Revista Ibero-Americana de Ciências Ambientais
Ibero-American Journal of Environmental Sciences

Jul 2022 - v.13 - n.7

ISSN: **2179-6858**

This article is also available online at:
www.sustenere.co

Phenology of five plant species with potential for fruit resources in the Pantanal

The phenology of plant species is directly reflected by the environmental conditions, which benefits a straight relationship between fish and fruit, for instance. The present study relates the phenology of five plant species at an ecological station in the Pantanal regarding the rainfall and different flooding seasons. The study was conducted in the Paraguay river in the Northern Pantanal, following an entire hidrologic cycle of full and dry. A positive correlation was found for the species Spondias mombin, Inga vera, Bactris riparia, and Bactris brongniartii with flooding, in which unripe fruits occurred at the beginning of the rainy season and ripe fruits occurred at high water. On the other hand, the production of unripe fruits of Erythrina fusca species was negatively correlated with the water table level, with the flowering, and fruiting occurring during the dry period. The fruiting period of the species S. mombin, I. vera, B. riparia, and B. brongniartii can benefit ichthyofauna which consume its fruits and seeds during the wet season, whereas E. fusca contributes to the dry season. There is a need to further the knowledge of plant phenology in the Pantanal and this information must be taken into account in conservation units for management.

Keywords: Plant phenology; Riparian plants; Water dynamics; Wetlands.

Fenologia de cinco espécies de plantas com potencial para recursos de frutos no Pantanal

A fenologia das espécies vegetais reflete-se diretamente nas condições ambientais, o que favorece uma relação direta entre peixes e frutos, por exemplo. O presente estudo relaciona a fenologia de cinco espécies vegetais em uma estação ecológica no Pantanal quanto à pluviosidade e diferentes épocas de cheias. O estudo foi realizado no rio Paraguai no Pantanal Norte, seguindo todo um ciclo hidrológico de cheia e seca. Foi encontrada correlação positiva para as espécies Spondias mombin, Inga vera, Bactris riparia e Bactris brongniartii com a inundação, em que os frutos verdes ocorreram no início da estação chuvosa e os frutos maduros ocorreram na cheia. Por outro lado, a produção de frutos verdes da espécie Erythrina fusca correlacionou-se negativamente com o nível do lençol freático, com a floração e frutificação ocorrendo no período seco. O período de frutificação das espécies S. mombin, I. vera, B. riparia e B. brongniartii pode beneficiar a ictiofauna que consome seus frutos e sementes durante a estação chuvosa, enquanto E. fusca contribui para a estação seca. Há necessidade de aprofundar o conhecimento da fenologia vegetal no Pantanal e essas informações devem ser levadas em consideração nas unidades de conservação para o manejo.

Palavras-chave: Fenologia vegetal; Plantas ribeirinhas; Dinâmica da água; Zonas úmidas.

Topic: **Conservação da Biodiversidade**

Reviewed anonymously in the process of blind peer.

Received: **02/07/2022**
Approved: **26/07/2022**

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DOI: 10.6008/CBPC2179-6858.2022.007.0003

Referencing this:
FURLAN, A. O.; MUNIZ, C. C.; OLIVEIRA JUNIOR, E. S.; LÁZARO, W. L.; CAMPOS, D. V. S.; CARNIELLO, M. A.. Phenology of five plant species with potential for fruit resources in the Pantanal. **Revista Ibero Americana de Ciências Ambientais**, v.13, n.7, p.27-39, 2022. DOI: http://doi.org/10.6008/CBPC2179-6858.2022.007.0003

INTRODUCTION

The Pantanal is considered as the largest continuous humid area in the world (CUNHA et al., 2015), being very important for the conservation of species and ecological services (RESENDE, 2008; ALHO et al., 2019), such as the preservation of water resources, fauna, and flora. Its extensive wetland is marked by periods of drought and flood, that are regulated by the annual flood pulse (LÁZARO et al., 2020). This promotes marked changes in the aquatic and terrestrial habitats of this biome (JUNK et al., 2014).

