



Reproductive phenology of aquatic macrophytes in the Cerrado-Pantanal ecotone

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Received: July 30, 2020

Accepted: October 29, 2020

ABSTRACT

Studies of plant phenology have been performed predominantly with terrestrial species and rarely so with aquatic communities. Such plants are fundamental for the aquatic ecosystems, representing a valuable source of resources when they are scarce in terrestrial environments for the fauna. Studies of phenology help to understand the reproduction rhythms of plant communities and provide fundamental support to management and conservation. This study aimed to describe the reproductive phenology of 15 species of aquatic plants and determine how it is related to climatic factors and physicochemical variables of water. Plants were collected every 15 days throughout a single year, from two ponds in the Cerrado-Pantanal ecotone, Central-West Brazil. Species were observed in flower and fruit throughout the year with varying phenophases among life forms (amphibious, emergent, rooted, floating and rooted submerged). Photoperiod stood out among climatic variables for flowering and fruiting times. Phenophases were explained by climatic factors, as well as by physicochemical variables of the water. Nitrogen and pH were the variables most related to the highest number of phenophases of different life forms. Such information is relevant to understanding how physicochemical alterations to water by pollution, eutrophication and siltation, among others, can change the phenology of aquatic macrophytes.

Keywords: aquatic plants, flowering, fructification, limnology, physicochemical water variables

Introduction

Phenology is the study of the temporal occurrence of phases or activities of plants or animals' life cycle over the year (Morellato 1995). In the case of plants, it investigates the patterns of fall and emission of leaves and the production of flowers and fruits in temporal cycles (Morellato 1995). Phenological studies contribute to understanding the rhythms of plant reproduction and regeneration, the temporal organization of the resources

within the communities and the life cycle of animals that depend on plants for food, such as herbivores, pollinators and dispersers (Morellato 1995; Talora & Morellato 2000). Phenology is considered one of the best parameters to characterize ecosystems (Lieth 1974; Morellato *et al.* 2000) and to understand and overcome global environmental changes (Abernethy *et al.* 2018).

Information on phenology are available and have increased lately on distinct Brazilian domains, such as Cerrado (Mantovani & Martins 1988; Batalha *et al.* 1997;

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Batalha & Mantovani 2000; Batalha & Martins 2004; Tannus *et al.* 2006), Caatinga (Barbosa *et al.* 2003; Araújo *et al.* 2011), Atlantic Forest (Morellato & Haddad 2000; Morellato *et al.* 2000; Pereira *et al.* 2008; Freire *et al.* 2013), Amazon Forest (Pinto *et al.* 2008) and Pantanal (Fava *et al.* 2011; Neves & Damasceno-Júnior 2011; Freitas *et al.* 2013; Lima & Damasceno-Junior 2020). Those studies encompass trees, shrubs and herbs, mainly from terrestrial environments. However, reports on the phenology of aquatic macrophytes are scarce in Brazil, including only one or a few species (Santos *et al.* 2005; Brasil *et al.* 2007; Bertazzoni & Damasceno-Júnior 2011; Catian *et al.* 2017; but see Catian *et al.* 2019). The Pantanal, rich in aquatic environments, has a high diversity of aquatic plants but phenological studies for this group are yet incipient (available for less than 2% of the species), though necessary (Aoki *et al.* in press).

Studies on terrestrial communities indicate that the periods of flowering and fruiting are related to climatic seasonality, like rain, day length and temperature (Mantovani & Martins 1988; Batalha & Martins 2004; Lenza & Klink 2006; Oliveira 2008), besides fire (Felfili *et al.* 1999; Miranda *et al.* 2004), primary consumers (Mantovani & Martins 1988; Oliveira 2008; Marquis *et al.* 2002) and phylogenetic restrictions (Munguía-Rosas *et al.* 2011).

Since water at flood is a less restrictive factor for aquatic plants (compared with terrestrial plants), other intrinsic factors such as characteristics of the water, *e.g.*, pH, dissolved oxygen, temperature, availability of nutrients as phosphorous and nitrogen, influence their primary production (Fraser & Morton 1983; Biudes & Camargo 2006). Therefore, it is fundamental to understand which factors related to the establishment and growth of aquatic macrophytes in their habitats (Barko *et al.* 1991) influence their reproductive phenophases.

In this context, our work aimed to answer the following questions: 1) which are the patterns of flowering and fructification in an assemblage of aquatic macrophytes in the Cerrado-Pantanal ecotone?; 2) are the climatic variables and physicochemical water variables correlated to flowering and fructification of the assemblage of aquatic macrophytes?; and 3) can different life forms (amphibious, emergent, rooted floating and rooted submerged) respond distinctly to these variables?

Materials and methods

Study area

Our study was carried out between October 2014 and September 2015, in the Parque Natural Municipal da Lagoa Comprida (PNMLC; 20°27'44" S, 55°46'26" W) (Fig. 1) and Lagoa dos Bobos (LC; 20°27'1" S, 55°44'44" W), situated in the municipality of Aquidauana, Mato Grosso do Sul (MS), Central-West Brazil, in the Cerrado-Pantanal ecotone (Fig. 1).

The PNMLC covers 74.2 ha and its wet area, the Lagoa Comprida (LC), has 26.87 ha of water surface, with semi-lentic characteristics (Souza & Martins 2010). Although LC presents forested edges, it is under anthropic influence from the nearby urban growth. In turn, the LB has circa 2 ha of water surface, located in the rural area, and its surrounding has practically no forest and is utilized for cattle grazing.

