



## REPRODUCTIVE PHENOLOGY OF MACROPHYTE COMMUNITY IN RESPONSE TO WETLAND FLOODING CYCLE

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**Abstract:** The phenology of macrophytes in response to environmental stressing factors is easily evidenced in wetlands under seasonal floods, such as the Pantanal. In these environments, the survival and establishment of seedlings of aquatic plants are restricted, limited to episodes with the presence of water, resulting in posterior sexual propagation for dispersal of seeds adapted to hydrochory, overcoming the dry period dormant in the sediment. We described the reproductive phenology of the macrophyte community in relation to the phases of flooding and between the species life forms. We sampled monthly the phenology of the macrophyte community of twenty ponds in the Pantanal, during two years, during the four phases of the flood pulse: 'drought', 'rising', 'flood' and 'receding'. The peak of flowering and fruiting in species of community occurred at the begin of rising, under the influence of the water depth variation on flowering. The species with different life forms develop flowers and fruits in the phases with water (flooded). Amphibious species present wider phenological amplitude, flowering also in the drought phase. There is a correlation between the species flowering in the community and the water depth in the ponds, not observed when considering the life forms of the species. There is a correlation between flowering of amphibious plants and temperature, and rainfall; and a correlation between flowering rooted floating plants and temperature. The macrophyte community presents phenology associated to seasonal alterations of the flooding cycle, such as the presence and depth of water, by means of the diversified life histories and life forms, determining the dynamics, resistance and resilience of this flora in the Pantanal.

**Keywords:** aquatic plants; floodplain; flowering; fruiting; Pantanal; sexual propagation.

### INTRODUCTION

Among the abiotic factors, water stress exerts the major role on the phenology of tropical plants (Van Schaik *et al.* 1993, Armstrong *et al.* 1994). The phenological reaction in response to environmental stressing factors (Schat & Van Beckhoven 1991, Haugaasen & Peres 2005) is easily evidenced in wetlands under seasonal floods (Junk & Piedade 1997, Thomaz *et al.* 2007). In the Pantanal, the water regime strongly influences the phenology of the vegetation (Grace 1989, Maia & Piedade

2000, Nunes-da-Cunha & Junk 2001, Bertazzoni & Damasceno-Júnior 2011, Fava *et al.* 2011, Marestoni 2011, Catian *et al.* 2017, Uriu *et al.* 2017), organizing mainly the macrophyte community by function of seasonal flood (Prado *et al.* 1994, Gratani 2014, Ortega *et al.* 2015, Catian *et al.* 2018).

In these environments, the establishment and survival of seedlings is restricted, limited to short episodes of favourable conditions (Eriksson & Fröborg 1996, Coelho *et al.* 2008), *i.e.*, in periods with water (Catian *et al.* 2017), resulting in posterior sexual propagation for dispersal of seeds

adapted to hydrochory, overcoming the dry period dormant in the sediment (Junk 1980, Coelho *et al.* 2005). Crawford (1992) mentioned the importance of the tolerance and response of the communities to different environmental conditions, resulting in changes in spatiotemporal distribution and composition of the species, what often reflects in the propagation strategy. In addition to the terrestrial vegetation (Silva *et al.* 2000), the Pantanal plain is constituted by aquatic vegetation in the permanent and temporary ponds, bays, seasonal streams and old riverbeds (Almeida & Lima 1959, Almeida *et al.* 2003), water bodies subjected to depth fluctuations between flooding phases.

Since the phenology encompasses the periodical variations in the life cycle of the populations, resultant from the selective pressure under the environmental conditions (Lieth & Schultz 1976, Almeida & Alves 2000), the study of phenological patterns of the aquatic macrophytes aggregates information for the understanding of their temporal biology over the flood cycle of the Pantanal. The annual flood pulse of the Pantanal encompasses floods and droughts (Abdon *et al.* 1998), of short or long duration, with great or small amplitude (Junk *et al.* 1989), and is divided into four well defined phases: *drought* (water in the riverbed and dry floodplain), *rising* (the riverbed overflows toward the floodplain), *flood* (peak of flood on the floodplain) and *receding* (water drawdown from the floodplain to the riverbed) (Prado *et al.* 1994). Little has yet been discussed upon the relation of the phenology of macrophytes in response to the different flood phases (Bertazzoni & Damasceno-Júnior 2011, Catian *et al.* 2017). In addition, there is considerable interest in the conservation of wetlands since changes in water regime threaten the maintenance of the diversity of the aquatic ecosystems.

Due to the annuality of the flood cycle in the Pantanal, the community of macrophytes adjusted its development to the water level fluctuation (Pott *et al.* 1989, Pott & Pott 1994, Rebellato & Nunes-da-Cunha 2005, Catian *et al.* 2018). Various studies (*e.g.*, Junk & Piedade 1993, Piedade *et al.* 1994, Penha *et al.* 1999, Catian *et al.* 2017, 2018) observed a synchronism between the phenology of aquatic macrophytes and depth variation, possibly due to the adaptations to the flood-and-dry cycles. Therefore, we described the phenology of the

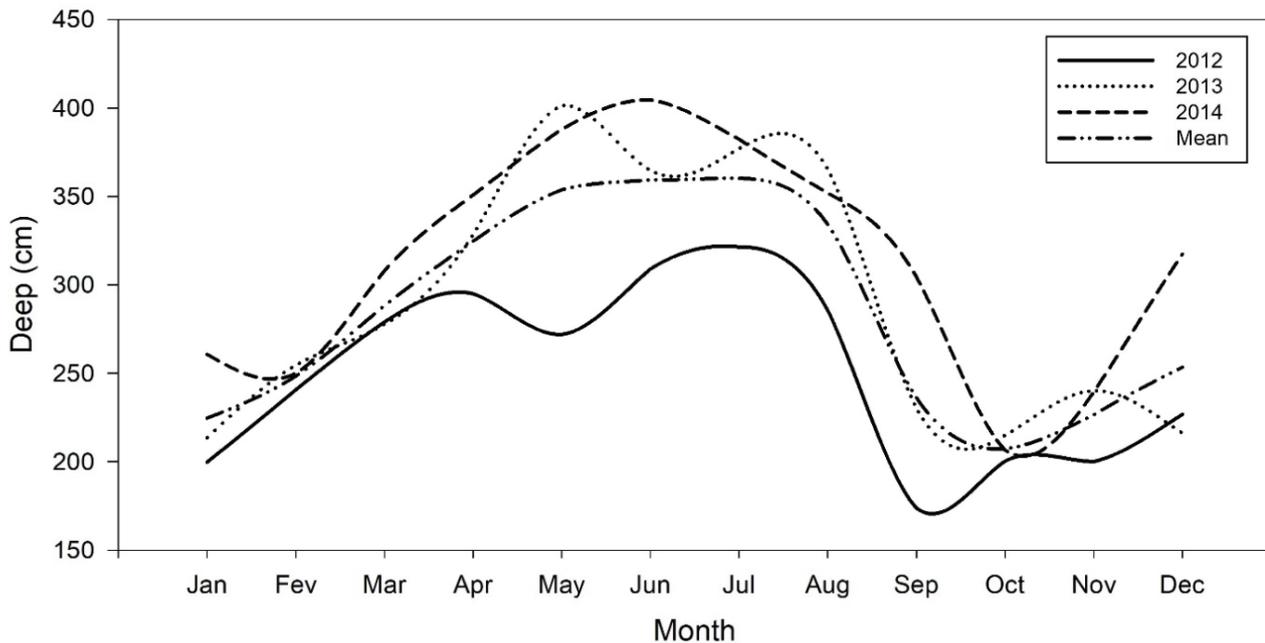
community of macrophytes and the life forms of the species in relation to the flood cycle in the Pantanal, analysing the phenophases of flowering and fructification between the phases of the flood pulse (*drought, rising, flood* and *receding*).