Large rivers as Paraguay, with a great floodplain, have high potential for fisheries production, since these areas constitute environments where fish find food and shelter. In the Pantanal, there are approximately 270 species of fish, which, in addition to their socio-economic role, are ecologically important actors (CATELLA et al., 2001; BRITSKI et al., 2007). Environments that are affected by temporary floods lead to peculiarities among the individuals inhabiting them because of the need to develop strategies for adaptation and tolerance to environmental changes (NASCIMENTO, 2001; FERREIRA JUNIOR et al., 2016). Studies performed by Junk et al. (1999), Maia (2001) and Anderson et al. (2011), reveal close ecological relationship between plant species and frugivorous fish from flooded areas suggesting the coevolution of some plant species and fish (CORREA et al., 2007; CORREA et al., 2015). Recent studies showed a straight relationship between plant phenology, river water level and seed dispersal by fish (DANTAS et al., 2021). These authors suggest that the flooding is a start point when the tree is stimulated to bear fruits, which are significantly dispersed by different fish species.

The knowledge about the supply of fruits in the diet of fauna throughout the year constitutes a relevant contribution to understand the dynamics, maintenance, and conservation of forest formations (BENCKE et al., 2002a; STEVENSON, 2011; FERREIRA et al., 2011). Riparian forests are of high importance for the maintenance of the fish community, being benefited by the better water quality and the food they offer, not only the food-web (PUSEY et al., 2003; CASATTI et al., 2012; KUPLIAS et al., 2021), but also the elements from the plants itself (fruits, flowers, leaves, etc. e.g. Reys et al. (2009)).

Although most of the studies relating plant-fish interactions show diets based on fruit consumption (e.g. REYS et al., 2009; PEREIRA et al., 2011; PEREIRA, 2017), also flowers are part of the diet of many of the tropical freshwater fish (OLIVEIRA et al., 2013; MONTAÑA et al., 2013; OLIVEIRA et al., 2014), highlighting the importance of studies showing the entire phenology of riparian trees. Phenological studies show relationship with the plants and the environmental conditions, such as temperature, humidity, displaying that the species phenology can be further than an endogenous condition, where the environment act as a start point for the plant development (AZEVEDO et al., 2014). In fact, the plant phenology may be related to changes in environmental conditions such as water level, and the duration of water in the system, precipitation (FERREIRA et al., 2007; SCHÖNGART et al., 2002; WITTMAN et al., 1999), on which the plant may produce flowers or fruits (CASCAES et al., 2012). The period and quantity of fruit production is not the same for all tree species, depending on the environmental characteristics and the neighbouring to bear fruit (MINOR et al., 2019; COSTA et al., 2021). Moreover, each species responds differently to the environmental conditions, where some species may flower or fruit first than others, even belonging to the same genus (CASCAES et al., 2012). Water level in riparian forest seems to be an important variable to be considered for the phenophase analysis, not only during the growing phase (MOUNGSRIMUANGDEE et al., 2017), but also during the flowering and fruiting period (FERREIRA et al., 2007).

The high-water level promotes the entry of fish into the flooded areas, favoring fruit feeding strategies (MAIA, 2001). There is a straight relationship between plant phenology and fish in the Pantanal, which is widely known by local communities (MORAIS et al., 2010). Furthermore, studies carried out in the northern Pantanal demonstrate that there is an exclusivity in the diet of *Piaractus mesopotamicus* and *Brycon hilarii* for food resources coming from the vegetation of the flood area (MUNIZ et al., 2014; FURLAN et al., 2017; BERTOLINO et al., 2021). Thus, it is believed that there is a close relationship between the phenology of vegetation in the Pantanal and the seasonality of this biome, and the potential supply of fruits to the ichthyofauna. Thus, we analyse the reproductive phenology of plant species widely present in the Pantanal environment and relate their potential for food supply for fish fauna.

MATERIALS AND METHODS

Study area

The study was carried out at the Taiamã Ecological Station (hereafter, TES), a conservation unit located in the Pantanal of Brazil on the border strip with Bolivia, and 180 km away from the urban perimeter. The TES has an area of 11,200 ha and covers the islands of Taiamã and Sararé, which are delimited by the bifurcation of the Paraguay and Bracinho rivers (Figure 1).