The region is characterized by a humid tropical climate (Peel *et al.* 2007) presenting seasonal rainfall, with a summer rainy season from November to March and dry winter from April to September (Marengo *et al.* 2015), a mean annual rainfall of 1,200 mm and maximum and minimum temperatures of 33 and 19 °C, respectively (Schiavo *et al.* 2010). The climatic data for the study period were obtained from CEMTEC-MS and the meteorological station of the Universidade Estadual de Mato Grosso do Sul; the photoperiod data were gathered on the On-line Photoperiod Calculator (Lammi 2001). In the sampling period, the average recorded temperature was 26.3 °C, January was the warmest month (36.3 °C maximum) and June the coolest (14.7 °C minimum). The accumulated annual rainfall was 1,098.4 mm, and the highest precipitation was recorded in December (342 mm) (Fig. 2). January (13h22min) and July (10h54min) were the months with the longest and shortest photoperiods, respectively.

Sampling

In the ponds, we marked 10 individuals of 15 plant species, selected regarding their abundance in each pond, totaling nine species in LB and six in LC. We did not choose Poaceae and Cyperaceae for our study. We contemplated four life forms: amphibious [*Bacopa myriophylloides* (Benth.) Wettst. and *Desmoscelis villosa* (Aubl.) Naudin], emergent [*Aeschynomene fluminensis* Vell., *Bacopa salzmännii* (Benth.) Wettst. ex Edwall, *Hydrolea spinosa* L., *Ludwigia decurrens* Walter, *L. lagunae* (Morong) H. Hara, *L. nervosa* (Poir.) H. Hara, *L. tomentosa* (Cambess.) H. Hara, *L. torulosa* (Arn.) H. Hara and *Xyris jupicai* Rich.], rooted floating [*Eichhornia azurea* (Sw.) Kunth, *Ludwigia sedioides* (Humb. & Bonpl.) H. Hara and *Nymphoides humboldtiana* (Kunth) Kuntze] and rooted submerged [*Egeria najas* Planch.], classified according to Irgang *et al.* (1984). The individuals were marked with numbered tags. We used iron rods, line and plastic screen for rooted floating and rooted submerged species, placed close to the tagged individuals, helping to find them. We recorded the phenological observations every 15 days, counting buds and flowers (flowering), and immature and ripe fruits (fructification). Flowering and fructification were analyzed regarding period and duration; duration was characterized as brief (1 month), intermediate (between two and five months) or extended (above five months), adapted from Newstrom *et al.* (1994).

Botanical material was collected and processed, and the exsiccatae incorporated into the collection of the Herbarium CGMS of the Universidade Federal do Mato Grosso do



Sul. The species were identified consulting the pertinent bibliography, botanists and the Herbarium. The taxonomic nomenclature followed Angiosperm Phylogeny Website 2016 (APG IV 2016), and Flora do Brasil 2020 (2020).

To explain phenological patterns, we obtained data of rainfall, temperature (Fig. 2) and photoperiod (Tab. 1). In each sampling, we collected water samples at all three different points. The samples were placed in polyethylene bottles for

laboratory analysis of each pond's physical and chemical variables of total nitrogen and total phosphorus (Tab. 1). The collection time of water samples was between 9h and 14h. The analyses were performed in the laboratory of environmental Hydrology of the Universidade Federal de Mato Grosso do Sul, Campus of Aquidauana. The electric conductivity, dissolved oxygen (DO) and pH (Tab. 1) were measured with a multiparameter sampler, also in three points per pond.

