showed acquisitive strategy in less flooded sites and conservative strategy in more flooded sites. The trend towards an acquisitive strategy in less flooded areas represent greater productivity (Reich et al. 1997; Poorter & De Jong 1999; Luo et al. 2004). Higher productivity can be related to greater functional diversity (Cadotte et al. 2009; Xu et al. 2018). However, we did not find a clear relation between flood and functional diversity.

The variations of traits along the flood gradient and their interaction with the soil variables show that, despite the apparent homogeneity of the monodominant communities, there is environmental filtering that causes functional zoning and niche differentiation in the forest patches dominated by *L. parvifolius*. That variation can be explained by the plant economic spectrum (Wright et al. 2004; Freschet et al. 2010; Reich 2014; Pan et al. 2020), which is related to the difference in speed in which plants absorb and use nutrients and therefore is associated with the rate of growth. Acquisitive plants have faster nutrient cycling, so they grow faster and store lower amounts of nutrients, reflecting higher SLA values and lower LT and LDMC values. In turn, conservative plants have opposite characteristics (Lavorel 2013).

The economic spectrum is sometimes treated as a fixed factor within species (Wright et al. 2004) due to the variation in traits being associated with species composition changes (Souza et al. 2019). However, it can vary within the same species in an environmental gradient (Niinemets 2015). Given that our study was conducted in patches of monodominant forest and, making use of the mass ratio hypothesis (Grime 1998), we can conjecture that, the variation in trait values occurs mainly due to individual variation in *L. parvifolius*. For this reason, considering that size of individuals is a relevant factor in their participation in the ecosystem processes of a community (Hikosaka & Hirose 2001), we assume that the method of individual trait measurement along with community averages weighted by individual basal area (individual-weighted approach), best represents the values of the functional traits in communities with monodominant species.

Thus, our results show that plants have acquisitive behaviour in low flooded areas and conservative in more floodable areas. That may be an important fact for the dominance of *L. parvifolius* since it has similar photosynthetic rates between dry and flood seasons and high efficiency in water use in the dry season (Dalmagro et al. 2016). That also indicates a broader range of flood-tolerance to flooding than some other monodominant species in the Pantanal (Dalmagro et al. 2016). In addition, even though

Specific leaf area had negative relation, whereas leaf dry matter content (LDMC) had positive relation with flood. However, it varies depending on pH levels. Flooding causes CO<sub>2</sub> to accumulate in the soil (Kozlowski 1997), hindering water absorption by the roots, which can alter the structure of aboveground plant tissues (He et al. 2019). Consequently, there may be a reduction in photosynthetic rate (Pociecha et al. 2008; Al-Traboulsi et al. 2012) and transpiration, reducing the SLA (Al-Traboulsi et al. 2012). In addition, flooding can significantly interfere with the soil nutrient availability, for example, reducing the availability of organic carbon (Zhao et al. 2017), N and P (Souza et al. 2019), and plant ability to uptake nutrients, hindering growth (Fu et al. 2014; Zhao et al. 2017). Therefore, this may have resulted in lower SLA values and higher LDMC values in our most flooded plots (Fig. 1b, c). This result is in agreement with (Souza et al. 2019), who studied functional traits in islands of mixed forest vegetation ("capões") in the same sub-region. I.e., the negative relationship with SLA and positive with LDMC shows that flooding is a limiting factor that reduces nutrient absorption and use rates.

L. parvifolius is tolerant, its rates of absorption and use of nutrients and, therefore, its

growth rate varies in the flood gradient and concerning soil nutrients.

Likewise, the association of soil pH with SLA and LMDC depends on flood levels. For example, pH, had a positive relationship with SLA, but only in less flooded areas. In flooded soils, low pH levels can inhibit the absorption of nutrients by plants (Kozlowski 1984b). Therefore, in low-flood areas a slight increase in pH could represent higher nutrients uptake, and thus, larger SLA. Changes in soil pH levels due to submersion depend on the pH itself and other components. The general trend under flood (except for iron-deficient soils) is the pH stabilisation towards neutral values, around 7 (Ponnamperuma 1972). Given that flooding has a negative effect and the increase in pH has a positive effect on nutrient absorption, this can be interpreted in two ways: firstly, higher levels of flooding may be neutralising the positive effect of pH; secondly, higher pH levels may be counteracting the negative effect of flooding on nutrient absorption. In addition, the fact that throughout the study area, the pH values were low and had slight variation (3.9 to 4.5) shows that, in addition to flood, pH was also relevant for the variation in SLA and LDMC.

Besides pH, K and Mg levels, and livestock disturbance also interfered with the flood-LDMC relation. The positive effect of flooding on LDMC occurred at high levels

of Mg and low levels of K. That means that in more flooded areas, the higher the K, the greater the acquisition of nutrients (lower LDMC) and the higher the Mg, the lower the acquisition of nutrients. In less flooded areas, the higher the K, the lower the acquisition of nutrients (higher LDMC). The last statement is supported by the fact that negative relationships between K availability and photosynthetic capacity seem to be a pattern along savanna-forest ecotones in the Amazon (Lloyd et al. 2015). The availability of nutrients in the soil and their absorption by plants depends both on their proportions and ratios, as well as on several other factors such as pH and water availability (Kozlowski 1984a; Reid & Hayes 2003; Laekemariam et al. 2018). However, between K and Mg, generally, the relationship is, when there are high levels of K, the absorption of Mg is reduced (Hovland & Caldwell 1960). Magnesium is a structuring element and can play a vital role in forming dry matter (Cakmak et al. 1994). Thus, the high availability of Mg may favour conservative strategies in more flooded areas (higher LDMC).

Since both SLA, LDMC and height are indicators of productivity (Wright et al. 2004) and resistance to disturbances (Oddershede et al. 2018), flooding may reduce the productive capacity of species with high growth rates like *L. parvifolius* and, concomitantly, inducing conservative characteristics. *Leptobalanus parvifolius* is a pioneer species (Santos et al. 2006; Pott & Ratter 2011) with relatively rapid growth (Nunes da Cunha & Junk 2004), characteristic of an acquisitive species, with faster absorption of nutrients than secondary trees (Bizuti et al. 2018). In addition, *L. parvifolius* appears to have an advantage over other species with increased flooding (Nunes da Cunha & Junk 2004; Dalmagro et al. 2016), indicating a lower negative effect of the flood on acquisitive strategies in *L. parvifolius*.