The study area has four well-defined hydrological periods (drought, flooding, full flood, and ebb) which is clearly related to the amount of rainfall that can reach 500 mm in January (month with more rainfall) to 0 mm in August (month with less rainfall; see Lázaro et al. (2020)). This region has an average annual temperature of 26 °C and higher temperatures during the wet period (NEVES et al., 2011).

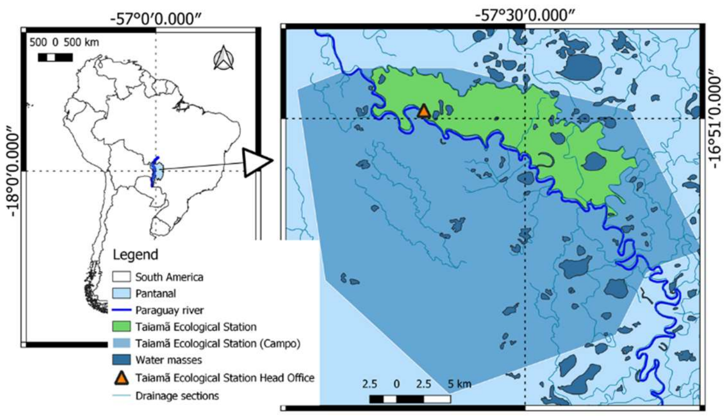

Figure 1: Taiamã Ecological Station located in the Paraguay river - northern Pantanal.

Data sampling

Phenological observations of the vegetation were undertaken on the right side of the TES island, over

12 km of river for vegetation monitoring, with individuals selected from the right and left banks of the Paraguay River. Five native fruit plant species were selected: three arboreal species and two palm trees, *Erythrina fusca* Lour., established in a monospecific forest environment, *Inga vera* (DC.) Penn., *Spondias mombin* L. (Figure 2), and *Bactris brongniartii* Mart., in a polyspecific forest; and *Bactris riparia* Mart. in a polyspecific swamp, as proposed by Cunha et al. (2015)[1].

The meteorological data of rainfall and air temperature were obtained from the Aqua Satellite for the meridians 57° 24′ W and 45° 40′ W and parallels 16° 48′ S and 16° 58′ S, following the location of the TES. Data on the level of the Paraguay River was obtained from the Port Authority in the city of Cáceres.

Figure 2: Studied species showing the flowering and fruiting. From the left to the right - *Erythrina fusca* Lour., *Inga vera* (DC.) Penn., *Spondias mombin* L., *Bactris riparia* Mart and *Bactris brongniartii* Mart. Source: Muniz et al. (2020)[2].

Phenology of species

Phenological monitoring was carried out monthly from September 2014 to September 2015. The main river channel in the right portion of the TES was used to establish the observation points, following the order of sighting of the specimens. Observations were made from boat using binoculars (10mm × 42 mm). Twenty-five individuals of each species were monitored, following the methodological recommendations of Morellato et al. (2010), except for *B. riparia*, of which only 15 individuals were monitored due to unfavourable access conditions. The specimens were sampled up to 15 m from the river bank, excluding individuals covered by lianas and in a compromised phytosanitary condition.

The phenophases were analysed were flowering (flower buds and flowers at anthesis) and fruiting (unripe and ripe fruits). The intensity of phenological events was individually estimated using the intensity index developed by Fournier (1974), characterised by a semi-quantitative scale of five categories (0 to 4), defined by an interval of 25% between the phenophases. In each month, the intensity values obtained for all individuals of each species were added and divided by the maximum possible value (number of individuals multiplied by four). The value obtained was then multiplied by 100 to convert it into a percentage.

The activity index was also obtained, which, according to Bencke et al. (2002a), is complementary to the intensity index facilitating the analysis and interpretation of phenological behaviour and helps to understand the animal-plant interactions by information regarding the synchrony. Phenological events were considered asynchronous when < 20 % of individuals were in the phenophase, with little or low synchrony if

[1] see more information about the plant species in http://floradobrasil.jbrj.gov.br/
[2] http://www.bichosdopantanal.org/wp-content/uploads/2020/11/Livro-Peixes-e-Plantas.pdf

20 % - 60 % of individuals were in the phenophase, and as highly synchronous when > 60 % of individuals were in the phenophase according to Bencke et al. (2002b).