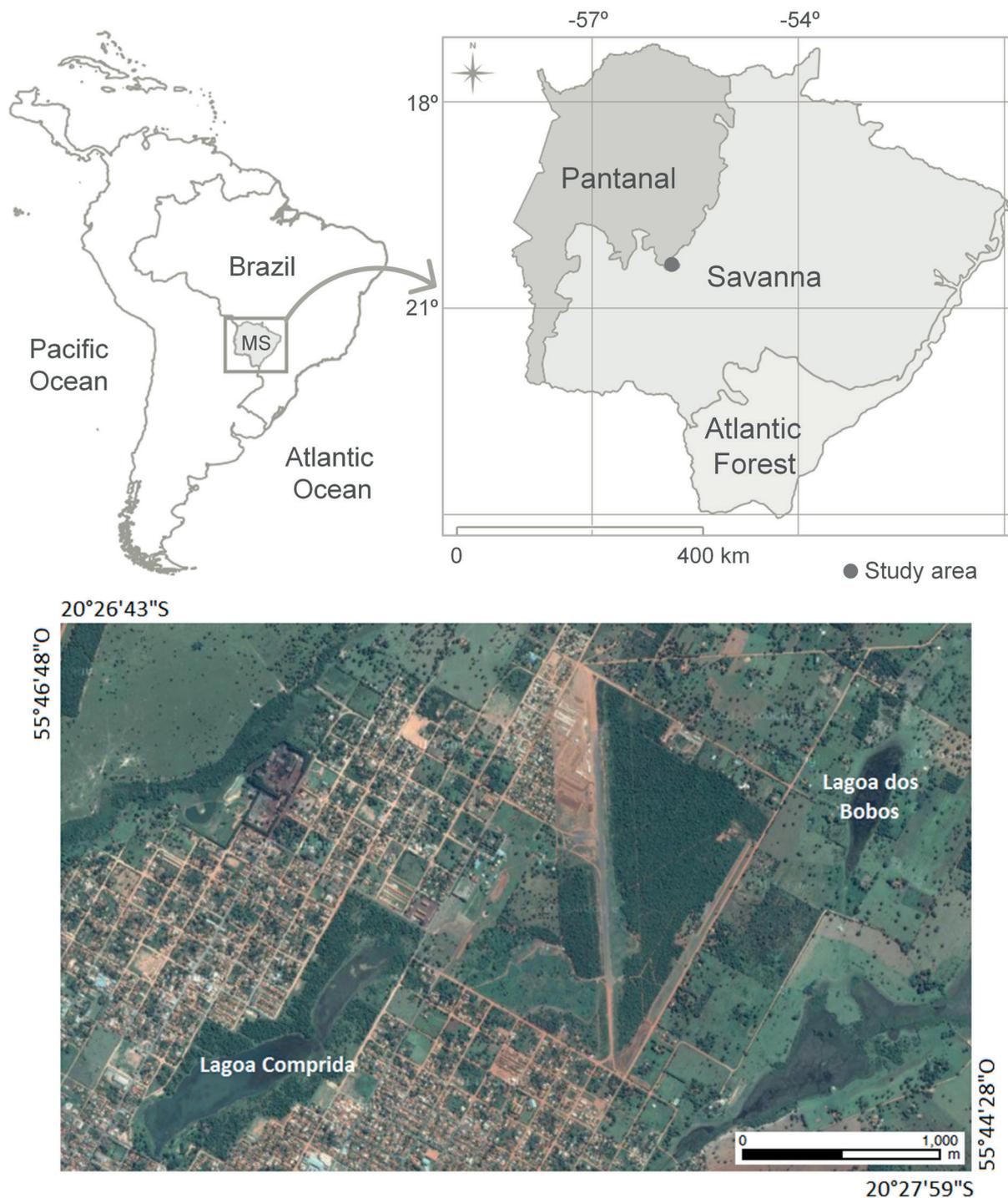


Figure 1. Location of the study area in the Pantanal-Cerrado (Savanna) ecotone, in Mato Grosso do Sul, Brazil; satellite image with Lagoa Comprida (next to the urban area) and Lagoa dos Bobos in rural site in the municipality of Aquidauana.

Table 1. Methods and measuring units utilized for the climatic variables and physicochemical water variables obtained for two studied ponds in Aquidauana, Mato Grosso do Sul.

	Parameters	Measuring units	Method of obtention
Climatic variables	Rainfall	mm	CEMTEC-MS and EM-UEMS
	Mean monthly temperature	°C	CEMTEC-MS and EM-UEMS
	Photoperiod	hours	Online-Photoperiod Calculator
Physicochemical water variables	Total phosphorous	mgL ⁻¹	Valderrama1981
	Total nitrogen	mgL ⁻¹	Valderrama1981
	Electric conductivity	µScm ⁻¹	Multiparameter sampler (Hanna HI9828 or YSI 556MPS)
	Dissolved oxygen	DO Mg	
	pH		

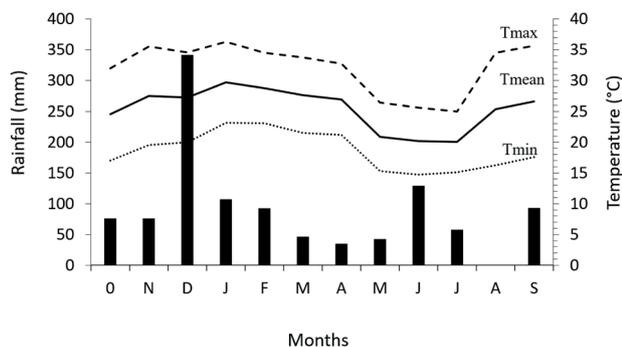


Figure 2. Climatic pattern for the municipality of Aquidauana, Mato Grosso do Sul, from October 2014 to September 2015. Climatic data of Aquidauana for the period of October 2014 to September 2015. (Sources: CEMTEC Mato Grosso do Sul and meteorologic station of the Universidade Estadual de Mato Grosso do Sul).

Data analysis

To verify the patterns of flowering/fructification, we produced circular histograms with the percentage of species or individuals with flowers/fruits. The medium date of flowering/fructification of the species, synchrony (r) and the Rayleigh test (Z) were calculated utilizing the program Oriana 2.0 (Kovach 2004). The synchrony is relative to the concentration around the medium date. The Rayleigh test (Z) calculates the probability of the data being distributed uniformly over the year. Thus, a probability value below the significance level ($p=0.05$) indicates the H_0 hypothesis that the data are uniformly distributed along the circumference (year) was rejected with a chance of error lower than 5%. The circular histograms were built utilizing the language R (ggplot, R Development Core Team 2018).

An initial multiple regression was applied to verify how climatic and physicochemical water variables influence the reproductive phenophases. Next, the selection of models based on the theory of information criteria was utilized to select the simplest and most parsimonious model supported by the data (Burnham & Anderson 2002). The Akaike Information Criterion (AIC) is a tool that has been widely utilized for the selection of models in ecology, being useful when experimentation is unviable (Johnson & Omland 2004).

Results

Phenology of the assemblage of aquatic macrophytes

We observed species of aquatic macrophytes flowering throughout the year (Fig. 3). This phenophase showed low synchrony ($r = 0.08$) and seasonal pattern ($Z = 8.83$, $p < 0.05$), with highest records of the activity in July, October and November (Fig. 3).

Production of immature and ripe fruits was also recorded throughout the year, with the highest percentage of species fructifying during the rainy season, from October to December (Fig. 3). Production of immature fruits showed low synchrony ($r = 0.07$) and seasonal pattern ($Z = 5.83$, $p = < 0.05$), whilst the ripe fruits also presented seasonal pattern ($Z = 36.50$; $p < 0.01$), but median synchrony ($r = 0.2$).

Most species exhibited seasonal (40%) and extended flowering (66.7%). *Eichhornia azurea* and *Ludwigia sedioides* presented peak in the transitional rainy to dry season; *Nymphoides humboldtiana*, *Ludwigia nervosa*, and *L. torulosa* had their peak the rainy season, whereas *L. tomentosa* exhibited its peak in the transitional dry to the rainy season (Tab. 2, Fig. 4). The species *Aeschynomene fluminensis*, *Egeria najas* and *Ludwigia lagunae* showed extended, not seasonal flowering (Tab. 2, Fig. 4).