There was also a negative relationship between flooding and plant height in areas disturbed by livestock. More prolonged flooding can shorten the growth period and thus the ability of the plants to compete for light (Fu et al. 2014). In turn, livestock can reduce plant height by tramping or browsing on juvenile plants. That can cause greater sprouting due to stimulation of lateral buds (Scogings & Sankaran 2020) and reduce the rate of growth in height (Sankaran et al. 2013). The plant height reduction by browsing is outstanding without associated fire effect (Staver et al. 2009). In addition, plants with conservative characteristics (In our work, those in more floodable areas) and subjected to herbivory tend to have slower growth compensation rates (Schuldt et al. 2017). In other words, cattle and flooding act as additive effects in reducing plant height growth. Height also was related positively to K and negatively to Mg. Nutrient availability can be an

indicator of growth conditions, albeit little evidence of positive relationships between forest height and nutrient availability (Huston 1980; Aiba & Kitayama 2020). Moreover, livestock can reduce plant density, mainly by browsing on seedlings (Scogings & Sankaran 2020).

The effect of flood and soil were observed in the leaf thickness (which usually is negatively related to SLA). In flooding conditions, water absorption is limited by anoxia (Kozlowski 1984). Thus, plants with less SLA and thicker leaves can improve the conversion of available water, generating production even with water stress. However, without water stress, thicker leaves can limit production. Following the logic of conservative at the detriment of acquisitive strategies, a higher LT would be expected in more floodable areas (e.g., with greater stress), i.e., a positive relationship between flooding and leaf thickness (Oddershede et al. 2018; Souza et al. 2019). In contrast, flooding had a negative relationship with leaf thickness, but only at lower Ca levels. In turn, Ca had a positive relationship with LT at high levels of flooding.

Ca has a fundamental role in maintaining the integrity of membranes and cell walls and in high concentrations might reach more than 10% of the dry weight in mature leaves. Also, high amounts of Ca can inhibit the photophosphorylation process (Marschner 2002). In addition, flooding appears to inhibit the accumulation of Ca by plants in a less pronounced way than other elements such as N, P and K (Fu et al. 2014). Thus, it seems that Ca may hampering the acquisition strategy at high flood levels. Even so, we can consider that the relationship between flood-calcium interaction with leaf thickness was not clear, because in our study area, Ca levels in the soil were low (between 4 and 13 mmolc/dm3), which is a symptom of high acidity (low pH) (Albrecht et al. 1941), also common in the Cerrado soils (Lopes & Cox 1977). Therefore, higher Ca levels, and thus, a more neutral pH could facilitate acquisitive strategies.

In general, flooding had a negative relationship with the bark thickness (BT), with a positive relationship at high levels of K and low levels of P (Fig. 2d, g). However, flooding can induce the production of low-density cells, with more intercellular spaces to facilitate oxygen transport (Coder 1994), increasing BT. Flooding sometimes increases stem thickness because the growth of bark tissues is increased more than the production of xylem cells (Yamamoto et al. 1987; Gomes & Kozlowsk 1988) which could also increase the relative bark thickness (RBT). However, we did not detect a relationship between RBT and flood. In non-flooded environments, BT and RBT can represent a trade-off between mechanical support and water and nutrient storage (Rosell et al. 2014). For example, K is stored in higher amounts in the wood and Ca in higher quantities in the bark (Fromm 2010). Potassium has high mobility in the phloem; however, it is immobile in the xylem where it accumulates, having great importance in forming cell wall and cell expansion and, therefore, in increasing of the size of the xylem vessels (Fromm 2010). This higher concentration of K in the xylem than in the bark (Fromm 2010) may be the reason for the negative relationship between K availability in the soil and RBT in our work. However, it is necessary to emphasise that, in flood conditions, the absorption of water and nutrients can be hindered, making these relationships very complex (Kozlowski 1984a).

The positive relationship between BDMC and flooding indicates increased dry matter production in the bark in areas that flood more. However, this relationship was not clear when interacting with pH (Fig. 2j). In addition, we found a negative relationship between BT and flooding, despite that, under the effect of flooding, greater production of lower density cells is expected, with larger intercellular spaces and production of hypertrophied lenticels to facilitate gas exchange. Thus, a positive relationship between BT and flood would be expected (Yamamoto et al. 1987; Coder 1994; Yáñez-Espinosa et al. 2001; Souza et al. 2019).

Both, Ca and OM were positively correlated with functional diversity in less flooded areas. OM is the leading nutrient supplier agent for plants. In less floodable areas are expected less stress, which facilitates the absorption and use of available nutrients (Kozlowski 1997). higher availability of nutrients, such as P, can generate higher productivity (Cleveland et al. 2011).

We found that functional traits are strongly related to the interaction between flood and soil nutrients. Flood and soil are relevant agents to plant acquisitive or conservative strategies. The influence of flood and soil on measures of functional traits indicates that the monodominant stands of *L. parvifolius* are niche-structured. Plants in less flooded areas tend to have more acquisition and use of nutrients strategy, meaning faster growth, that can be proxied by higher SLA and lower LDMC, while in more flooded areas, they have a more conservative strategy.

## **Chapter 3**

# Establishment and growth of a monodominant tree species affected by flooding and *El Niño*-Southern Oscillation

## Abstract

Interannual climatic variations can define the establishment epoch of the individuals and the patterns in tree physiology, leading to alterations in ring annual growing rhythm. We evaluated the influence of El Niño events, flood and rainfall on the establishment and growth of Leptobalanus parvifolius (Huber) Sothers & Prance (Chrysobalanaceae). We collected dendrochronological samples from 76 individuals of monodominant patches within an area of approximately 97 km<sup>2</sup> in the Pantanal floodplain. The samples were polished to visualize the rings. The samples were cross-dated, and the best time series were used to build the final chronology. We compared the height of the watermark in the individuals in the collection year with the maximum flood height of the Paraguay River recorded at Ladário gauge in the same period. Afterwards, we estimated the flood duration for each individual in previous years. We verified the relationship between flooding time and tree establishment, comparing the flood duration in that year of establishment with the averages and percentiles of the complete series of the Paraguay River levels. We relate the ring widths with flood duration in the year of formation of each ring. We calculated Pearson's correlations between the L. parvifolius chronology and the occurrence of El Niño, rainfall and flood data. The annual flooding duration suitable for the establishment of L. parvifolius is from 30 to 110 days. The flood occurred in all establishment years, showing that flood is mandatory for establishment. The direct relationship between ring width and flood was slightly negative. The flood in August of the current year has a positive influence on growth. The rainfall in February of the previous year has a negative influence on growth, but in March and April of the current year, the influence of rainfall was positive. The drought phase (May-September), when simultaneous with the lack of flooding (August-September), is the stress factor that reduces the growth of *L. parvifolius*. El Niño has a significant negative influence on the growth of L. parvifolius. Considering the predictions of increased frequency and intensity of El Niño events, it is likely that these will tend to cause remarkable changes in landscapes dominated by L. parvifolius by altering species composition and required conditions to achieve monodominance.