Fruit resources

The production of fruits of the species *S. mombin* and *E. fusca* was evaluated by "crown count", which consists of counting or estimating the number of fruits in each specimen (GALETTI et al., 2006). For this study, the average production was estimated by counting the number of fruits per branch and multiplying by the average number of branches. For palm trees, the number of fruits per infructescence was counted and multiplied by the average number of infructescence and stipe per individual sampled. Fruit production was not estimated for *I. vera* because of the irregularity of the crown, for which this method could not be applied. As fruit production occurred when the sample sites were completely flooded, it was impossible to use fruit collectors.

With the estimated number of fruit production for species and the identification of the monthly fruiting intensity, it was possible to calculate the fruit production for the dry and flood seasons.

Statistical analysis

The relationship between the phenophases of the species and the environmental variables (rainfall, temperature, and river level) were analysed using Pearson's correlation (r). Linear regressions were performed after the identification of significant correlations ($P < 0.01$) between plant species and environmental variables. All data were analysed using R software (R Development Core Team, 2015).

RESULTS

Rainfall varied from only 9.26 mm in June/2015 to 220.36 mm in January/2015, which reflected to the water level from the Paraguay river, which reached the lowest level in September/2015 (1m), and the highest in March/2015 (4.60m). The lowest temperature was 27.69 °C in May and 37.83 °C in October. A significant relationship between water level from the river and rainfall was found (simple linear regression: $R^2 = 0.20$; $P < 0.01$), and with the temperature (simple linear regression; $R^2 = 0.44$; $P < 0.05$; Figure 3).

The flower buds were present from September to November 2014, with higher values recorded in October and recurrence in 2015 from July to September. For both the species, this phenological event showed a negative correlation with the river level ($r = -0.69$ and $r = -0.75$, respectively for the two species, and $P < 0.05$). The first anthesis was recorded for *S. mombin* in September 2014 and extended to January 2015, and for *I. vera* from September 2014 to February 2015, and was recorded again from June 2015, influenced mainly by the increase in temperature ($r = 0.74$ and $r = 0.86$, respectively for the two species, and $P < 0.05$).

In this study, the rainfall was shown to be correlated with the presence of unripe fruits of *S. mombin* ($r = 0.79$; $P < 0.001$) and *I. vera* ($r = 0.67$; $P < 0.05$). These events were registered in the months of October 2014 to April 2015. The beginning of the production of ripe fruits was from February 2015 to April 2015 for

S. mombin, whereas the production for *I. vera* was observed in February and March 2015. The high waters of the Pantanal positively influenced the appearance of ripe fruits (r = 0.65 and r = 0.60, for the two species respectively, and P <0.05).

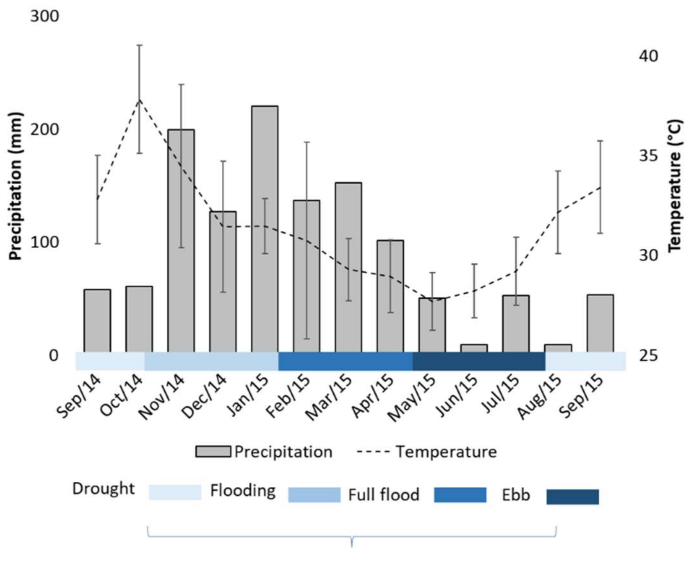

Figure 3: Monthly rainfall sum and monthly mean temperature for the studied period (Sep/2014 to Sep/2015) in the Taiamã Ecological Station. Bars denote SD.