Seasonal and intermediate flowering was observed in *Hydrolea spinosa*, *Xyris jupicai* (flowering peak in the rainy season), *L. decurrens* (in the rainy season and transitional rainy to dry), *Bacopa myriophylloides*, *Bacopa salzmännii* (flowering peak in the transitional dry to the rainy season) and *Desmoscelis villosa* (flowering peak in the dry season). We did not record short duration flowering.

Seasonal and extended fructification was shown by most species (53.3% and 80%, respectively), including *A. fluminensis*, *L. nervosa*, *L. torulosa*, *N. humboldtiana* (peak in the rainy season), and *E. azurea* and *L. sedioides* (peak in the transitional rainy to dry season) (Tab. 2, Fig. 4). *Ludwigia lagunae* and *L. tomentosa* did not present seasonal fructification (Tab. 2, Fig. 4).

Seasonal and intermediate fructification was observed in *B. myriophylloides*, *B. salzmännii*, *D. villosa*, *E. najas*, *H. spinosa*, *X. jupicai* (fructification peak in the rainy season)

and *L. decurrens* (peak in the rainy season and transitional rainy to dry). We did not record brief fructification.

Phenology by life form

The period of flowering and fructification varied between the studied life forms (Fig. 4). The reproductive phenophases were explained as much by climatic factors and water physicochemical variables, and the models varied according to life form (Tab. 3).

Amphibious species had their reproductive phenophases restrict to the period of July to December (Fig. 5) with marked seasonality ($Z > 275.32$; $p < 0.001$) and high synchrony ($r > 0.6$), and had median date of flowering and fructification in the middle and end of September,

respectively. The production of buds and flowers in this life form was influenced negatively by temperature, rainfall and electric conductivity, and positively by photoperiod, total nitrogen and pH, as well as dissolved oxygen acting negatively on the production of flowers (Tab. 3). The production of buds and immature fruits was influenced by the same variables, and the production of ripe fruits also follows the same pattern, except rainfall (Tab. 3).

Emergent aquatic macrophytes flowered and fructified throughout the year and presented median date for flowering and fructification in the beginning and end on November, respectively (Fig. 5). The phenophases are seasonal ($Z > 15.64$; $p < 0.005$), but showed low synchrony ($r > 0.1$). The pH was the parameter that most influenced the phenophases

Table 2. Studied species of aquatic macrophytes, classified for duration of flowering (buds and flowers) and fructification (immature and ripe fruits) (Ext= extended and Int= intermediate).

Family	Species	Phenophase duration		Voucher
		Flowering (n. of months)	Fructification (n. of months)	
Fabaceae	<i>Aeschynomene fluminensis</i> Vell.	Ext (12)	Ext (9)	78486
Hydrocharitaceae	<i>Egeria najas</i> Planch.	Ext (6)	Int (2)	78498
Hydroleaceae	<i>Hydrolea spinosa</i> L.	Int (3)	Int (3)	78499
Melastomataceae	<i>Desmoscelis villosa</i> (Aubl.) Naudin	Int (4)	Int (5)	78495
Menyanthaceae	<i>Nymphoides humboldtiana</i> (Kunth) Kuntze	Ext (12)	Ext (9)	78485
Onagraceae	<i>Ludwigia decurrens</i> Walter	Ext (6)	Int (5)	78489
Onagraceae	<i>Ludwigia lagunae</i> (Morong) H. Hara	Ext (12)	Ext (12)	78490
Onagraceae	<i>Ludwigia nervosa</i> (Poir.) H. Hara	Ext (8)	Ext (9)	78491
Onagraceae	<i>Ludwigia sedioides</i> (Humb. & Bonpl.) H. Hara	Ext (12)	Ext (12)	78492
Onagraceae	<i>Ludwigia tomentosa</i> (Cambess.) H. Hara	Ext (12)	Ext (12)	78493
Onagraceae	<i>Ludwigia torulosa</i> (Arn.) H. Hara	Ext (8)	Ext (9)	78494
Plantaginaceae	<i>Bacopa myriophylloides</i> (Benth.) Wettst.	Int (5)	Int (4)	78487
Plantaginaceae	<i>Bacopa salzmännii</i> (Benth.) Wettst. ex Edwall	Int (5)	Int (4)	78488
Pontederiaceae	<i>Eichhornia azurea</i> (Sw.) Kunth	Ext (6)	Ext (6)	78497
Xyridaceae	<i>Xyris jupicai</i> Rich.	Int (3)	Int (4)	78496