Keywords: Dendrochronology, monodominance, monodominant, *Licania parvifolia*, Pantanal, ring width, tree growth, tropical forest.

## Resumo

Variações climáticas interanuais podem definir a época de estabelecimento dos indivíduos e os padrões na fisiologia das árvores, levando a alterações no ritmo de crescimento anual dos anéis. Neste estudo, avaliamos a influência dos eventos El Niño, inundação e precipitação sobre o estabelecimento e crescimento de indivíduos de Leptobalanus parvifolius (Huber) Sothers & Prance (Chrysobalanaceae). Coletamos amostras dendrocronológicas de 76 indivíduos em manchas monodominantes cobrindo uma área de aproximadamente 97 km<sup>2</sup> na planície de inundação do Pantanal. As amostras dendrocronológicas foram polidas para visualização dos anéis. As amostras foram crossdatadas e as melhores séries temporais foram usadas para construir a cronologia final. Comparamos a altura da marca d'água nos indivíduos no ano de coleta com a altura máxima de inundação do rio Paraguai na régua de Ladário no mesmo período. Posteriormente, estimamos o tempo de inundação em cada indivíduo nos anos anteriores. Verificamos a relação entre duração de inundação e estabelecimento comparando o tempo de cheia no ano de estabelecimento com as médias e percentis das séries completas de altura do rio Paraguai. Relacionamos as larguras dos anéis com a duração da inundação no ano de formação de cada anel. Calculamos correlações de Pearson entre a cronologia de L. parvifolius e El Niño, precipitação e inundação. O tempo de inundação anual adequado para o estabelecimento de L. parvifolius é de 30 a 110 dias, ligeiramente acima da altura média do rio da série histórica completa do rio Paraguai. Em todos os anos de estabelecimento ocorreu inundação, evidenciando que a inundação é obrigatória para o estabelecimento. A relação direta entre a largura do anel e a inundação foi ligeiramente negativa. A enchente de agosto do ano corrente tem influência positiva no crescimento. A precipitação de fevereiro do ano anterior influencia negativamente o crescimento, no entanto, nos meses de março e abril do ano corrente, a influência da precipitação foi positiva. A fase de seca (maio-setembro) quando simultânea com a ausência de inundação (agosto-setembro) é o fator de estresse que reduz o crescimento de L. parvifolius. El Niño tem influência negativa significativa no crescimento de L. parvifolius. Considerando as previsões de aumento da frequência e intensidade dos eventos El Niño, é provável que eles tendam a causar grandes mudanças nas paisagens dominadas por L. parvifolius devido às mudanças na composição de espécies e nas condições necessárias para que L. parvifolius atinja monodominância.

Palavras-chave: Dendrocronologia, monodominante, monodominância, largura de anel, *Licania parvifolia*, Pantanal, crescimento arbóreo, floresta tropical.

## Introduction

Most tropical floodplains have markable flood pulse, with distinct terrestrial and aquatic phases and markable rainfall seasonality, with a dry and a rainy season (Junk et al. 1989; Ivory et al. 2019). However, intensity, duration of flood and rainfall can vary interannually. These variations are chiefly attributed to sea surface temperatures oscillations (SST) in many oceanic regions (Cai et al. 2020).

In the tropical Pacific, variations in the sea surface temperature (SST), called *El Niño*-Southern Oscillation (ENSO), are the main factor that causes interannual changes in the climate of South America (Andreoli et al. 2017; Cai et al. 2020). ENSO can cause variations in temperature and rainfall, which leads to changes in hydrological conditions and alterations in the intra- and interannual dynamics of floods in south American floodplains (Jeltsch et al. 2000; Grimm & Tedeschi 2009; Thielen et al. 2020).

These climatic and environmental oscillations can change the annual pattern in tree physiology, leading to increased or reduced ring annual growing rhythm (Schöngart et al. 2002; Silva et al. 2017; Gris et al. 2020). Besides, these interannual variations can define the establishment epoch to tree individuals from several species (Nunes da Cunha & Junk 2004; Manrique-Pineda et al. 2021).

Flooding induces conditions of anoxia which leads to a reduction in physiological activities and, therefore, a reduction in radial increment of trees (Schöngart et al. 2002). However, in floodplains, tree species have a wide range of adaptations that allow them to tolerate flooding (Parolin 2012). For example, carbohydrate reserves during the growth phase, adventitious roots, hypertrophied lenticels, changes in pressurization for gas transportation, regrowth and leaf shedding, among others (Graffmann et al. 2008; Parolin 2012). Thus, despite meaning a period of stress, unfavourable for growth, these plants are highly adapted to these environments, and their physiological processes are not entirely prevented by flooding (Schöngart et al. 2002).

Rainfall and flooding are important in determining growth patterns in some areas in floodplains, especially in less floodable parts or in those without flooding (Worbes 1999). Some species seem to benefit more from rainfall, with reduced growth in the dry season and zero (Paixão 2018), or negative relation with flooding in lower areas (Ishii 1998), while others have shown a positive relationship between growth and flooding (Gris et al. 2020). The climatic and hydrological dynamics in the Pantanal floodplain in the centre of South America are strongly influenced by ENSO, with interannual and decadal variations in rainfall and flood patterns (Thielen et al. 2020). Years with *El Niño* occurrences can alter seasonality and reduce rainfall, causing changes in flood dynamics. Studies on climate change have predicted an increase in frequency and intensity of *El Niño* events with reduced rainfall and increased temperature (Marengo et al. 2015; Thielen et al. 2020). As a result, it is likely that there will be an increase in the frequency and intensity of the Pantanal (Thielen et al. 2020).

The reduction in rainfall may cause drastic changes in the hydrological cycle and increased fire frequency. With this, drastic changes in landscapes are expected, with a spread of species more adapted to fire, besides a loss of biodiversity (Alho 2008; Alho & Silva 2012; Thielen et al. 2020). These extreme conditions between periods of drought and flood, and great seasonal variations of temperature due to its central location in the continent in addition to other climatic factors (Marengo et al. 2015; Thielen et al. 2020) make the Pantanal an ideal environment to explore the drivers of growth in trees and the monodominant formations structures.