## MATERIAL AND METHODS

In the northern part of the Pantanal, the flood of the Paraguay river occurs from January to March, moving south in April-June, caused mainly by overflow of the riverbed and not by local rainfall – peaks of floods produced by the discharge of the river in the South occur four months after the peaks of rainfall on the headwaters (Hamilton *et al.* 1996). The study area is not under the direct influence of the Paraguay River, but of its affluents Miranda and Negro and in years of higher flood the seasonal stream Corixinha. The main river near the study area is Miranda and its fluvioigram (Figure 1). Climate: Aw (tropical subhumid – Peel *et al.* 2007) – dry winters and rainy summers, mean annual rainfall concentrated between November and April (1,000 to 1,200 mm) (Soriano *et al.* 2001).

The study was carried out for two years, from November (2012) to September (2014), when we collected monthly in 20 ponds near the Estrada Parque (19°24'21.89" S, 57°01'44.57" W, datum SAD69 and 19°14'45.14" S, 57°02'18.00" W, datum SAD69), in the Pantanal, subregions Abobral and Nhecolândia (Silva & Abdon 1998), municipality of Corumbá, Mato Grosso do Sul State, Brazil. We considered the four phases of the flooding cycle: *drought* (November/2012 to January/2013; November/2013 to March/2014); *rising* (February and March/2013; April to May/2014); *flood* (April to July/2013; June and July/2014); and *receding* (August to October/2013; August to October/2014).

Information on climate was obtained from the Centro de Monitoramento de Tempo, do Clima e dos Recursos Hídricos de Mato Grosso do Sul (CEMTEC MS). For the collected period the average temperature was 26.07°C, the coolest in August 2013 (17.1°C minimum) and the warmest in October 2014 (34.73°C maximum), both in *receding* inundation phase. In both years, an accumulated rainfall of 2,484 mm was recorded with lowest rainfall (1.6 mm) in August 2013, in the *receding* inundation phase, and the highest rainfall (300.4 mm) in May 2014, *flood* inundation phase. The



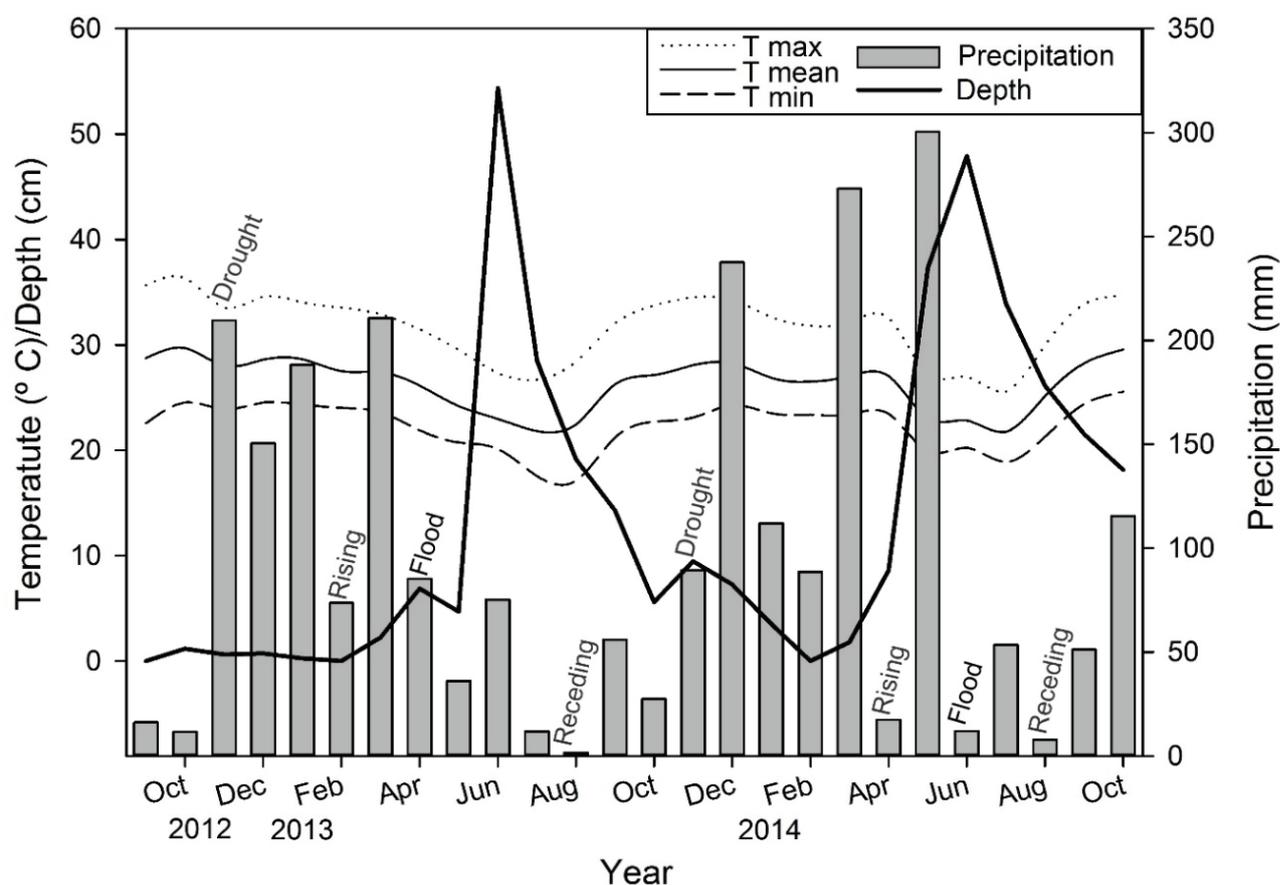
**Figure 1.** Fluviogram of the Miranda river based on data collected (2012-2014) daily at the research station Base de Pesquisa do Pantanal – Universidade Federal de Mato Grosso do Sul, municipality of Corumbá, Mato Grosso do Sul State, Brazil.

first year of sampling (2012-2013) with an average temperature of 25.9°C, the warmest month in December (34.6°C), *drought* inundation phase and coolest month in August (17.1°C), beginning of *receding* inundation phase. Annual accumulated rainfall of 1125.8 mm, with the highest rainfall in March (210.8 mm), at *rising* inundation phase and lowest rainfall in August (1.6 mm), begin of *receding* inundation phase. The second year of sampling (2013-2014), the average recorded temperature was 26.2°C with the warmest month in October (34.7°C), *receding* inundation phase and coolest month in July (18.9°C), end of the *flood* inundation phase. Annual accumulated rainfall of 1358.2 mm, with the highest rainfall in May (300.4 mm), end of *rising* inundation phase and lowest rainfall in June (1.6 mm), beginning of *rising* inundation phase (Figure 2). The phases were considered in relation to the water level in the ponds, not straightly rainfall, the reason why in November/2012 the pond depth was still at the *drought* phase, despite the rainy season had started because the low water table had to be replenished. A similar lag occurs at the end of the rainy season when the ponds are yet filled. The water table fluctuation and the pond depth are influenced by the accumulated rainfall of the previous year or years.

### Phenology

For the phenology, we considered the plant communities of the ponds, sampling phenological data (flowering and fruiting) (Morellato *et al.* 2010) of different individuals for two years. Each pond was divided into 26 plots, which were sampled monthly, without resample of the plots, utilizing 0.5 x 0.5 m quadrats of PVC pipe, placed every 2 m, from the margin to the centre, the number of quadrats being relative to the distribution of the stand of macrophytes on the margin and within the pond. Water depth was measured monthly in each plot (Figure 2).

We utilized the quantitative (presence or absence) method (Bencke & Morellato 2002a, D'Eça-Neves & Morellato 2004), recording the fundamental units of the reproductive phenology (number of flowers/buds and ripe/immature fruits) per month in each individual of each species per plot. The plants were not labelled, sampling different individuals every month, to better assess the populational variation. The macrophyte life forms were classified according to Irgang *et al.* (1984). The taxonomic classification followed the Angiosperm Phylogeny Group (APG IV 2016) and the scientific nomenclature was updated by the Lista de Espécies da Flora do Brasil (REFLORA).