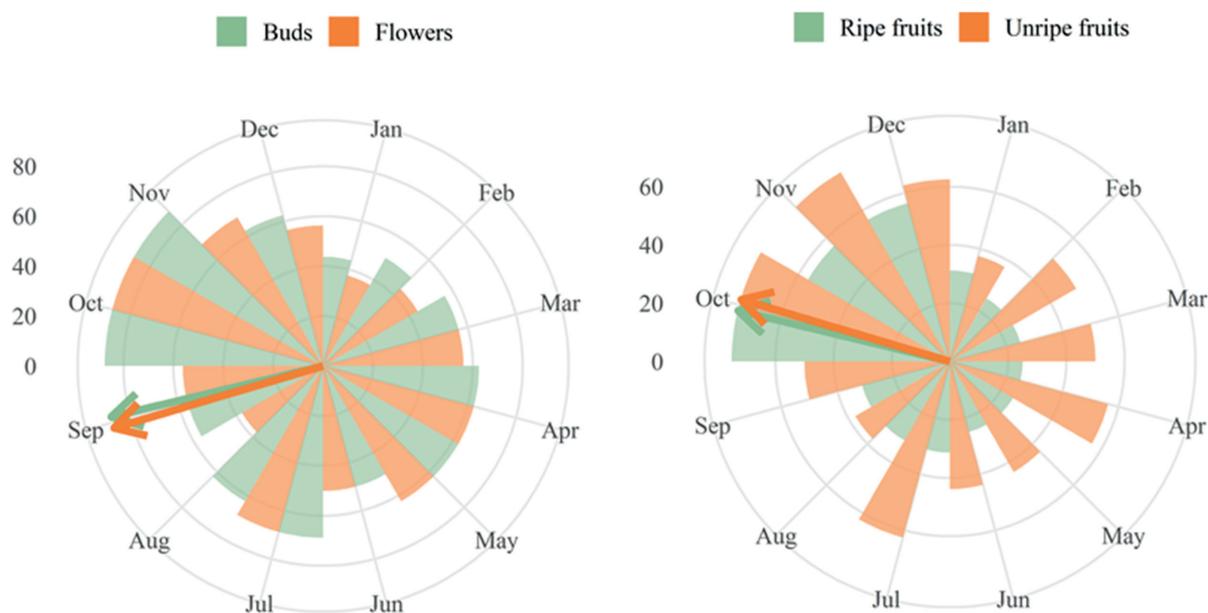


Figure 3. Circular histogram of the percentage of species in flowering and fructification over an annual cycle in ponds, in the Cerrado-Pantanal ecotone, Aquidauana, Mato Grosso do Sul, Brazil.



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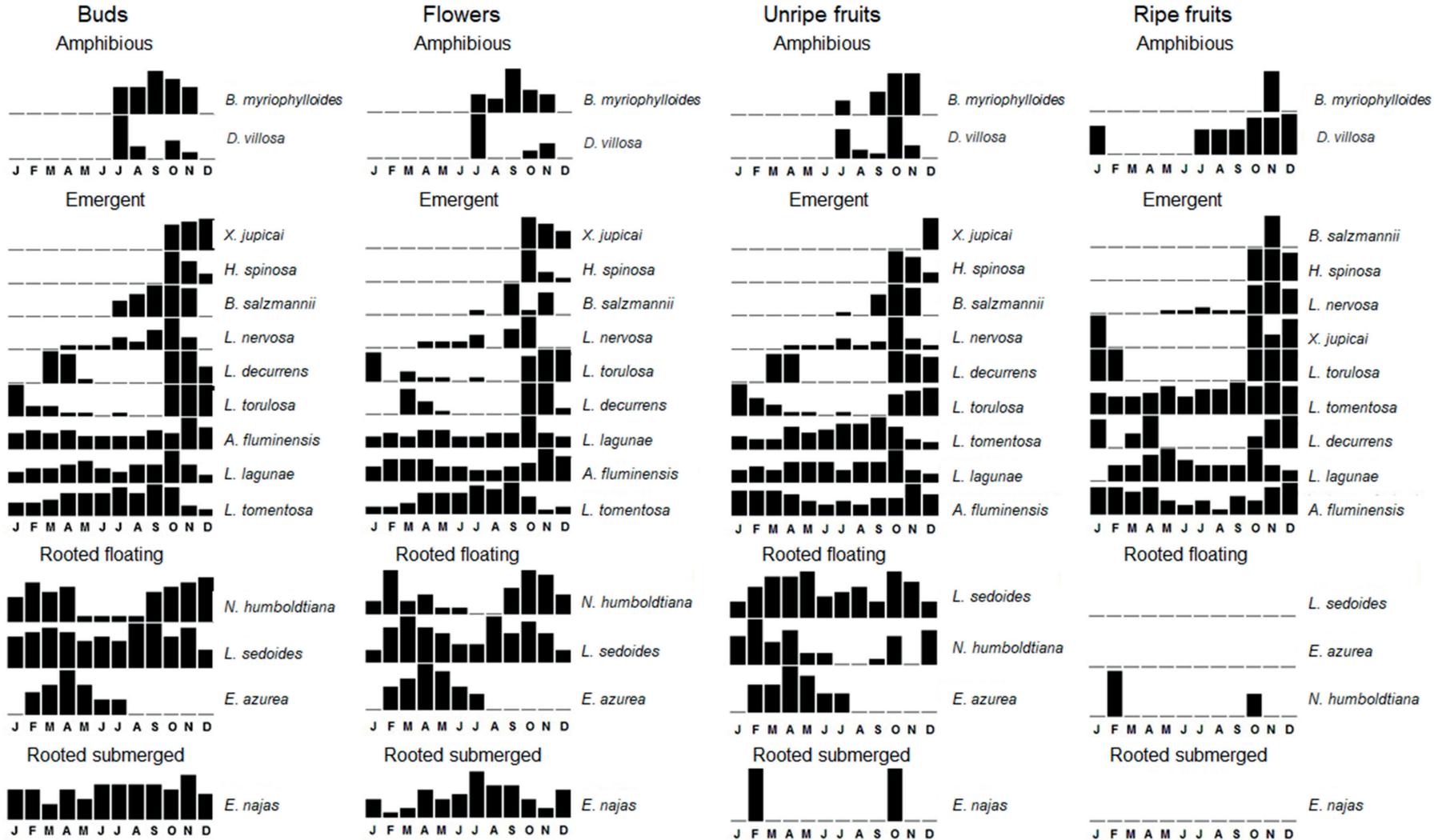


Figure 4. Direct ordination considering the frequency of individuals of each species of aquatic macrophyte, in each phenophase (A: bud, B: flower, C: immature fruits, D: ripe fruits), over an annual cycle (Aquidauana, Mato Grosso do Sul, Brazil).