Leptobalanus parvifolius is a widespread species, occurring mainly in the northern and central-western Brazilian regions. This species forms monodominant stands in seasonally flooded areas (Nunes da Cunha & Junk 2004; Pott et al. 2011; Dalmagro et al. 2016). In the Pantanal is considered a pasture invader, therefore, being undesired by cattle ranchers (Allem & Valls 1987). Due to great vigour and sprout capacity, the spreading of these monodominant stands is difficult to be controlled (Santos et al. 2006). The growth of *L. parvifolius* seems to be faster than some other typical monodominant species of the region (Nunes da Cunha & Junk 2004). In addition, *L. parvifolius* has an effective photosynthetic rate and high-water use efficiency with low leaf water potential during dry seasons, besides little variation in photosynthetic performance between dry and flooded seasons (Dalmagro et al. 2016). Moreover, farmers have already observed its advance in years of greater flooding (Nunes da Cunha & Junk 2004). Thus, above-average flooding can benefit this species.

Understanding the relationship between climatic conditions and growth of tree species and the consequences of changes in the hydrological cycle for the establishment and growth of monodominant species is a key factor to think about management and conservation strategies, in harmony with extensive livestock in this region. Therefore, in this study, we evaluate the influences of *El Niño*, flood and rainfall events on the establishment and growth of *L. parvifolius* in the Pantanal floodplain. In addition, we determined an adequate flood time interval for the establishment of these individuals. Considering that *El Niño* reduces rainfall in the Pantanal and that longer flood can be a stress factor to growth, we expected that higher *El Niño* oscillation and higher flood negatively influence and that higher precipitation positively influences the growth of *L. parvifolius*. Since there is evidence that *L. parvifolius* advances in years with higher flooding, we expect that most individuals in our study had established themselves in years when flooding occurred.
# Methods

## Study area and studied species

The data were collected in monodominant stands of *Leptobalanus parvifolius* in the Pantanal floodplain, approximately 20 km eastwards from the Paraguay river (Fig. 1). The climate of the region is tropical with dry winter (Aw), with rainfall between 1000-1200 mm (Thielen et al. 2020), and annual average temperature between 24 and 26 °C (Alvares et al. 2013). *Leptobalanus parvifolius* is a tree with 3-7 m height, and a trunk usually branched at the base (Fig. 2a). The monodominant stands of *L. parvifolius* occur in riparian forests and areas with intermittent water systems (Appendix 2), flooded up to eight months per year (Nunes da Cunha & Junk 2009). Some species associated are *Inga vera* Willd, *Calophyllum brasiliense* Cambess, *Erythroxylum anguifugum* Mart., and *Alchornea discolor* Poepp. (Nunes da Cunha et al. 2007; Pott et al. 2011). In our study area, the stands were located mainly in intermittent watercourses and sometimes alongside paleodykes (locally called "cordilheiras").



Fig. 1. Location of study area and sampled individuals of *Leptobalanus parvifolius* in the Pantanal floodplain. Colours in the upper right panel represent *El Niño* regions in the Pacific Ocean.

#### Data collection

In August/2017, we marked the eight individuals by mechanical wounding (Mariaux 1967) to obtain more accurate growth data and confirm the annual growth rhythm. The mechanical wounding method consists of small incisions in the bark that cause cambium damage (Fig. 2b). Between August and October 2018, we collected dendrochronological samples from 68 individuals by using an increment borer (Pressler borer) 5 mm in diameter (non-destructive sample), two cores per individual (Appendix 6). Two years after the mechanical wounding procedure (September 2019), the 68 trees were cut at the height of the mark to obtain three transversal disks (for each individual) with about 5 cm thick (Fig. 2c and Appendix 7). The disks and samples collected with the borer were dried at room temperature and then polished sequentially with sandpaper of 80, 100, 180, 220, 400, 600 and 1200 of granulation to better show the growth rings (Worbes 1985). Ring width was measured with a resolution of 0.001 mm using LINTAB-TSAP.

Samples without pith were analysed carefully. For samples where the increment borer captured the rings in the direction tangential to the pith, we calculated the distance from the last ring to the pith, using the angle of the radius. With the average number of rings for a given distance (this average number of rings was calculated from the samples that presented the pith), we estimate the number of rings missing in that distance. Thus, we could better estimate the age for those samples without the pith (Appendix 8).

Cross-dating of the rings was performed using the TSAP-WINTM program. We validated cross-dating visually and using the "Gleichlaeufigkeit" (GLK) and the T value (Pilcher 1990) coincidence coefficient. After cross-dating, the best individual time series was selected to construct the average time series (chronology) (Fig. 3).



Fig. 2. Internal overview of a monodominant stand of *Leptobalanus parvifolius* in the Pantanal floodplain, with yellow arrows showing the 2018 flood watermark (a). The mechanical wounding (b). Stem disc showing the ring formations after mechanical wounding in August/2017 (c). And anatomical cross section showing the delimitation of a growth ring (d). Photo: Evaldo B. Souza.



Fig. 3. Average ring-width chronology and ring-width curves of *Leptobalanus parvifolius* in the Pantanal floodplain.

To obtain a normal distribution to the ring time series, which is a basic prerequisite to perform correlations with climate variables, we settled a five-year moving average that converts tree ring time series into growth indices. That procedure is necessary to remove long-term growth trends related to increasing tree age and size (Cook & Kairiukstis 1990).

For the characterisation and better recognition and delimitation of the rings, we made transversal anatomical sections. The anatomical sections were stained and analysed under a microscope (Fig. 2d). To do that, we softened the wood by boiling the samples in glycerin solution (50%) for 3 hours. Then, we use a sledge microtome (Leica SM2000R) to prepared cross 15  $\mu$ m thickness planes sections. After, the sections were cleared, washed in sodium hypochlorite, distilled water and acetic acid (1%) and finally, stained with alcian blue and safranin.

### Flood data

We measured the height of the watermark of the last flood on each individual (Fig. 2b) and calculated the difference between the maximum height (max) of the Paraguay River (Ladário's gauge data, provided by the Brazilian navy – Fig. 4) in the year of collection and the watermark (WM) on trees with the formula: quota = max - WM. Thus, the quota is the minimum height of the river necessary for an individual to be reached by the flood. In sequence, we verified which daily values of Ladário's gauge in all years (1900-2018) were higher than the quota. With this analysis, we determined how many days per year each individual was reached by flood (R code to the calculation procedure is in Appendix 9). Considering that the Paraguay River is the main river in the region and thus responsible for the largest floodable area of the plain covering tens of kilometres and that the topography of the region is extremely flat (Adámoli 2000; Gonçalves et al. 2011), we assume that the water level in the study area varies according to that of the Paraguay River.