**Figure 2.** Climatic data in the study period from September/2012 to September/2014 in municipality of Corumbá, Mato Grosso do Sul State, Brazil (Source: Inmet/Seprotur/Agraer/Cemtec-MS) and water depth measured in the studied ponds. Year 1. 2012 – 2013 = Nov 2012 – Jan 2013; Feb – Mar 2013; Apr – Jul 2013; Aug – Nov 2013. Year 2. 2013 – 2014 = Dec 2013 – Mar 2014; Abr – May 2014; Jun – Jul; Aug – Oct 2014. Source of the graph: Catian *et al.* (2017).

For plant identification, we utilized Pott & Pott (1994) and Pott & Pott (2000) and for species author abbreviations, Brummitt & Powell (1992). Vouchers were incorporated into the Herbarium CGMS of UFMS (Appendix 1).

### Analyses

The description of the phenology of the plant community and of the life forms most representative of the species was tested applying Rayleigh's ( $Z$ ) for circular distribution (Morellato *et al.* 1989, Zar 2010), calculating the means of the dates for the frequency of species in flower or fruit, and the concentration of each event around that date (synchrony  $r$ ) (Morellato *et al.* 2000),  $Z$  being the reproductive probability (flower and fruit) uniformly over the year (flooding phases). If the mean of the angle is significant ( $p < 0.05$ ), the pattern is considered seasonal, corresponding to the mean date of the year around which the

phenological events are concentrated (Morellato *et al.* 2000, 2010). In our work, it indicates the production of flowers and fruits in the flooding phases. We plotted the distributions of frequencies of flowers and fruits in each phenophase, in monthly intervals, in circular histograms, the 365 days of the year corresponding to the  $360^\circ$  of the circumference. Vector length relates to the value of the coefficient of concentration ( $r$ ), varying from 0 to 1, and the angle where this is drawn indicates the mean angle, that corresponds to the mean date of occurrence of the phenophase, *i.e.*, the concentration of the production of flowers and fruits around the mean annual date or degree of seasonality of the phenophase (Morellato *et al.* 2000, 2010). Calculations were performed utilizing the software Oriana 2.0 (Kovach 2004). The intensity of synchrony of flowering and fructification was determined by the scale: values equal to 0 indicate absence of synchrony; 0.1 to 0.27 indicate minimum

synchrony; 0.28 to 0.45 indicate low synchrony; 0.46 to 0.69 indicate medium synchrony; 0.70 to 0.99 indicate high synchrony, and values equal to 1 indicate perfect synchrony (Augsburger 1983).

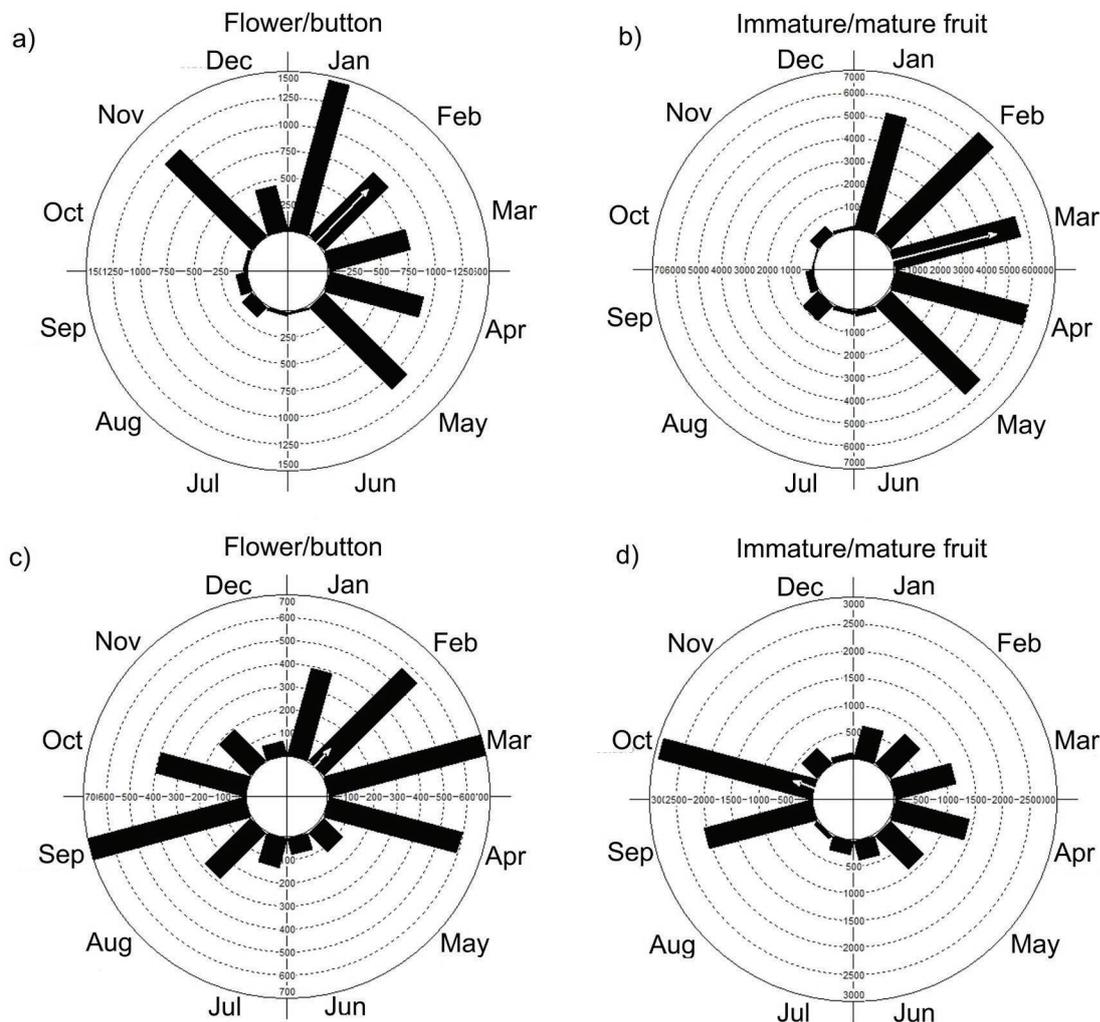
To verify if the frequency of flowers and fruits of the community (for each pond) and frequency of flowers and fruits of the species for life forms in a certain phenophase responds proportionally to the climatic seasonality, the degree of synchrony of each species in the flooding phases was calculated applying the proportion of flowers and fruits shown in certain phenophases in the four flooding phases, as suggested by Bencke & Morellato (2002a,b): asynchronous (< 20% of individuals exhibiting the phenophase); little synchrony/low synchrony

(20-60%); or high synchrony (> 60%). To evaluate the correlation between abiotic variables (depth, temperature and rainfall) and each phenological event, we utilized the correlation of Pearson (Zar 2010).

## RESULTS

### *Phenology of the community of aquatic macrophytes between flooding phases*

Seasonal flowering and fructification in the first year, flowering at the beginning of *rising*, with medium synchronism, and fructification at *rising* (Figure 3a-b), with medium synchrony (Table 1). However, in the second year, although both phenophases were seasonal, flowering occurred



**Figure 3.** Circular histogram of the community of macrophytes with the number of flowers/buds (a, c) and immature/ripe fruits (b, d) over two annual flooding cycles (2012 - 2014) in ponds of the Pantanal, municipality of Corumbá, Mato Grosso do Sul State, Brazil. Year 1. a and b (2012 – 2013) = Nov 2012 – Jan 2013 (*drought*); Feb – Mar 2013 (*rising*); Apr – Jul 2013 (*flood*); Aug – Nov 2013 (*receding*). Year 2. c and d = 2013 – 2014 = Dec 2013 – Mar 2014 (*drought*); Apr – May 2014 (*rising*); Jun – Jul (*flood*); Aug – Oct 2014 (*receding*). ( $r_a = 0.46$ ,  $p < 0.001$ ;  $r_b = 0.66$ ,  $p < 0.001$ ;  $r_c = 0.14$ ,  $p < 0.001$ ;  $r_d = 0.13$ ,  $p < 0.001$ ).