The species *E. fusca*, on the other hand, presented completely different phenological patterns, with peak production of unripe and ripe fruits related to the increase in temperature (r = 0.67 and 0.64, respectively for the two phenophases, and P < 0.05), although the presence of unripe fruits was negatively correlated with the river level (r = −79; P < 0.05). It was estimated that the individuals of *E. fusca* produced 3,343 fruits each, with the month of December having the highest intensity and activity (high synchronicity of 96 %). Moreover, *Erythrina fusca* presented flower bud and anthesis from June to August 2015, the driest months recorded in the study. These phenophases showed no correlation with the precipitation indices (r = −0.36. P < 0.05) and (r = −0.45. P < 0.05) flower bud and anthesis respectively. There was also no relationship between the presence of floral bud and river level (r = −0.13. P < 0.05), the same for anthesis (r = −0.31. P < 0.05). While *E. fusca* blooms only for two months of the year, the tree species *S. mombin* and *I. vera* bloomed during the ebb, drought, and flooding seasons (from May to December; Figure 4).

The flowering of *B. brongniartii* and *B. riparia* occurred with greater intensity in the dry period, during which the flowering buds were observed from September 2014 to January 2015. The anthesis of these species appeared exactly for the same period but differed in that the anthesis of *B. riparia* was positively related to the temperature (r = 0.69; P < 0.05), while the increase in river level had a negative influence on this phenophase (r = 0.62; P < 0.05). The peak intensity occurred in December 2014, while ripe fruits occurred from December 2014 to August 2015, with a peak of fruiting in February 2015. The ripe fruits of *B. riparia* and *B. brongniartii* appeared when the level of the Paraguay River was high (r = 0.67 and r = 0.60, respectively for the two species, and P < 0.05; Figure 5).

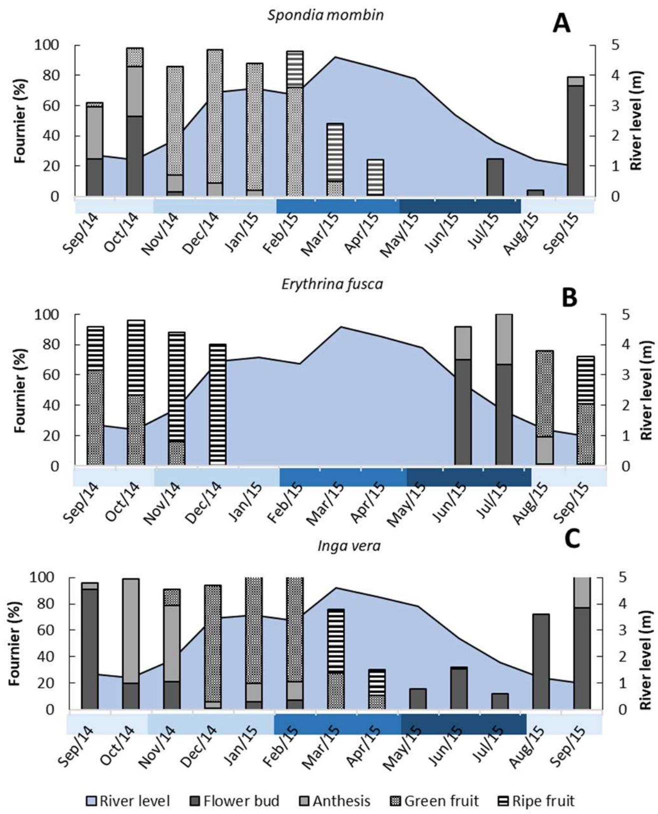

Figure 4: Phenology of tree species regarding the level of the Paraguay river, *(***A**) *Spondia mombin* L*.,* (**B**) *Erythrina fusca* Lour., (**C**) *Inga vera* Willd.