Fig. 4. Monthly average level of Paraguay River (1900-2018; data from Ladario Navy), and Miranda River (1995-2018, data from Base de Estudos do Pantanal-UFMS), and rainfall in Pantanal south. Rainfall data from Agência Nacional das Águas (ANA), see Appendix 10

### Climatic data

We obtained ENSO data (regions 1+2, 3, 3+4 and 4; see Fig. 1) from the Climate Explorer website (Trouet & Oldenborgh 2013), managed by the Royal Netherlands Meteorological Institute-KNMI (<u>http://climexp.knmi.nl/getstations.cgi</u>).

To build a database for the entire life span of the sampled individuals (1965-2018), we downloaded rainfall data from Agência Nacional das Águas-ANA website (http://www.snirh.gov.br/hidroweb/serieshistoricas) using the five nearest rainfall stations to the study area (Appendix 10). Since all stations lack data in several years interspersed in that period, we calculate the average rainfall for the five stations, thus minimising missing data.

#### Data analyses

To verify the relationship between the establishment of individuals and the flood time length, we obtained the age of individuals by counting the rings to determine in which year the individual was established. Then, to mitigate ring count errors, we calculated the average from three years: the year of establishment, the year before establishment, and the year after establishment, which we called Establishment Period (EP). We compared the flood duration in the EP with the average and percentiles of 50%, 75%, 100% of flood duration in the same areas for the complete series of the Paraguay River between 1965 and 2018. To test the difference in flood duration between EP and the other groups (average and percentiles of 50%, 75%, 100%), we used permutational tests with 10,000 iterations. With the flood time length of the EP of each individual, we also showed which periods (years between 1900 and 2018) were more favourable for *L. parvifolius* populations establishment.

We related the ring widths to the flood duration of each individual in each year. For this analysis, we used a generalised linear model (GLM) with a log-normal distribution. We used Pearson's correlation to relate the chronology of *L. parvifolius* to temperature anomalies in the southern Pacific (*El Niño* Southern oscillation), flood and rainfall.

# Results

The wooden structure of *Leptobalanus parvifolius* presents rings demarcated mainly by a band of fibrous cells, often accompanied by a band of radial parenchyma. In cross-section composed of libriform wood fibres, radial parenchyma with one to two layers of cells, axial paratracheal parenchyma confluent with vessel elements dispersed in the xylem, and frequent occurrence of annular apotracheal axial parenchyma. In many rings, it was possible to verify the reduction in size and quantity of vessels from earlywood to latewood (Fig. 2d). False rings were not included in the measurements. False rings were those with bands of fibres very close to each other and without vessels and parenchyma bands between them.

*Leptobalanus parvifolius* presents annual rings, with reduced growth in the dry season (August-September). The ring formation begins during the dry season since the mechanical wounding was done in August and coincided with the reduced growth season (Fig. 2c). The age of the trees varied between 12 and 54, with 27.2 years in average (Appendix 11)

The average height of the watermark was 47.6 and varied between 13 and 135 cm. The time of flooding on the individuals for all the years ranged between 0 and 207 days per year. The establishment of *L. parvifolius* individuals occurs mainly in years with flooding duration between 30 and 110 days and 64.9 days on average (Fig. 5a). The averages of EP were higher than the complete series averages and medians (50% percentile) of the complete series (Fig. 5b, c). However, the EPs were less than the 75% and the 100% percentiles of the complete series (Fig. 5d and 5e, respectively).



Fig. 5. Relationship between establishment of *Leptobalanus parvifolius* individuals and flood duration. Each point represents an individual. EP = flood duration average for the Establishment Period of each individual. TS = flood duration average for the Complete Series of the Paraguay River between 1965 and 2018 in the same areas of each individual. P50, P75 and P100 are respectively 50%, 75% and 100% percentiles of flood time for each individual for the series of the Paraguay River between 1965 and 2018. The horizontal blue trace in (a) indicate the means. Panels (b) to (e) are results of permutation tests; comparison between observed means (red line) and randomizations (histogram).

Considering the 30-110 flooding days as favourable for the establishment of *L. parvifolius*, we can indicate which intervals were more favourable for such establishment. This estimate showed that several years in the periods 1944-1963 and 1998-2017 were the most favourable for the establishment of *L. parvifolius* populations in the Pantanal, besides other years that occurred in more dispersed way (Fig. 6). Thus, the width of the rings tended to decrease with increasing flooding time of the same ring growth year (Fig. 7).



Fig. 6. Time series of water levels of the Paraguay River in Ladário gauge between 1900 and 2018. Vertical bars are water level amplitude of the years and black dots are averages. Blue vertical bars are the estimate of favourable years to *L. parvifolius* populations establishment. Horizontal black line represents the limit that river overflows.



Fig. 7. Relationship between ring width of *Leptobalanus parvifolius* and annual duration of flood in the Paraguay River in the Pantanal floodplain.

*El Niño* regions 1+2, 3 and 3+4 had negative correlations with growth. The negative correlations occurred between January and June of the current year (Fig. 8). The flood in August of the current year positively correlated with the chronology (Fig. 8). In turn, rainfall presented a negative correlation with growth in February of the previous year and a positive correlation in March and April of the current year (Fig. 8).



Fig. 8. Correlations between the chronology (ring width index) of *L. parvifolius* and four regions of *El Niño*-Southern Oscillation (ENSO), Paraguay River water level and accumulated monthly rainfall (between 1969 and 2017). (-1) indicate growth season in the previous year and (+1) indicates calendar year after growth season in the current year (growth season begins in October). Dashed blue lines represent thresholds for p < 0.05.

## Discussion

Our major findings were that the growth of *L. parvifolius* is reduced when *El Niño* oscillation is higher. Flood is essential for the establishment of *L. parvifolius* individuals. Flood that begins at the end of the rainy season can be positive for growth in non-rainy periods. The growth reduction occurs in August-September when the dry season coincides with the terrestrial phase. Rainfall can influence growth positively in March and April of the current year or negatively in February of the previous year.