**Table 1.** Synchrony (*r*) and Rayleigh test (*Z*), of phenophases of macrophyte community, per year, in flowering and fructification, of ponds of the Pantanal, municipality of Corumbá, Mato Grosso do Sul State, Brazil. Months: Feb = February; Mar = March; Oct = October. Fl = Flowering; Fr = Fructification; *p* < 0.05. Year 1. a and b (2012 – 2013) = Nov 2012 – Jan 2013 (*drought*); Feb – Mar 2013 (*rising*); Apr – Jul 2013 (*flood*); Aug – Nov 2013 (*receding*). Year 2. c and d = 2013 – 2014 = Dec 2013 – Mar 2014 (*drought*); Apr – May 2014 (*rising*); Jun – Jul (*flood*); Aug – Oct 2014 (*receding*).

|        | Phenophase | Vector month | Flooding phase      | r     | Z        | P     |
|--------|------------|--------------|---------------------|-------|----------|-------|
| Year 1 | Fl         | Feb          | Beginning of rising | 0.461 | 1473.538 | P = 0 |
|        | Fr         | Mar          | Rising              | 0.657 | 13329.25 | P = 0 |
| Year 2 | Fl         | Feb          | Drought             | 0.145 | 88.348   | P = 0 |
|        | Fr         | Oct          | End of receding     | 0.132 | 191.396  | P = 0 |

at *drought* and fructification at the end of *receding* (Figure 3c, d), both with low synchronism (Table 1).

For the flooding phases, flowering showed low synchronism at *drought*, *rising* and *flood*, and asynchrony at *receding*, while fructification had low synchronism at *rising* and *flood* and asynchrony in the other phases (Table 2), in the first year. There was a negative correlation between depth and flowering (*r* = -0.646; *p* = 0.023), and positive for rainfall (*r* = 0.637; *p* = 0.026), but no correlation with temperature (*r* = 0.556; *p* = 0.061); fructification did not present any correlation (depth *r* = -0.469; *p* = 0.124; temperature *r* = 0.28; *p* = 0.378; rainfall *r* = 0.253; *p* = 0.428). The synchrony of flowering was low at *drought* and *receding*, with asynchrony in the other phases, while fructification showed asynchronism only at *flood*, with low synchrony in the other phases (Table 1; Figure 3), in the second year. Depth and flowering were negatively correlated (*r* = -0.569; *p* = 0.054), but no correlation with temperature (*r* = 0.503; *p* = 0.096) and rainfall (*r* = -0.081; *p* = 0.804); fructification had no correlation (depth *r* = -0.129; *p* = 0.689; temperature *r* = 0.540; *p* = 0.070; rainfall *r* = 0.014; *p* = 0.965).

**Phenology of the community of macrophytes per representative life form between flooding phases**

**Amphibious plants:** Seasonal phenology, flowering at the beginning of the *rising* phase, medium synchronism and fructification at *rising* with high synchrony (Table 3; Figure 4a-b). In contrast, in the second year, seasonality, with flowering and at *drought*, flowering showing medium synchrony and fructification low synchronism (Table 3; Figure 4c-d). In the first year, regarding synchronism in the flooding phases, flowering was low at *drought*, *rising* and *flood*, with asynchrony at *receding*, while for fructification the synchronism was low at *drought* and *receding* and occurred asynchrony in the other phases (Table 4). There was a correlation between flowering and temperature (*r* = 0.582; *p* = 0.047) and rainfall (*r* = 0.703; *p* = 0.011), but not for depth (*r* = 0.232; *p* = 0.468); whereas for fructification was no correlation (depth *r* = 0.53; *p* = 0.076; temperature *r* = 0.245; *p* = 0.443; rainfall *r* = 0.258; *p* = 0.419). Between phases, in the second year, the synchronism of flowering was low at *rising* and *flood*, with asynchrony in the other phases, while

**Table 2.** Synchrony of phenophases per flooding phases (*drought*, *rising*, *flood* and *receding*), per year, in percentage of flowers/buds (flowering) and immature/ripe fruits (fructification), for the macrophyte community of ponds of the Pantanal, municipality of Corumbá, Mato Grosso do Sul State, Brazil. Degree of synchrony: a = asynchronous, b = low synchrony, c = high synchrony (Bencke & Morellato 2002a).

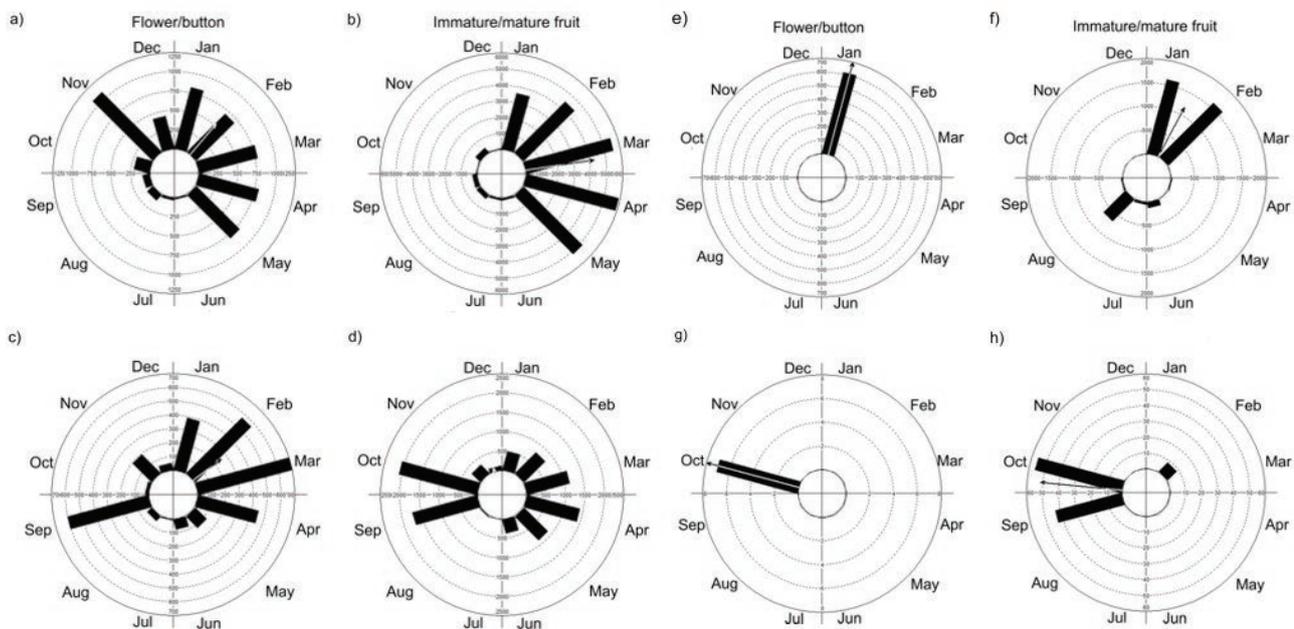
|        | Flowering         |                    |                   |                   | Fructification     |                    |                    |                    |
|--------|-------------------|--------------------|-------------------|-------------------|--------------------|--------------------|--------------------|--------------------|
|        | Drought           | Rising             | Flood             | Receding          | Drought            | Rising             | Flood              | Receding           |
| Year 1 | 43.6 <sup>b</sup> | 23.2 <sup>b</sup>  | 29.2 <sup>b</sup> | 3.89 <sup>a</sup> | 18.97 <sup>a</sup> | 38.55 <sup>b</sup> | 38.22 <sup>b</sup> | 4.24 <sup>a</sup>  |
| Year 2 | 45.5 <sup>b</sup> | 16.85 <sup>a</sup> | 4.8 <sup>a</sup>  | 3.85 <sup>b</sup> | 27.63 <sup>b</sup> | 20.7 <sup>b</sup>  | 5.55 <sup>a</sup>  | 46.12 <sup>b</sup> |

fructification showed asynchronism only at *flood* and low synchronism in the other phases (Table 4), and we found no correlation between flowering (depth  $r = -0.383$ ;  $p = 0.22$ ; temperature  $r = 0.459$ ;  $p = 0.133$ ; rainfall  $r = 0.103$ ;  $p = 0.750$ )/fructification (depth  $r = -0.215$ ;  $p = 0.501$ ; temperature  $r = 0.539$ ;  $p = 0.071$ ; rainfall  $r = 0.072$ ;  $p = 0.823$ ) and the parameters.