Table 3. Models according to the Akaike Information Criterion (AIC) between the abiotic variables and the phenophases of different life forms sampled in ponds in the municipality of Aquidauana, Mato Grosso do Sul, Brazil.

Life form	Phenophase	Model	Δ AIC	R ²	F	p
Amphibious	Buds	- 888.46 Intercept - 13.80 Temp. - 0.26 Precip. + 73.10 Photop. + 158.95 TNitr - 0.90 Conductiv. + 56.42 pH	2.32	0.71	9.4	0.0003
	Flowers	- 786.93 Intercept - 13.83 Temp. - 0.20 Precip. + 65.26 Photop. + 120.35 TNitr - 0.83 Conductiv. - 2.98 DO + 58.09 pH	2	0.85	17.8	0.00001
	Immature fruits	- 877.72 Intercept - 9.80 Temp. - 0.19 Precip. + 66.91 Photop. + 172.60 TNitr - 1.07 Conductiv. + 50.51 pH	3.76	0.69	8.4	0.0005
	Ripe fruits	- 607.36 Intercept - 8.80 Temp. + 55.32 Photop. + 129.38 TNitr - 0.69 Conductiv. + 25.32 pH	3.21	0.55	5.9	0.003
Emergent	Buds	- 143.47 Intercept + 31.56 pH	9.65	0.29	17.58	0.0001
	Flowers	- 147.54 Intercept + 31.36 pH	9.95	0.22	12.48	0.001
	Immature fruits	- 110.97 Intercept - 35.90 TNitr + 0.12 Conductiv. + 27.87 pH	8.28	0.28	6.48	0.001
	Ripe fruits	- 115.30 Intercept - 63.65 TNitr + 0.24 Conductiv. + 28.83 pH	9.15	0.3	6.98	0.0007
Rooted floating	Buds	414.35 Intercept - 15.83 Photop. + 0.23 Conductiv. - 24.03 pH	6.99	0.24	3.08	0.05
	Flowers	54.75 Intercept + 63.04 TNitr - 803.98 Tphos	8.48	0.24	4.13	0.03
	Immature fruits	182.70 Intercept + 0.074 Precip. + 65.60 TNitr - 106.70 Ptotal - 19.02 pH	7.69	0.57	7.69	0.001
	Ripe fruits	43.14 Intercept + 17.36 TNitr - 7.54 pH	10.44	0.2	3.51	0.05
Rooted submerged	Buds	53.23 Intercept + 5.64 Temp. + 0.10 Precip. - 22.01 Photop. - 0.15 Conductiv. + 2.82 DO + 15.39 pH	3.15	0.26	2.15	0.11
	Flowers	- 11.09 Intercept - 16.17 Photop. - 61.95 TNitr + 3.29 DO + 36.14 pH	7.05	0.6	8.41	0.0007
	Immature fruits	0.95 Intercept	12.02			

Conductiv.: Electric conductivity (μScm^{-1}), DO: Dissolved oxygen (mgL^{-1}), Photop.: Photoperiod (min), Precip.: Precipitation (mm), Tphos: Total phosphorous (mgL^{-1}), TNitr: Total nitrogen (mgL^{-1}), Temp.: Mean monthly air temperature ($^{\circ}\text{C}$).

of this life form. The production of buds and flowers had as predictor the pH influencing positively; in contrast, the production of immature and ripe fruits was influenced positively by electric conductivity and pH, and negatively by total nitrogen (Tab. 3).

Rooted floating species showed buds, flowers and immature fruits throughout the year, with higher intensity of these phenophases between February and June with the mean date for production of buds and flowers at the end of April, and immature fruits the beginning of that month (Fig. 5). We observed ripe fruits only in February and October, but with low synchrony (Fig. 5). The production of buds and flowers and immature fruits is seasonal ($Z > 23.38$; $p < 0.008$), but showed low synchrony ($r > 0.1$), whereas that of ripe fruits is seasonal ($Z = 66$; $p < 0.001$), with high synchrony among species ($r = 1$).

For production of buds, the most relevant predictor variables were photoperiod and pH (influencing negatively) and electric conductivity (positively). The production of flowers was correlated with total nitrogen and phosphorous positive and negatively, respectively. The formation of immature fruits was correlated with the same variables as flowers and was also influenced by rainfall (positively) and pH (negatively). The production of ripe fruits was influenced by total nitrogen (positively) and pH (negatively) (Tab. 3).

Only one rooted submerged species was investigated (*Egeria najas*) (Fig. 5). The production of buds, flowers and immature fruits were seasonal ($Z > 19.28$; $p < 0.003$), showing low synchrony for buds and flowers ($r > 0.1$) with

the mean date for flowering in the mid-August; in contrast, for immature fruits, the synchrony was high ($r = 1$). Flower emission was negatively influenced by photoperiod and total nitrogen and positively influenced by dissolved oxygen and pH. The selected model did not significantly explain the production of buds and immature fruits (Tab. 3). We did not observe ripe fruit throughout the study.

Thus, the main predictor variables of the phenophases of the various life forms were pH, that influenced 80 % of the analyzed phenophases, total nitrogen (53 %), electric conductivity (46.7 %) and photoperiod (40 %). Dissolved oxygen and total phosphorous were the variables selected in the lowest number of explicative models of the phenophases (20 %). We point out that total phosphorous only influenced phenophases of the rooted floating life form.