In all years beneficial for the establishment of *L. parvifolius*, the height of the Paraguay River exceeded the minimum limit for overflow of water from the channel (4 m), i.e., there were floods (Fig. 6). In general, the favourable years to the establishment of *L. parvifolius* had averages very close and often slightly above the general average of the complete series. This result shows that flooding is mandatory for the establishment of *L. parvifolius*. Periods with prolonged droughts such as 1964-1973 are cited as hostile for other monodominant species in the Pantanal (Nunes da Cunha & Junk 2004). However, higher flood periods such as 1976-1985 also were unfavourable to the establishment of *L. parvifolius*.

In the study region, several species need an interannual hydrological window to establish themselves (Nunes da Cunha & Junk 2004; Damasceno-Junior et al. 2021). An example is *Tabebuia aurea*, which also forms monodominant stands. This species needs years with low flooding to become established or small elevations in the terrains that are less frequently flooded (Bueno et al. 2014; Manrique-Pineda et al. 2021). It also seems to happen with other woody species considered pasture invaders, which advance over the grasslands in drier years (Nunes da Cunha & Junk 2004; Silva et al. 2016).

In contrast, *L. parvifolius* is established in years with somewhat above-average flooding. The same seems to happen with *Vochysia divergens* in the northern Pantanal (Nunes da Cunha & Junk 2004), where periods with higher water levels seem to favour the advancement of monodominant stands of this species, and several years of drought can cause a significant decline in its populations (Nunes da Cunha & Junk 2004). Likewise, *Erythrina fusca*, another monodominant species in northern Pantanal, seems to have its establishment favoured by longer periods of flooding, with durations between 97 and 117 days (Gris et al. 2020). Changes in the flood regime could modify or restrict the distribution of these monodominant stands (Marengo et al. 2015; Gris et al. 2020).

Relating the flood time in the year of formation of each ring directly with the width of the rings, we found a slightly negative correlation. However, we found a positive relationship between flood time and ring indexed growth in August of the current year. There are reports that, in this region, the negative effect of flooding on tree growth occurs in areas with flooding times of at least 180 days per year (Ishii 1998), as occur in the lower areas of the Pantanal. The time of flooding in the individuals we sampled was between 0 and 207 days per year, rarely exceeding 180 days (Fig. 7). Some studies have shown that during the high floods, the cambial dormancy suppresses or wholly ceases the stem diameter increase during the terrestrial phase, there are high rates of monthly increase (Schöngart et al. 2002). The relationship between flood and growth is more evident in lower areas in the Amazon, where flooding induces anaerobic conditions in the roots, which is the main factor affecting growth (Schöngart et al. 2002; Schöngart et al. 2005).

A study addressing the effect of flooding on the community structure and individuals in monodominant stands of *Tabebuia aurea* showed that at higher levels of flooding, the basal area of *T. aurea* is smaller. However, this negative effect interacts with other environmental factors such as fire and small differences in elevation on the ground caused by earth mounds (Manrique-Pineda et al. 2021). Dendrochronological studies with *Tabebuia aurea* have shown that flooding within the monodominant stands in southern Pantanal positively affects the growth of individuals (Paixão 2018). The same was not observed in the North Pantanal region (Paixão 2018), where besides *T. aurea*, other species with wide distribution also did not have the growth hinder by flood (Leite 2012; Paixão 2018).

That may be because flooding in the southern region occurs at the beginning of the dry season (i.e., without rain), approximately three months delayed in relation to the north due to slow drainage from north to south (Hamilton et al. 1996). Such condition provides water availability for a longer time in the southern region, explaining the positive relationship of *L. parvifolius* ring width index with flood in August. In this small range of time, when the terrestrial phase coincides with the phase without rain from August to September, less flooded areas are subject to lower soil water potential causing water stress and consequently reduced growth. Therefore, any prolongation of the flooding phase can reduce the stress by drought. As we realize, in specific years, several individuals can still be reached by the flood in August and, sometimes, even in September (Appendix 12).

Thus, the drought phase (May-September) concomitant with the lack of flooding (August-September) must be the stressor that reduces the growth of *L. parvifolius*. This statement is supported by mechanical wounding, which showed that the ring growth was strangled in the dry season since the procedure was done in August and coincided with the growth reduction, producing the ring boundary. Whether less intense, and occurring at the beginning of the dry season, the flooding can provide a longer time of soil water availability favouring the growth of *L. parvifolius*. Considering that in our study region, the rainy season occurs between October and April (the growing season) and that floods occur between March and August, the growing season can be prolonged if the flood is not very intense and does not last long enough to affect growth (Parolin 2010).

Another possible scenario, the negative effect of more severe flooding after the growth phase, would have the same effect as the drought. For consecutive years with exceptionally long floods can be a realistic scenario, as is the case, for example, in some of the most flooded areas of the Amazon floodplain (Schöngart et al. 2002). Furthermore, the opposite scenario would be a sequence of years without flooding.

Unlike other flooded areas with greater flooding amplitude, such as in the Amazon, the duration of the flooding in the Pantanal does not seem to be sufficient to reduce the growth of *L. parvifolius* and other species (Paixão 2018; Gris et al. 2020). Parolin (2012) pointed out that significant growth reductions for floodplain species occur in flood duration with 90-210 days, an interval far above the flood average in our study area. In addition, although flooding is unfavourable for growth in some evergreen species, it appears that their physiological processes are not entirely hindered by flooding (Maia 1997; Schöngart et al. 2002; Dalmagro et al. 2016). Thus, we can consider that floods that occur in areas of *L. parvifolius* are insufficiently long to show a strong influence on its growth.

Our results showed that ENSO events are negatively correlated with the growth of *L. parvifolius*. The climatic effects of ENSO vary according to the region (Ropelewski & Halpert 1987; Thielen et al. 2020) and, therefore, on the growth of trees between regions (Cai et al. 2020; Li et al. 2020). In the Neotropics, most studies have reported negative relationships between tree growth and ENSO (Schongart et al. 2004; Gris et al. 2020). In the Pantanal, the negative effects of ENSO on the growth of tree species have been demonstrated for other species (Paixão 2018; Gris et al. 2020).

As shown by our analyses, the negative correlations occurred between January and June of the current year. ENSO events, characterized by an increase in the surface temperature of the southern Pacific Ocean, takes place in December. Therefore, the effect of *El Niño* in the Pantanal happens a month late. This period (January to June) also coincides with the growth phase of *L. parvifolius*, which seems to start in October, with a reduction starting in August when the dry phase begins (without rain and flooding). Similarly, in the North Pantanal, the beginning of the growth period of *E. fusca* occurs between December and January, coinciding with the peak of rainfall and the beginning of the flooded phase (Gris et al. 2020).. The negative effect of ENSO on the growth of *E. fusca* occurs between February and September for region 1 + 2 and from November to June for region 3 (Gris et al. 2020).