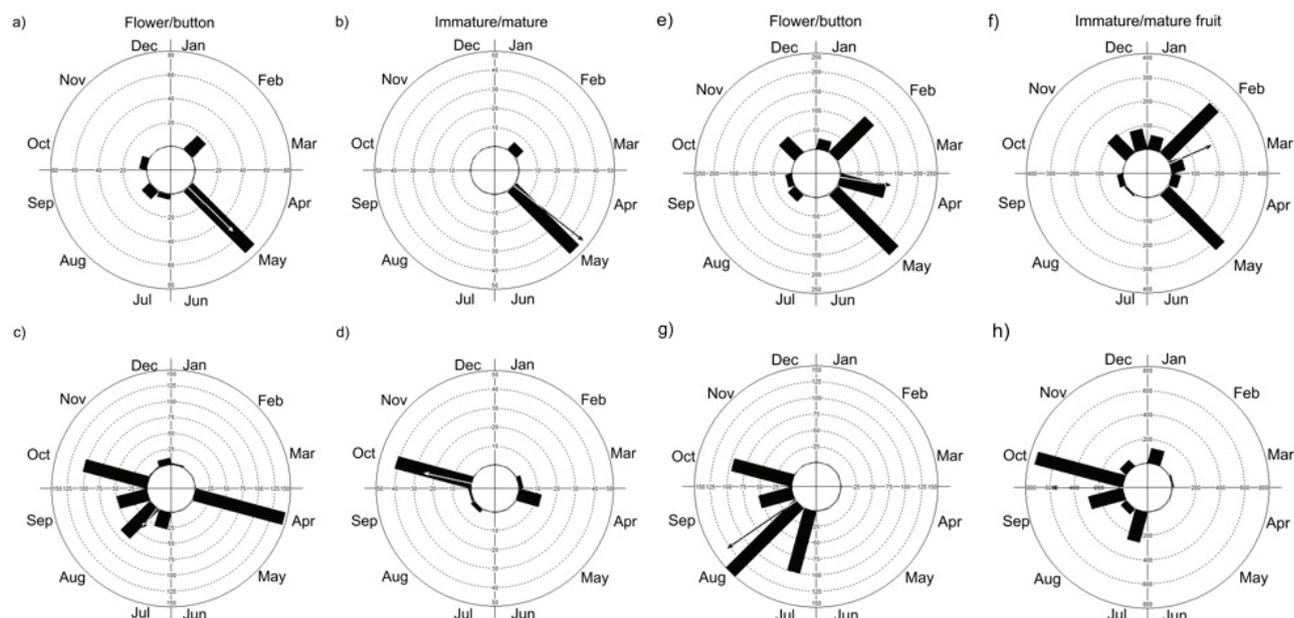
**Emergent plants:** In the first year occurred seasonal phenology, when flowering occurred in the transition between *drought* and *rising*, with elevated synchronism, and fruiting at *rising*, with high synchrony (Table 3; Figure 4e-f). However, in the second year, the phenologies were seasonal with flowering and fruiting at the end of *receding*, with elevated synchronism for both flowering and fruit set (Table 3; Figure 4g-h). The synchronism of flowering, in the first year, was high at *drought* and synchronic in the other phases, while for fructification the synchronism was low at *drought* and *rising* and had asynchrony in the other phases (Table 4). Between phases, the synchronism of flowering was high at *receding*, with asynchrony in the other phases, while for fructification occurred high synchronism only at *receding*, with asynchrony

in the other phases (Table 4), in the second year. We found no correlation between flowering (year 1 - depth  $r = -0.063$ ;  $p = 0.845$ ; temperature  $r = 0.349$ ;  $p = 0.266$ ; rainfall  $r = 0.388$ ;  $p = 0.212$ ; year 2 - depth  $r = -0.211$ ;  $p = 0.510$ ; temperature  $r = 0.427$ ;  $p = 0.166$ ; rainfall  $r = 0.007$ ;  $p = 0.983$ )/fructification (year 1 - depth  $r = -0.199$ ;  $p = 0.535$ ; temperature  $r = 0.102$ ;  $p = 0.752$ ; rainfall  $r = 0.247$ ;  $p = 0.438$ ; year 2 - depth  $r = 0.007$ ;  $p = 0.982$ ; temperature  $r = 0.530$ ;  $p = 0.076$ ; rainfall  $r = -0.126$ ;  $p = 0.696$ ) and the parameters in both years.

**Rooted floating plants:** Seasonal phenology showed flowering and fruiting in the first year at *flood*, with high synchronism for both flowering and fructification (Table 3; Figure 5a-b). For the second year, seasonal, with flowering and fruiting at the end of *flood* and beginning of *receding*, medium synchrony for both flowering, but low synchronism for fructification (Table 3; Figure 5c-d). The synchronism per phase was high at *flood* for flowering and fructification, occurring asynchrony in the other phases (Table 4). No correlation was detected between flowering (depth  $r = 0.003$ ;  $p = 0.992$ ; temperature  $r = -0.254$ ;  $p = 0.426$ ; rainfall  $r = -0.349$ ;  $p = 0.266$ )/fructification (depth  $r = 0.080$ ;  $p =$



**Figure 4.** Circular histogram of the species with amphibious (a-d) and emergent (e-h) lives forms of the community of macrophytes with the number of flowers/buds (a, c, e, g) and immature/ripe fruits (b, d, f, h) over two annual cycles (2012 - 2014) in ponds of the Pantanal, Mato Grosso do Sul State, Brazil. a and b = 2012 - 2013; c and d = 2013 - 2014. (Amphibious –  $r_a = 0.41$ ,  $p < 0.001$ ;  $r_b = 0.71$ ,  $p < 0.001$ ;  $r_c = 0.36$ ,  $p < 0.001$ ;  $r_d = 0.047$ ,  $p < 0.005$ ); (Emergent –  $r_a = 1$ ,  $p < 0.001$ ;  $r_b = 0.58$ ,  $p < 0.001$ ;  $r_c = 1$ ,  $p < 0.001$ ;  $r_d = 0.85$ ,  $p < 0.001$ ). Sep 2012 – Jan 2013 (*drought*); Feb – Mar 2013 (*rising*); Abr – Jul 2013 (*flood*); Aug – Nov 2013 (*receding*); Dec 2013 – Mar 2014 (*drought*); Apr – May 2014 (*rising*); Jun – Jul (*flood*); Aug – Oct 2014 (*receding*).



**Figure 5.** Circular histogram of the species with rooted floating (a-d) and free-floating (e-h) life forms of the community of macrophytes with the number of flowers/buds (a, c, e, g) and immature/ripe fruits (b, d, f, h) over two annual cycles (2012 - 2014) in ponds of the municipality of Pantanal, Mato Grosso do Sul State, Brazil. a and b = 2012 - 2013; c flowering and d = 2013 - 2014. (Rooted floating –  $r_a = 0.65$ ,  $p < 0.001$ ;  $r_b = 0.85$ ,  $p < 0.001$ ;  $r_c = 0.26$ ,  $p < 0.005$ ;  $r_d = 0.51$ ,  $p < 0.005$ ); (Free-floating –  $r_a = 0.51$ ,  $p < 0.001$ ;  $r_b = 0.46$ ,  $p < 0.001$ ;  $r_c = 0.85$ ,  $p < 0.001$ ;  $r_d = 0.73$ ,  $p < 0.001$ ). Sep 2012 – Jan 2013 (*drought*); Feb – Mar 2013 (*rising*); Abr – Jul 2013 (*flood*); Aug – Nov 2013 (*receding*); Dec 2013 – Mar 2014 (*drought*); Apr – May 2014 (*rising*); Jun – Jul (*flood*); Aug – Oct 2014 (*receding*).