Discussion

Phenology of the assemblage of aquatic macrophytes

The occurrence of species in flowering and fructification throughout the year in the studied assemblage can be explained by the presence of different life forms with distinct substrates of nutrient absorption and resource obtention strategies (Irgang *et al.* 1984; Pott & Pott 2000) in the studied areas. Thus, the permanence and maintenance of the fauna dependent on flowers and fruits' resources are favored by the aquatic vegetation.



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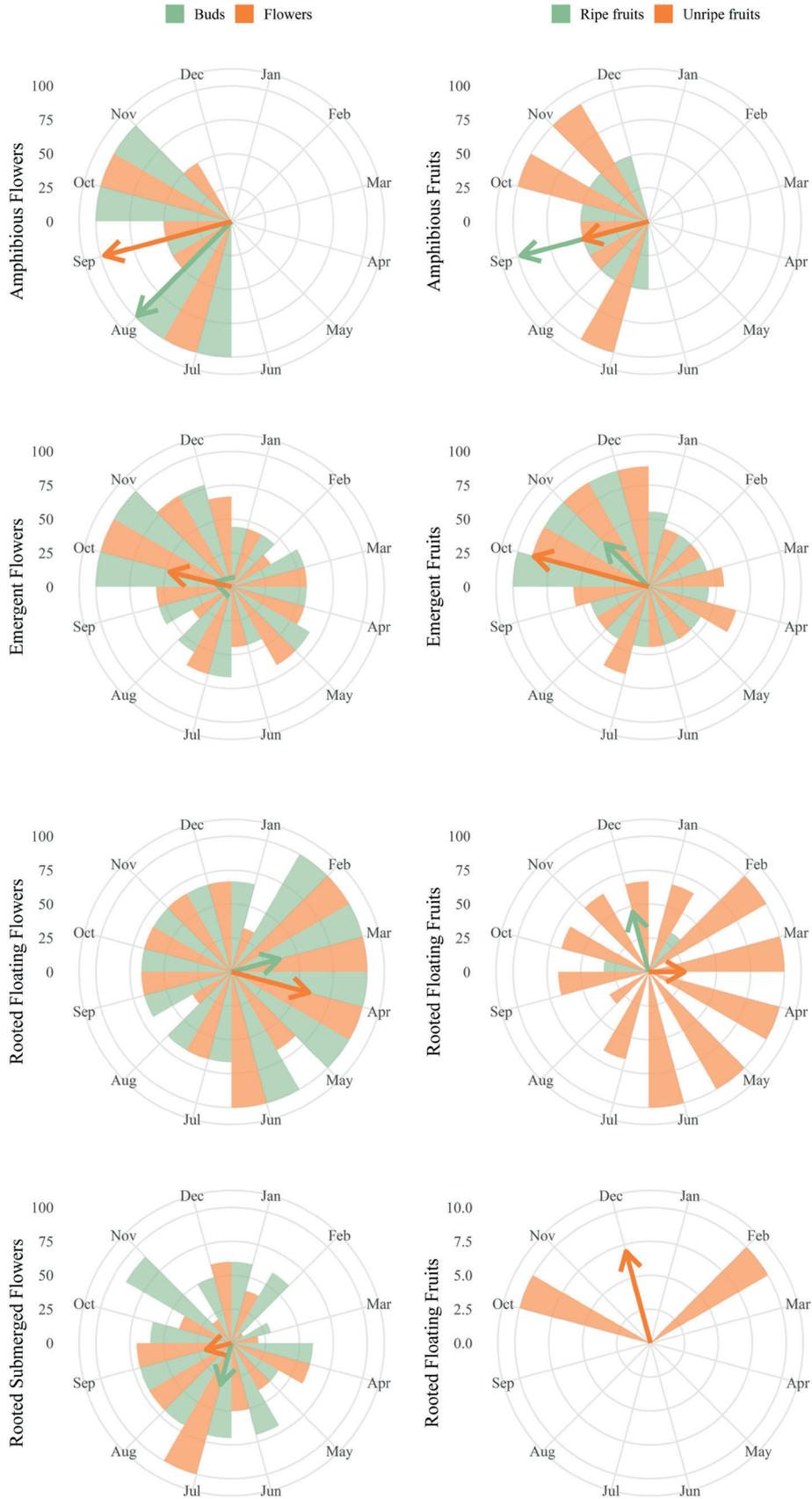


Figure 5. Circular histograma of percentage of amphibious, emergent, rooted floating and rooted submerged species in flowering and fructification over an annual phenological cycle in ponds in Aquidauana, Mato Grosso do Sul, Brazil.



The most intense flowering in the rainy season has been related to the increased temperatures and rainfall, which increase nutrient availability to the plants, that then invest resources in flower production (Morellato & Leitão-Filho 1992). Variation in radiation (Wright & Schaik 1994; Adler & Kielipinski 2000) and pollinators' activity also influence (Wikander 1984; Morellato 1991). A similar flowering pattern occurs in the rainy season in terrestrial plants of the Caatinga (Barbosa *et al.* 2003; Araújo *et al.* 2011), Cerrado grassland (Mantovani & Martins 1988; Batalha *et al.* 1997; Batalha & Mantovani 2000; Batalha & Martins 2004; Tannus *et al.* 2006), Atlantic Forest (Morellato & Haddad 2000; Morellato *et al.* 2000; Pereira *et al.* 2008; Freire *et al.* 2013) and Pantanal (Freitas *et al.* 2013).

Among the studied species, only *Desmoscelis villosa* showed flowering in the dry season. That seems to be the flowering inductor factor of several species of Melastomataceae (Borges 1991). Phenological rhythms related to phylogenetic issues have a dominant role in the flowering of some plants (Kochmer & Handel 1986) and were already observed in several families like Myrtaceae and Rubiaceae (*e.g.* Lobo *et al.* 2003; Bulhão & Figueiredo 2002; Martin-Gajardo & Morellato 2003; Gressler 2005).