That negative effect of *El Niño* on tree growth in the Pantanal is mainly attributed to the reduction in rainfall that ENSO causes in the floodplain (Thielen et al. 2020). The reduction of rainfall is the main stressor for tree growth in the tropics (Worbes 1999; Schöngart et al. 2002; Schongart et al. 2004). This reduction in growth can occur when rainfall is below 50 mm per month, causing a decrease in water potential in the soil (Worbes 1999). Therefore, reducing the nutrients absorption Thus, most tropical species have their growth phase related to the rainy seasons.

Although positive relationships between rainfall and growth are common in the tropics, negative relationships also occur (Clark et al. 2003; Schongart et al. 2004; Grogan & Schulze 2012; Rahman et al. 2018). The negative relationship between growth and rainfall in February of the previous year may have occurred because the increase in rainfall in that month in the entire basin contributes to more flooding, which generally occurs between April and July. However, flooding at that period was not related to growth.

The chronology showed a positive relationship with rainfall only in February and April of the current year. In the region, rainfall occurs between October-April and the dry season (without rain) between May-September. In the driest years (e.g., 1936 to 1939 and 1964 to 1974, see Fig. 6), the dry season can extend until mid-November, with rainfall below 50 mm in that month. In addition, there can be a wide variation in rainfall between months, and there may also be sequences of several days without rain (locally called *veranicos*) from January to March (Pereira et al. 2021). Therefore, the variation in rainfall in these months may cause a delay and therefore, a reduction in the length of the growing season, that may be relevant for tree growth in the region.

As shown by the cambial wounding, the growth reduction phase occurs in the dry season (August-September). The leaf shedding in the dry season due to soil water deficit

leads to the reduced photosynthesis and consequent cambial dormancy, thus reducing growth (Schöngart et al. 2002). *L. parvifolius* is considered an evergreen species (Pott & Pott 1994). According to our field observation, maximum leaf shedding occurs at the end of September, but it does not drop more than c. 30% of its leaves. Unlike deciduous species, evergreen species change their leaves almost continuously during the dry phase (Schöngart et al. 2002). In addition, the growth of evergreen species, such as *L. parvifolius*, extends for a few weeks after the beginning of the dry season, with only a short period of growth interruption by drought end (Worbes 1999). However, albeit this dry period being brief, our stem disk samples showed limited growth at precisely that time.

As observed by Schöngart et al. (2002), in the Amazon, few species subjected to flooding strongly correlate between radial increment rates and precipitation. The positive effect of rainfall on growth is higher in Amazon evergreen species, but it can also occur in deciduous tree species such as *Pseudobombax munguba* (Mart.) Dugand (Schöngart et al. 2002). Rainfall has an influence mainly on the growth of trees in areas with short flooding or without flooding ("terra firme") (Schöngart et al. 2002; Schongart et al. 2004). Contrary to what seems to happen in the Pantanal (Paixão 2018), most tree species in the Amazon floodplain are influenced more by the flood pulse than by rainfall (Schöngart et al. 2002).

*El Niño* strongly affects rainfall in the Amazon, and these changes in rainfall dynamics in the Amazon directly affect the rainfall cycle in the Pantanal (Bergier 2010). Thus, the effect of flooding and rainfall in the Pantanal may be due an indirect effect of *El Niño* and the rain cycles in the Amazon. According to climatic forecasts, *El Niño* events will occur with higher frequency and intensity. The increase in the frequency of occurrence of *El Niño* plus direct interferences of human actions in the upper basin, such as intensive livestock husbandry (Araujo et al. 2018), improper land use (Guerra et al. 2020) and hydroelectric dams (Rocha et al. 2020), can lead to the worst scenario within the predictions of loss of landscape with drastic changes in the climate and hydrology of the Pantanal, such as reduced rainfall and floods. Those climatic and environmental changes, like Flood reduction, may cause great transfigurations in the landscape, such as replacing natural grasslands with tree and shrub vegetation leading. Such loss of native pasture, can lead ranchers to convert native vegetation into cultivated pastures, accelerating the loss of landscape and species diversity and floodplain functionality (Erwin 2009). The impact of those events on wetlands can be catastrophic, leading to a

severe change in conditions for the establishment of characteristic monodominant vegetation of the Pantanal. Therefore, the conservation of these monodominant landscapes depends on the maintaining climatic and hydrological conditions in the Pantanal.

The conservation and management of areas with *L. parvifolius* monodominance depends primarily on knowledge of flooding dynamics and how it affects the establishment and growth of this species. Many areas are deforested in dry years for livestock use. However, in years of greater flooding, these areas become unviable for this purpose. Therefore, local predictions about the intensity of floods and also the climatic variations that influence them can assist less destructive and more economically efficient management strategies. Thus, the results found here, can develop conservation plans that mitigate climate change effects to maintain the necessary conditions for the stability of these formations in line with the economic activities in the region.

## **General conclusion**

Our results showed that cattle and edaphic characteristics in interaction with seasonal flooding are essential influential factors for *L. parvifolius* monodominance. That is, flood is not the only structuring factor of monodominant stands. Even so, we also observed that, in the Pantanal, the marked variations between periods of drought and flooding are essential for this tree species to reach monodominance. Thus, classic monodominance, which occurs under low intensity endogenous and exogenous disturbances, does not apply to the species of the studied floodplains, which depend on strong influence of environmental filters to achieve monodominance,

Functional traits are also strongly related to the interactions between flood and nutrients to which plants respond by modulating between nutrient acquisitive and conservative strategies. In less flooded areas, plants are more acquisitive, which provides them faster growth (proxied by higher SLA and lower LDMC). In turn, plants in more flooded areas are more conservative, i.e., they grow slower.

Flooding in the Pantanal has a slightly negative influence on the ring width of *L*. *parvifolius* individuals, though flooding can have positive influences when it occurs in the non-rainy season. However, as shown by the dendrochronology analysis, interannual climatic variations caused by temperature fluctuations in the tropical Pacific (*El Niño* Southern Oscillation) have a significant negative effect on growth of *L. parvifolius*.

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## Appendix



Appendix 1 Flowers (a) and fruits (b) of *Leptobalanus parvifolius* in the Pantanal floodplain. Photo: Evaldo B. Souza.