0.805; temperature  $r = -0.202$ ;  $p = 0.529$ ; rainfall  $r = -0.248$ ;  $p = 0.437$ ) and the parameters. The second year presented between the phases low synchronism of flowering at *receding*, with asynchrony in the other phases, while for fructification we found high synchronism at *receding*, low at *rising*, with asynchronism in the other phases (Table 4). We detected a correlation between flowering and depth ( $r = 0.625$ ;  $p = 0.030$ ), but not for temperature ( $r = 0.311$ ;  $p = 0.324$ ) and rainfall ( $r = -0.438$ ;  $p = 0.155$ ); whereas for fructification was no correlation (depth  $r = 0.277$ ;  $p = 0.384$ ; temperature  $r = 0.462$ ;  $p = 0.131$ ; rainfall  $r = -0.076$ ;  $p = 0.815$ ).

**Free-floating plants:** First seasonal year, with flowering at the beginning of the *flood*, with medium synchronism, and fructification between the end of *rising* and beginning of *flood*, with medium synchrony (Table 3; Figure 5e-f). Second seasonal year, with flowering at the beginning of *receding*, high synchronism, and fructification at *receding*, with high synchrony (Table 3; Figure 5g-h). Between phases, the synchronism of flowering was low at *rising* and *drought* and asynchronous in

the other phases, while for fructification occurred asynchrony only at *receding*, being low in the other phases (Table 4) in the first year. And in the second year, the synchronism of flowering was high at *receding*, low at *flood* and asynchronous in the other phases, while fructification had high synchronism only at *receding* and asynchronism in the other phases (Table 4). No correlation was found between flowering (year 1 - depth  $r = 0.173$ ;  $p = 0.591$ ; temperature  $r = -0.017$ ;  $p = 0.957$ ; rainfall  $r = -0.166$ ;  $p = 0.605$ ; year 2 - depth  $r = 0.205$ ;  $p = 0.524$ ; temperature  $r = -0.119$ ;  $p = 0.713$ ; rainfall  $r = -0.414$ ;  $p = 0.181$ )/fructification (year 1 - depth  $r = -0.149$ ;  $p = 0.644$ ; temperature  $r = 0.192$ ;  $p = 0.550$ ; rainfall  $r = 0.028$ ;  $p = 0.932$ ; year 2 - depth  $r = 0.292$ ;  $p = 0.357$ ; temperature  $r = 0.355$ ;  $p = 0.258$ ; rainfall  $r = -0.156$ ;  $p = 0.629$ ) and the parameters, in both years.

## DISCUSSION

### *Phenology of the community of macrophytes between flooding phases*

In the first year, because the peak of flowering occurred at the begin of *rising*, what leads us to

**Table 3.** Synchrony ( $r$ ) and Rayleigh test ( $Z$ ), per year, in percentage of flowers/buds (flowering) and immature/ripe fruits (fructification), for the life forms of macrophytes of ponds of the Pantanal, municipality of Corumbá, Mato Grosso do Sul State, Brazil. Months: Jan = January; Feb = February; Mar = March; Apr = April; Aug = August; Sep = September; Oct = October; Dec = December. Fl = Flowering; Fr = Fructification;  $p < 0.05$ . (Fphase = Flooding phase; Beg = beginning; E = end; Drou = drought).

| Year 1       |            |              |            |            |                 |              |               |              |
|--------------|------------|--------------|------------|------------|-----------------|--------------|---------------|--------------|
| Life form    | Amphibious |              | Emergent   |            | Rooted floating |              | Free-floating |              |
| Phenophase   | Fl         | Fr           | Fl         | Fr         | Fl              | Fr           | Fl            | Fr           |
| Vector month | Feb        | Mar          | Jan        | Jan        | May             | May          | Apr           | Mar          |
| Fphase       | Beg rising | Rising       | Beg rising | Rising     | Beg flood       | Beg flood    | Flood         | Flood        |
| R            | 0.413      | 0.71         | 1          | 0.583      | 0.654           | 0.918        | 0.517         | 0.465        |
| Z            | 992.673    | 13001.247    | 612        | 1365.448   | 46.164          | 42.953       | 158.484       | 212.507      |
| P            | P = 0      | P = 0        | P = 0      | P = 0      | P = 0           | P = 0        | P = 0         | P = 0        |
| Year 2       |            |              |            |            |                 |              |               |              |
| Life form    | Amphibious |              | Emergent   |            | Rooted floating |              | Free-floating |              |
| Phenophase   | Fl         | Fr           | Fl         | Fr         | Fl              | Fr           | Fl            | Fr           |
| Vector month | Feb        | Dec          | Oct        | Oct        | Aug             | Aug          | Aug           | Sep          |
| Fphase       | Drou       | Drou         | E receding | E receding | Beg receding    | Receding     | E flood       | Beg receding |
| R            | 0.362      | 0.047        | 1          | 0.855      | 0.257           | 0.509        | 0.851         | 0.728        |
| Z            | 419.553    | 20.393       | 7          | 78.181     | 26.38           | 15           | 286.381       | 819.051      |
| P            | P = 0      | P = 1.39E-09 | P = 0      | P = 0      | P = 3.49E-12    | P = 3.06E-07 | P = 0         | P = 0        |

**Table 4.** Synchrony of phenophases per flooding phases (*drought, rising, flood* and *receding*), per year, in percentage of flowers/buds (flowering) and immature/ripe fruits (fructification), for the life forms of macrophytes of ponds of the Pantanal, Corumbá, Mato Grosso do Sul, Brazil. Degree of synchrony: a = asynchronous, b = low synchrony, c = high synchrony (Bencke & Morellato 2002a). Bigger synchrony in bold.

| Year 1          | Flowering                |                    |                          |                          | Fructification           |                    |                          |                          |
|-----------------|--------------------------|--------------------|--------------------------|--------------------------|--------------------------|--------------------|--------------------------|--------------------------|
|                 | Drought                  | Rising             | Flood                    | Receding                 | Drought                  | Rising             | Flood                    | Receding                 |
| Amphibious      | <b>41.44<sup>b</sup></b> | 26.06 <sup>b</sup> | 28.65 <sup>b</sup>       | 3.84 <sup>a</sup>        | 15.53 <sup>a</sup>       | 38.62 <sup>b</sup> | <b>43.5<sup>b</sup></b>  | 2.4 <sup>a</sup>         |
| Emergent        | <b>99.83<sup>c</sup></b> | 0 <sup>a</sup>     | 0 <sup>a</sup>           | 0.16 <sup>a</sup>        | <b>39.74<sup>b</sup></b> | 39.42 <sup>b</sup> | 4.33 <sup>a</sup>        | 16.51 <sup>a</sup>       |
| Rooted floating | 0 <sup>a</sup>           | 14.81 <sup>a</sup> | <b>71.3<sup>c</sup></b>  | 13.9 <sup>a</sup>        | 0 <sup>a</sup>           | 9.8 <sup>a</sup>   | <b>90.2<sup>c</sup></b>  | 0 <sup>a</sup>           |
| Free-floating   | 14.19 <sup>a</sup>       | 22.13 <sup>b</sup> | <b>57.26<sup>b</sup></b> | 6.42 <sup>a</sup>        | 25.5 <sup>b</sup>        | 34.96 <sup>b</sup> | <b>36.58<sup>b</sup></b> | 2.95 <sup>a</sup>        |
| Year 2          | Flowering                |                    |                          |                          | Fructification           |                    |                          |                          |
| Amphibious      | <b>56.2<sup>b</sup></b>  | 16.65 <sup>a</sup> | 2.26 <sup>a</sup>        | 24.9 <sup>b</sup>        | 30.5 <sup>b</sup>        | 24.4 <sup>b</sup>  | 3.81 <sup>a</sup>        | <b>41.32<sup>b</sup></b> |
| Emergent        | 0 <sup>a</sup>           | 0 <sup>a</sup>     | 0 <sup>a</sup>           | <b>100<sup>c</sup></b>   | 7.48 <sup>a</sup>        | 0 <sup>a</sup>     | 0 <sup>a</sup>           | <b>92.52<sup>c</sup></b> |
| Rooted floating | 3.17 <sup>a</sup>        | 11.3 <sup>a</sup>  | 6.52 <sup>a</sup>        | <b>53.93<sup>b</sup></b> | 3.45 <sup>a</sup>        | 20.7 <sup>b</sup>  | 0 <sup>a</sup>           | <b>75.9<sup>c</sup></b>  |
| Free-floating   | 0 <sup>a</sup>           | 0 <sup>a</sup>     | 25.1 <sup>b</sup>        | <b>74.94<sup>c</sup></b> | 13 <sup>a</sup>          | 0 <sup>a</sup>     | 16.5 <sup>a</sup>        | <b>70.5<sup>c</sup></b>  |