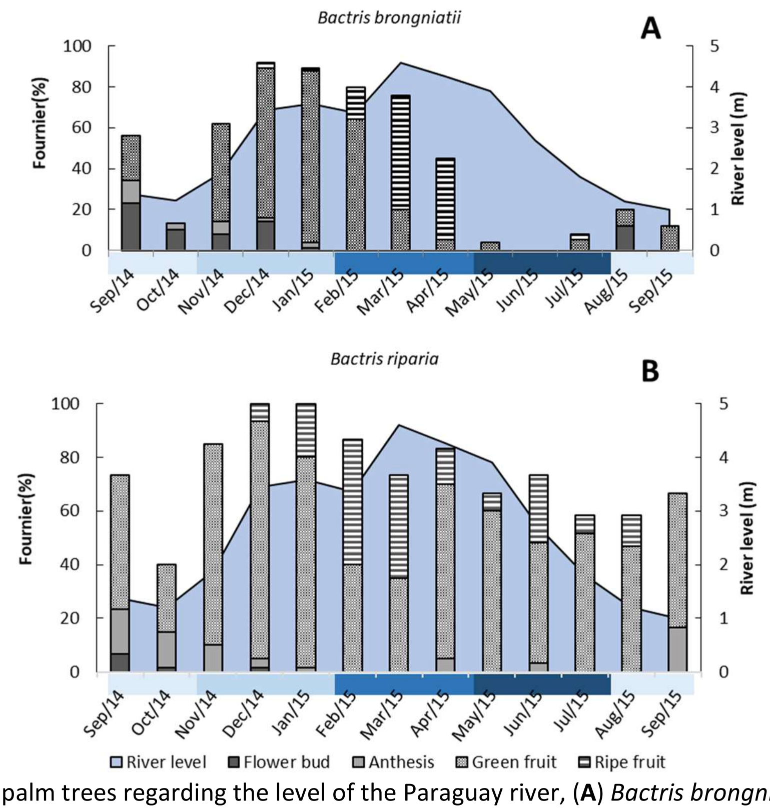

Figure 5: Phenology of palm trees regarding the level of the Paraguay river, (**A**) *Bactris brongniartii* Mart., e (**B**) *Bactris riparia* Mart.

Bactris brongniartii developed floral buds from September 2014 to January 2015 and the anthesis was recorded in the same period. Neither phenophase showed a significant correlation with rainfall and river level. Unripe fruits were recorded from September 2014 to September 2015 and ripe fruits were recorded from December/ 2014 to April/ 2015 with peak intensity in March, the month with the highest level recorded for the Paraguay River during the study period. The synchrony was high among individuals in March (76%), a period of greater fruiting activity. The fruit production for *B. brongniartii* was estimated to be approximately 8,930 fruits per individual.

In parallel with the correlation results for unripe and ripe fruits of the species *S. mombin*, *I. vera*, *B. riparia*, and *B. brongniartii* with temperature, rainfall, and river level, a general linear model was applied to better represent this relationship. It was possible to identify a rise in the number of ripe fruits with an increase in the level of the river, except for *E. fusca* (Figure 6).

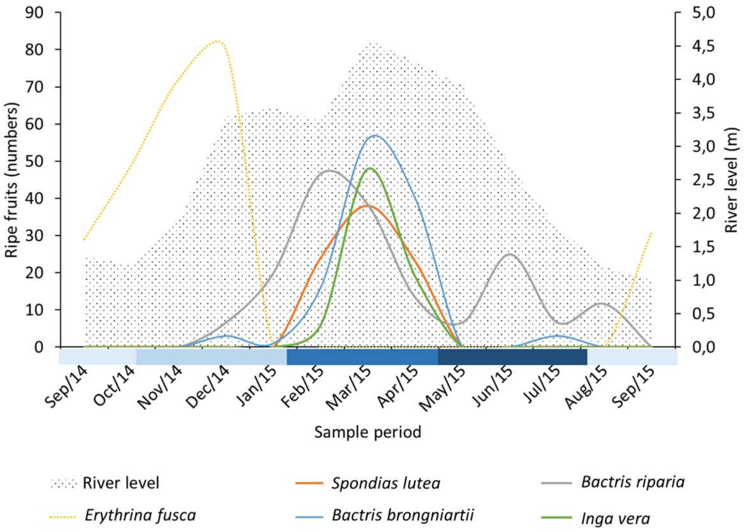

Figure 6: Relationship between the number of ripe fruits of the studied species and the level of the Paraguay river.