Appendix 2 *Leptobalanus parvifolius* individuals inhabiting the periphery of a semidecidual forest patch (locally called "capão") in the Abobral subrregion (a); and, a monodominant stand of *L. parvifolius* occupying an intermitent watercourse in the Nhecolandia subrregion (b). Photo: Evaldo B. Souza.



Appendix 3 *Leptobalanus parvifolius* monodominance (dark green inside yellow lines) involving a monodominant patch of *Couepia uiti* (light green inside red lines). Source: Google earth (coordinates: -19.366371 W, -57.047702 S)

Family	Species	Abundance
Apocynaceae	Tabernaemontana siphilitica (L. f.) Leeuwenb.	1
Arecaceae	Copernicia alba Morong	1
Bignoniaceae	Bignoniaceae Juss.	1
	Handroanthus heptaphyllus (Vell.) Mattos	4
Cactaceae	Cereus bicolor Rizzini & A. Mattos	11
Chrysobalanaceae	Couepia uiti (Mart. & Zucc.) Benth. ex Hook. f.	51
	Leptobalanus parvifolius Huber	368
Erythroxylaceae	Erythroxylum anguifugum Mart.	36
Euphorbiaceae	Alchornea discolor Poepp.	7
Fabaceae	Andira inermis (W. Wright) Kunth ex DC.	11
	Inga vera Willd.	5
	Machaerium acutifolium Vogel	1
Lauraceae	Ocotea diospyrifolia (Meisn.) Mez	6
Malpighiaceae	Byrsonima crassifolia (L.) Kunth	1
	Byrsonima cydoniifolia A. Juss.	3
Malvaceae	Sterculia apetala (Jacq.) H. Karst.	1
Moraceae	Ficus calyptroceras (Miq.) Miq.	3
	Sorocea sprucei (Baill.) J.F. Macbr.	1
Myrtaceae	Eugenia egensis DC.	1
	Eugenia florida DC.	2
	Eugenia sp. Juss.	1
	Myrcia splendens (Sw.) DC.	9
Nyctaginaceae	Neea hermaphrodita S. Moore	4
Ochnaceae	Ouratea purpuripes S. Moore	2
Olacaceae	Dulacia egleri (J.O. Rangel) Sleumer	2
Polygonaceae	Ruprechtia brachystachya Benth.	1
Rubiaceae	Alibertia edulis (Rich.) A. Rich.	1
	Genipa americana L.	2
	Tocoyena formosa (Cham. & Schltdl.) K. Schum.	18
Rutaceae	Zanthoxylum rigidum Humb. & Bonpl. ex Willd.	5
Urticaceae	Cecropia pachystachya Trécul	8

Appendix 4 Species list of *Leptobalanus parvifolius* monodominant stands in the Pantanal floodplain



Appendix 5. Correlations between functional traits before (a) and after (b) the reduction to generate the kernel alpha diversity (hypervolume).



Appendix 6. Core extraction from *L. parvifolius* trunk in the Pantanal Floodplain. Photo: Evaldo B. Souza.



Appendix 7. Stem disc of *Leptobalanus parvifolius* in the Pantanal floodplain. Photo: Evaldo B. Souza.

Distance from the last ring to the centre



Appendix 8. Scheme of the distance estimation method for samples with displaced pith.

Appendix 9. R code to the calculation procedure for the differences between the maximum height (max) of the river (Ladário's gauge data, provided by the Brazilian navy) in the year of collection and the watermark (WM) on trees and to calculate how many days per year each individual was reached by flooding.

# Requisites:

# The data frame with the values of the gauge of the river. # The data frame needs to be with months and days in the # rows and years in the columns (named here as dataD) # See an example:

dataD

	Months	Days	1900	1901	1902	 2018
1	Jan	1	77	90	151	 116
2	Jan	2	64	187	159	 67
3	Jan	3	111	120	9	 4
4						 
5	Dec	31	57	113	45	 87

# Remove Months and Days columns
dataD2 <- dataD[,-c(1,2)]</pre>

# We also need the data frame with the sample identities #(Individuals) and the Water Mark values (named here as # Sample). Example:

## Sample

samp WM 1 I\_01 55 2 I\_02 47 3 I\_03 22 4 I 04 86

## calculate the flood quota of the individuals

```
# quota = the minimum height of the river necessary for an
# individual to be reached by water.
# That is, the quota is the difference between the maximum
# river water level in the year of the collection and the
# watermark on the trees. Thus, quota = max - WM
# Being max = Maximum water level of the river in the year
# of collection.
# with the 'max' function we extract the maximum value of
# the river height in the collection year.
# And, from this value, we subtract the watermark value on
# the trunk in the year of collection (here is 2018).
quota <- max(dataD2[,"2018"], na.rm=T) - Sample$WM</pre>
# Sample$WM = The column with watermark values in the trunk
# in the year of collection.
# The next code will loop across the data frame and
# calculate the number of days with values above the quota
# for every year and for every individual.
nDays = list()
for(j in 1:length(quota)) {
  resul <- as.numeric()</pre>
  for(i in 1:length(dataD2)){
    resul[i] <- length(which(dataD2[,i] > quota[j]))
  }
  nDays[[j]] <- resul</pre>
}
# Convert list to data.frame
nDays <- (data.frame(nDays))</pre>
```

```
# Naming the columns
colnames(nDays) <- Sample$samp
```

```
# add years column (line names)
nDays <- data.frame(year=as.numeric(names(dataD2)), nDays)
# Now we have a data frame with sample in columns, and values
# above the quota for all samples in all years.
# See
head(nDays[,1:3])</pre>
```

Appendix 10. Identification of the stations used in the collection of rainfall data. Source: Agencia Nacional das Águas (ANA)

Station code	Station name	Municipality	Active since	Latitude	Longitude
1956005	Bodoquena	Miranda	1953	-19.87	-56.98
2056005	Guaicurus	Miranda	1920	-20.10	-56.80
1957000	Corumbá	Corumbá	1912	-19.00	-57.65
1957005	Piraputanga	Corumbá	1972	-19.31	-57.59
2057001	São Simão	Corumbá	1977	-20.05	-57.32

(http://www.snirh.gov.br/hidroweb/serieshistoricas)



Appendix 11 Tree individual ages and histogram of number of individuals per age (embedded graph).



Appendix 12 Average rainfall and monthly average flood period for each individual between 1965 and 2018. Each point represents an individual.



Appendix 13. Field working team. From left to right, Pedro Isaac, Anahi Cerzósimo, Daniel Manrique-Pineda and Evaldo Benedito de Souza. Photo: Evaldo B. Souza.