observe such phenological “behaviour”, besides the presence of water for future dispersal, as had been recorded in two species of *Polygonum* L. (Caryophyllales, Polygonaceae) (Catian *et al.* 2017). Abiotic conditions are important environmental signs for the beginning of the reproductive process (Borchert *et al.* 2005), a fact observed here. Thereby,

essentially aquatic species, which do not survive in absence of water, show hydrochory, needing it for dispersal of their diaspores. This group of plants is represented by most life forms (rooted floating and submerged, free-floating and submerged, epiphytic and some emergent), even some amphibious species. The dynamics of species distribution and

the succession of species in the ponds in relation to depth (Pott & Pott 1986, 2003, Van Geest *et al.* 2005), ends up influencing the peaks of flowering, which explains the negative correlation between flowering and depth. As we observed in the field, shallow depths allow more species of the essentially aquatic life forms, such as floating, emerge and submerged, resulting in peaks of simultaneous flowering, what explains the concentration of the peaks at the begin of *rising*, nearly all species explore this essential post-*drought* resource. For the colonization of new areas is essential a wider amplitude of transport of diaspores (Hamilton & May 1977, Hughes *et al.* 1994).

Analysing the flooding phases separately, we observe that the species invest differently in flowers and fruits, given the temporal appearance of the species in ponds, influencing the functionality of the community, as reported by Catian *et al.* (2018). The duration of the aquatic and terrestrial phases for the herbaceous plants, such as amphibious, is of great importance, determining the composition of species and growth habits of the plants over the year (Junk & Piedade 1997).

In the second year, in spite of the mean of flowering being high in February, it was representative in September, reflecting in the peak of fructification. However, different from the first year, February/2014 was still dry, when essentially aquatic plants did not occur yet, except in permanent ponds. Nevertheless, we believe that the species were responding to the cycle that year, then in the previous year, the *drought* was prolonged, somehow interfering with opening of flowers. We observe that the same occurred for the synchrony per phases separately, due to the distribution of the individuals in relation to the water depth in the phases. The adaptations of plants to the hydrological regime generate temporal variations in richness, composition, cover and life forms of the species (Capon 2003). For both years the fructification did not have a correlation with the parameters, probably because it responds to the time of flowering; physical-chemical parameters of water and photoperiod, not measured in this work; or presence of pollinators. Pollinators forage in ponds, visiting flowered species and benefiting from the presence of water (Stewart *et al.* 2017)

and plants have different rates of flower opening influencing the attractiveness to pollinators (Harder & Johnson 2005).

### ***Phenology of the community of macrophytes per representative life form between flooding phases***

**Amphibious plants:** Amphibious species developed flowers at the begin of *rising*, in the first year, due to the environmental trigger of the presence of water for probable future dispersal of the diaspores, explaining the fact that most species invest in fructification at this phase, as we observed in the field for *Sesbania virgata* (Cav.) Pers., *Senna* spp. Mill., *Mimosa* spp. L. and *Aeschynomene* spp. L. (Fabales, Fabaceae). Some amphibious species set fruit in the aquatic phases, due to adaptative characteristics of the diaspores for hydrochory, fruits possessing tissue filled with air, for flotation, well observed in *S. virgata* and *Polygonum* spp., that present diaspores with air stored in the perianth to facilitate buoyancy (Staniforth & Cavers 1976). However, when we analyse the phases separately, we see a reduction of synchrony, probably by loss of amphibious species tolerant of lack of oxygen in the soil. Many amphibious species develop adaptative tissues and structures for hypoxia or anoxia, such as aerenchyma, hypertrophied lenticels and fissures on the stem (Drew 1997), nevertheless, some species die “drowned”, not finishing their phenological process. According to Boeger & Poulson (2003), amphibious species have morphophysiological variations due to different requirements of light and gases present in the water and in the air, related to those adaptations.

The correlation between temperature and rainfall was also observed by Simão (2016) for amphibious macrophytes. The fact that most amphibious species need water to flower at *drought* explains rainfall as an important requirement because it reduces the stress of water shortage. The relation with temperature is explained by its influence on the activity of pollinators since most plants are mellitophilous. Authors such as Rathcke & Lancey (1985) and Diekmann (1996) report that temperature and photoperiod are identified as factors of regulation of flowering. In the second year, we believe that the species responded to the phase with precedent water, that kept the soil wet, leading to the peak of flowering at *drought*. The fact that

there are amphibious species with characteristics of terrestrial plants, explains the results obtained per phases, the same observed by Simão (2016).

**Emergent plants:** In the first year, the species presented flowers and fruits in phases with low water depths and the period with high rainfall, though not correlated, this may have interfered with the sexual propagation and dispersal of fruits via hydrochory, what explains the high synchrony for the phenophases. According to Morellato & Leitão-Filho (1992), the intenser flowering in the rainy season can be related to the availability of resources such as light and nutrients, offering favourable conditions for germination of future seeds. Nonetheless, emergent species have the capacity to survive after *receding*, in wet soil, e.g., *Echinodorus* spp. Rich. (Alismatales, Alismataceae) and *Pontederia* spp. L. (Commelinales, Pontederiaceae) in our observation, and so they emit flowers to use the residual moisture, mainly that year with prolonged *drought*, to set fruits and release seeds to compose the bank. According to Pott & Pott (1986), these species do not depend on rains to flower, presenting flowers almost year-round.

In the second year, the flood cycle was temporally normal, emergent species flowered in the phase with the lowest water level, though without correlation, we observed in the field this phenological “behaviour” of emitting flowers at the end of *receding*, in shallower depths. Besides morphological and physiological adaptations, the plants present phenological strategies, allowing the synchronization of the reproductive phenophases, seed dispersal and leaf change under different seasonal conditions (Uriu *et al.* 2017), what can explain such investment of the emergent species in phases when the shortage of resources begins.

**Rooted floating plants:** These species need water to support their leaves, as we observed in the field for *Nymphaea* spp. (Nymphaeales, Nymphaeaceae). At the begin of *rising* in the first year, dormant seeds in the soil germinated and the seedlings grew in shallow depths, then at the peak of flood, the mature individuals emitted flowers, what would be the moment for pollination, once they have hydrochoric seeds with floating structures. The seed bank is responsible for maintaining a high

density of species such as *N. amazonum* Mart. & Zucc. (Nymphaeales, Nymphaeaceae) (Ferreira *et al.* 2016). It is known that species of this genus are dominant in a range of water depths between 0.5 and 3 m (e.g., Spence 1982), with a tolerance of significant water level changes, the phases with the presence of water being ideal for flowering. Some species, e.g., *N. gardneriana* Planch. (Nymphaeales, Nymphaeaceae), continue to grow with smaller leaves and to flower on the pond edge even after the surface water has drawn down, on waterlogged soil, yet underwater fruit set (Pott & Pott 2000) would not be feasible.

In the second year, as the phases were “normalized”, not preceded by a long dry spell, the water level was reduced slowly, this slower *receding* prolonged the wetness. The floating species follow the lowering water level and can flourish, once they developed floral stalks of various sizes and keep the leaves on the water surface by petiole elongation (Brock *et al.* 1987), which explains the correlation between flowering and depth. Bertazzoni & Damasceno-Júnior (2011) observed that water level and daylength interfere with the phenology of *Oryza latifolia* Desv. (Poales, Poaceae). However, pollination under higher temperatures would be involved with such a response since the temperature of the insect body is influenced by ambient temperature (Käpylä 1974).