A CCA summarizes our findings, highlighting the effect of the water (rainfall and river level) and temperature in the riparian plant species analyzed (Figure 7). The results show the opposition between the ripe fruits and unripe fruits of all the species, while the flooding season favors the unripe fruits, the full flood the ripe fruits are present. *Erythrina fusca* is the only species that is related to the low temperature during the drought, presenting the unripe and ripe fruits related to this season.

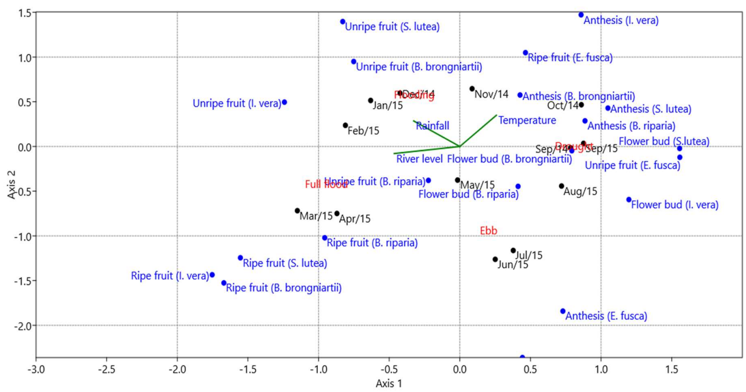

Figure 7: CCA for all the variables and the five different plant species phenophases. Axis 1 corresponded to 70.11% (Eingenvalue = 0.46) and Axis 2 to 29.78% (Eigenvalue (0.19) of the analysis. All the values were accreted to 1 to avoid zero values.

DISCUSSION

Our results showed species flowering and fruiting in the driest months, which may be related to the characteristics of the dehiscent dried fruit, with autochoric potential and spontaneous release of seeds in the soil. However, it was observed that the peak of fruiting occurred at the beginning of the flooding. The flowering of the species occurred in the transition from the dry to the rainy season, this result corresponds to the data obtained by Salis et al. (2009) for swampland plants whose flowering occurred mainly in spring (September to December), except for *E.fusca*, the only one that did not have this characteristic, whose flowering occurred in the driest months during this study (June to August/2015). Specifically for flowering in tropical palm trees, Jardim et al. (1994) point out the occurrence in both the dry and rainy seasons. This may depend on the characteristics of each taxonomic group. However, Damasceno et al. (2015), studying the same genus here studied, observed flowering in the rainy season for *Bactris bidentula* and *B. glaucescens*, while in this study the flowering of the two Bactris occurred with greater intensity in the dry season.

The tree species *S. mombin* and *I. vera* showed flowering patterns according to the data obtained by Salis et al. (2009) for plants in the southern Pantanal, whose flowering occurred mainly in the spring (September to December). This relationship between flowering and temperature is expected for tropical species, as reported in phenology studies carried out in other environments (e.g., MORELLATO et al., 1992; BENCKE et al., 2002b; MARTINI et al., 2010).

The pattern of flowering and fruiting in tropical plants has been attributed to biotic and abiotic factors, and the oscillation of rains may be the most significant climatic factor in the phenology of flowering and fruiting (MORELLATO et al., 1992; MARTINI et al., 2010). Rodrigues et al. (1993) suggested three distinct patterns of fruit ripening related to dispersion syndromes: (a) presence of immature fruits for an extended period, with ripening varying within and between individuals; (b) presence of immature fruits for an extended period, but with rapid and simultaneous maturation in the same individual; and (c) abundant fruit production, simultaneous ripening within the same individual, and short intervals between reproductive periods. From this perspective, *S. mombin* and *I. vera* can be classified in the second pattern, since following a long period of unripe fruit generation, ripe fruits were registered only in the period when the river level was high, during flooding at all points sampled. The degree of synchronism in the individuals of *S. mombin* with ripe fruits was considered low (48%) in February, the month of greatest activity. An evaluation of the production of fruits yielded approximately 2,457 fruits per individual. Among the fruited specimens of *I. vera*, the month of greatest activity had a high degree of synchronism (72%).

The results, for both palms and trees, correspond to the reports of Kubitzki et al. (1994) and Junk et al. (1999) regarding the fruiting of plant species in humid areas, occurring during the period in which they are flooded. This period favours the dispersion of its seeds by hydrocoria or ichthyocoria. These results are indicated by both the intensity and activity indices of *S. mombin*, *I. vera*, *B. riparia*, and *B. brongniartii*, in which the fruiting period started in the wet season, with the peak of ripe fruit production from January to March 2015, concomitant with the highest levels recorded for the Paraguay River.

The fruiting of *B. riparia* and *B. brongniartii* are in accordance with the first pattern according to Rodrigues et al. (1993), as they presented unripe and ripe fruits for a long period, and unripe fruits were observed during all months of study for *B. riparia*, except for October 2014 for *B. brongniartii*. This suggests that the exposure time is long for dispersers, which may favour the dispersion of seeds by fish, for example Muniz et al. (2014), Maia (2001) and Goulding et al. (2000) reported the importance of species that produce food resources for fish from flooded areas, since they are closely linked to fisheries production with the supply of fruits provided by vegetation. As reported by Van der Pijl (1982), the fruits or seeds of falling autochoric species can be secondarily dispersed by animals. Thus, it is suggested that seeds of *E. fusca* are carried by hydrocoria or small fish; the water depth allows lateral displacement to the river channel, since the seeds of this plant species have been described as one of the most important food resources for *Brycon hilarii* (FURLAN et al., 2017; BERTOLINO et al., 2021).

Maia (2001) suggested that species identified in fish feeding should be used as important elements of environmental recovery in humid areas, as they complement the vegetation and restore the food supply to ichthyofauna and other animals. Janzen (1974) previously pointed out the importance of the loss of interactions in tropical regions, and authors such as Jordano et al. (2006), Galleti et al. (2006) and Tabarelli et al. (2010) state that it is important to understand these relationships for the conservation of biodiversity.

Muniz et al. (2014), Reys et al. (2005) and Carmo et al. (2001) discussed the importance of furthering such studies to understand the dynamics of populations and the management and recovery of riparian ecosystems. Furthermore, studies relating the interactions of the biota increase the understanding of the existing networks in the landscape, favouring the development of actions for the conservation of native species in suitable areas and conditions, landscape projects, or commercial exploitation (MORELLATO, 2007). However, only with an understanding of the ecological processes responsible for productivity and biodiversity that exist in the floodplain of the Pantanal, is it possible to use them sustainably (RESENDE, 2008). This is particularly important since threats, such as deforestation and inadequate land management for agriculture and livestock, are significantly impacting its waters (PETRY et al., 2012).

CONCLUSIONS

Our study exposes the need to conserve the flood areas so that, consequently, there is protection of the fishing resource in the Pantanal in terms of the nutritional potential of other species. Thus, attention is needed in the elaboration of public policies for the conservation and management of this ecosystem, without isolating the elements that make up the interactions of the aquatic and terrestrial environments of the Pantanal.

Our results point out the concern regarding the synchronicity of this ecosystem service (provision) are raised regarding the hydrology changes that the Pantanal has been suffering, due to climate change and direct human alterations. The decrease in the amplitude and duration of flood pulses can also alter the phenological relationships of the species, as described here, with consequences for the fauna. Also, the possible entry of agricultural plantation areas in the Pantanal plain region may alter or decrease the supply of pollinators, which would also lead to a decrease in the supply of fruits and flowers to the fish community.

Finally, this research was conducted prior to the intense wildfires in the Pantanal that occurred in 2019 and 2020 and serves as important documentation of the vegetation in the Taiamã Ecological Station, which was severely damaged by the fire. We do not yet know the extent of damage caused by the fires, and how it altered or reduced the supply of fruits and flowers of the species under study. Further clarifications should be made in this regard, with the phenological monitoring of specimens already documented by this research.

ACKNOWLEDGEMENTS

We would like to thank the Chico Mendes Institute for Biodiversity Conservation (ICMBio). We also thank the team of the ichthyology laboratory of the North Pantanal (LIPAN), botany laboratory, and Herbarium of the Pantanal (HPAN). The team of the SojaMaps extension project at the State University of Mato Grosso was also important in understanding the ecosystem.

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