**Free-floating plants:** Species of this life form not rooted in the soil and obtain nutrients directly from the water, therefore, phases with the presence of water are necessary for survival. Many species invest in cloning, producing stolons before flower emission (Catian 2015), this interval can explain the medium synchrony found in the first year. At the end of *receding*, we observed in the field that the free-floating species come in contact with the soil and then they flourish and often already set fruit, before dying.

Although without correlation between depth and phenology, in the second year, at *receding*, we observed in the field a high density of the free-floating *Pistia stratiotes* L. (Alismatales, Araceae) and *Limnobium laevigatum* (Humb. & Bonpl. ex Willd.) Heine (Alismatales, Hydrocharitaceae), with a simultaneous flowering of all species and often investment in cloning and fructification at the same time (Catian 2015). Junk & Piedade (1997) had

observed in *P. stratiotes* an increment in biomass, result of sexual and vegetative propagation at the begin of *receding*. The vegetative propagation assures fast colonization as the water level rises, being interrupted at low water level, overcoming the period of *drought* in the bank of diaspores and/or propagules (Junk 1980, Coelho *et al.* 2005), what is very common for free-floating species.

Owing to the fact that different species being grouped within the same life form and presenting different phenologies, the non-detection of a pattern related to the depth of the life forms reflects specific biological conditions. As can be observed in the graphs (Figures 4, 5), there are several months with a phenological active period, in distinct hydrological phases, therefore the lack of relationship with depth when analysed this way. The great variability of the sexual systems found in plants determines their reproductive characteristics and flowering synchrony (Otárola & Rocca 2014), an important fact that shall be taken into consideration.

We conclude that the community of macrophytes presents phenology associated with the response of the populations to seasonal and year-to-year alterations of the flood cycle, such as presence of water, by means of morphological plasticity, diversified life histories and life forms that, altogether, determine the dynamics, resistance and resilience of the aquatic vegetation in the Pantanal. Such knowledge helps to understand this ecosystem, to predict climate effects and other hydrologic changes for conservation purposes.

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**Appendix 1.** Angiosperm flora and life forms of the macrophytes occurrent within and on the margin of sampled ponds in the subregions Abobral and Nhecolândia, Pantanal, Mato Grosso do Sul State, Brazil, in two yearly flooding cycles (2012-2014). LF = life form (Am = amphibious; Em = emergent; FF = free-floating; RF = rooted floating). \*Vouchers incorporated into the Herbarium CGMS (Herbário de Campo Grande, Mato Grosso do Sul).

| Family                               | Specie   | LF    | Voucher* |
|--------------------------------------|--|-------|----------|
| Alismataceae                         | <i>Echinodorus longiscapus</i> Arechav.                              | Em    | 54571    |
|                                      | <i>Echinodorus paniculatus</i> Micheli                               | Em    | 54572    |
|                                      | <i>Helanthium tenellum</i> (Mart.) Britton                           | Am    | 54546    |
|                                      | <i>Hydrocleys nymphoides</i> (Willd.) Buchenau                       | RF    | 54537    |
|                                      | <i>Sagittaria guyanensis</i> Kunth                                   | RF    | 54519    |
|                                      | <i>Sagittaria montevidensis</i> Cham. & Schltldl.                    | Em    | 54573    |
| Araceae                              | <i>Pistia stratiotes</i> L.  | FL    | 54576    |
| Cannaceae                            | <i>Canna glauca</i> L.   | Am    | 54536    |
| Fabaceae                             | <i>Aeschynomene denticulata</i> Rudd                                 | Em    | 50234    |
|                                      | <i>Aeschynomene fluminensis</i> Vell.                                | Em    | 37514    |
|                                      | <i>Aeschynomene rudis</i> Benth.                                     | Em    | 54608    |
|                                      | <i>Aeschynomene sensitiva</i> Sw.                                    | Em    | 54524    |
|                                      | <i>Mimosa pigra</i> L.   | Am    | 54532    |
|                                      | <i>Mimosa polycarpa</i> Kunth  | Am    | 54714    |
|                                      | <i>Mimosa weddelliana</i> Benth.                                     | Am    | 54526    |
|                                      | <i>Senna aculeata</i> (Pohl ex Benth.) H.S. Irwin & Barneby          | Am    | 37172    |
|                                      | <i>Senna alata</i> (L.) Roxb.  | Am    | 54715    |
|                                      | <i>Senna obtusifolia</i> (L.) H.S. Irwin & Barneby                   | Am    | 37182    |
|                                      | <i>Senna occidentalis</i> (L.) Link                                  | Am    | 37181    |
|                                      | <i>Senna pendula</i> (Humb. & Bonpl. ex Willd.) H.S. Irwin & Barneby | Am    | 54567    |
| <i>Sesbania virgata</i> (Cav.) Pers. | Am   | 37504 |          |
| Hydrocharitaceae                     | <i>Limnobium laevigatum</i> (Humb. & Bonpl. ex Willd.) Heine         | FF    | 54583    |
| Marantaceae                          | <i>Thalia geniculata</i> L.  | Am    | 54544    |
| Nymphaeaceae                         | <i>Nymphaea amazonum</i> Mart. & Zucc.                               | RF    | 54521    |
|                                      | <i>Nymphaea gardneriana</i> Planch.                                  | RF    | 54520    |
| Onagraceae                           | <i>Ludwigia decurrens</i> Walt.                                      | Em    | 54525    |
|                                      | <i>Ludwigia grandiflora</i> (Michx.) Zardini                         | Em    | 54548    |
|                                      | <i>Ludwigia helminthorrhiza</i> (Mart.) H. Hara                      | FF    | 54584    |
|                                      | <i>Ludwigia lagunae</i> (Morong) H. Hara                             | Em    | 54518    |
|                                      | <i>Ludwigia leptocarpa</i> (Nutt.) H. Hara                           | Em    | 37511    |
|                                      | <i>Ludwigia octovalvis</i> (Jacq.) P.H. Raven                        | Em    | 37173    |
|                                      | <i>Ludwigia sedoides</i> (Humb. & Bonpl.) H. Hara                    | RF    | 54533    |
|                                      | <i>Ludwigia tomentosa</i> (Cambess.) H. Hara                         | Am    | 54542    |
| Plantaginaceae                       | <i>Bacopa arenaria</i> Loefgr. & Edwall                              | Am    | 54538    |
|                                      | <i>Bacopa australis</i> V.C. Souza                                   | Am    | 37180    |

Appendix 1. Continued on next page...

## Appendix 1. ...Continued

| <b>Family</b>         | <b>Specie</b>                             | <b>LF</b> | <b>Voucher*</b> |
|-----------------------|---|-----------|-----------------|
| <b>Polygonaceae</b>   | <i>Polygonum acuminatum</i> Kunth         | Am        | 54529           |
|                       | <i>Polygonum hispidum</i> Kunth           | Am        | 37176           |
|                       | <i>Polygonum ferrugineum</i> Wedd.        | Am        | 37167           |
|                       | <i>Polygonum hydropiperoides</i> Michx.   | Em        | 54605           |
|                       | <i>Polygonum punctatum</i> Elliot         | Am        | 37177           |
| <b>Pontederiaceae</b> | <i>Eichhornia azurea</i> (Sw.) Kunth      | RF        | 54547           |
|                       | <i>Eichhornia crassipes</i> (Mart.) Solms | FF        | 37502           |
|                       | <i>Pontederia parviflora</i> Alexander    | Em        | 54535           |
|                       | <i>Pontederia rotundifolia</i> L.f.       | RF        | 54550           |
|                       | <i>Pontederia subovata</i> (Seub.) Lowden | RF        | 54607           |
| <b>Rubiaceae</b>      | <i>Diodia kuntzei</i> K. Schum.           | Am        | 37513           |