Fruits were produced throughout the year, with different ripening periods among life forms. An intenser fructification in the rainy season is generally associated with more favorable seed germination conditions (Foster 1985). The species differ regarding seed dormancy time, that induces dispersal in distinct periods, to germinate in more favorable conditions (Smits *et al.* 1990). Except for the rooted submerged *E. najas*, the species' fructification is correlated with total nitrogen and pH, both variables that vary over the year (Necchi Jr. *et al.* 1996; Esteves 1998) and influence the species physiology, as we will discuss next. We did not evaluate the possible effects of consumers and dispersers of the studied macrophytes.

Phenology by life form

The patterns of flowering and fructification varied among different life forms of aquatic macrophytes. Amphibious plants exhibited patterns of flowering at the end of the dry season and extended to the middle of the rainy season, influenced by temperature, rainfall and photoperiod. Amphibious species generally occupy an interface of the terrestrial and aquatic environment, can exhibit phenological behavior similar to terrestrial plants. During this period, the flowering of terrestrial species has been attributed mainly to reduced water stress provided by the first rains after the dry season, to increased photoperiod and raised temperature (Morellato *et al.* 1989; Morellato 1991; 1995).

Emergent species produced buds and flowers year-round, more accentuated in the rainy season (October-December). Assemblages with such flowering pattern assure animals'

permanence (floral visitors/pollinators) depending on these resources (Morellato 1995). The assemblage of emergent aquatic macrophytes in our study encompasses several species of *Ludwigia*. A study in southern Brazil also reported a long flowering pattern for the genus, of 5-10 months (Vieira 2002).

The flowering pattern of emergent plants has a strict correlation with pH, a variable that influences aquatic plants' physiology (Esteves 1998). That was the parameter that showed influence in most flowering and fructification patterns of aquatic plants (80%) and can influence nutrient concentration and act on the synthesis of hormones that favor and induce the production of flowers and fruits. That variable can influence macrophyte communities' structure, *i.e.*, determine their species composition and abundance in water bodies (Fraser & Morton 1983; Catling *et al.* 1985; Arts & Leuven 1988; Pulido *et al.* 2015; Aoki *et al.* 2017).

The amphibious and emergent life forms fructify at the end of the dry season and the rainy season. That fructification pattern is generally related to adequate water availability for dispersal and germination in the subsequent period, characterized by high rainfall and temperature (Frankie *et al.* 1974; Schaik *et al.* 1993).

The seasonal flowering concentrated in the dry season, found in the rooted floating species, can be related to its advantages, *e.g.*, reducing florivory (Janzen 1967; Rathcke & Lacey 1985) and fewer damages on the reproductive structures caused by rain (Fernandes *et al.* 2011). It may also be an adjustment to the best period for seed germination. A study on seeds of *N. humboldtiana* demonstrated that the best germination rates occurred under high temperatures and moderate light (Batista *et al.* 2013). Those are characteristics of the transitional dry to the rainy season, after the fruit production of rooted floating species.

The rooted submerged *Egeria najas* showed an extended and non-seasonal flowering pattern. This species multiplies readily by stem fragmentation, that is very fragile, the reproduction from seeds being rare (Kissmann 1997). That was corroborated by our study, once we recorded fruits only in October and in February and, consequently, it did not show correlation with any of the analyzed variables. A study on this species analyzed the physicochemical water variables on processes of photosynthesis and growth, showing a positive relationship between nutrient availability and growth rate (Petracco 2006). We found that these variables, together with others, significantly influence the flower production of this life form.

Besides pH, already mentioned, a compound that influenced the phenophases of aquatic plants considerably was total nitrogen (53%). It is an essential element in the composition of molecules that act on metabolic processes in aquatic plants (Larcher 2006) and is also considered as one of the main factors that control the occurrence and the primary production of floating and rooted aquatic macrophytes (Van *et al.* 1999; Biudes & Camargo 2006;



Thomaz *et al.* 2006). Electric conductivity influenced 46.7% of the assemblage phenophases. Conductivity combined with pH determines the availability of carbon (Pulido *et al.* 2015), which is essential for growth and the plant support system's central element.

Photoperiod and temperature are cited as responsible for habitat occupation success by aquatic plants (Colares *et al.* 2007) and favor their primary production (Geneviève *et al.* 1997). Somehow, these factors also function as a trigger for the phenophases of aquatic plants (correlated positively or negatively), standing out photoperiod, that influenced 40% of the phenophases. Plants can obtain more pollination success when flowering occurs in high illumination periods (Schaik *et al.* 1993).

Another relevant parameter was rainfall. Although water at flood is a less restrictive factor for aquatic plants (compared with terrestrial plants), rainfall influences the transport of nutrients to the water and pH (Esteves 1998; Campos *et al.* 2012). One study on the phenology of aquatic macrophytes in the Pantanal reported flowering and fructification associated with inundation phases and a correlation of flowering of some life forms with temperature and rainfall (Catian *et al.* 2019).

Besides the parameters we evaluated, others still need investigation in aquatic communities. Phylogenetic restrictions (Kochmer & Handel 1986; Johnson 1992), availability of pollinators (Rathcke 1988; Newstrom *et al.* 1994; Bhat & Murali 2001) and adjustment to the optimal period of seed dispersal (Oliveira 2008), relevant for many terrestrial species, were not duly studied in aquatic environments.

In our study, we observed that physicochemical water variables help to explain the fructification patterns of aquatic plants. Once the primary elements responsible for eutrophication of water bodies are nitrogen and phosphorous, they can be responsible for changes in some species' reproductive behavior, some with invasive potential, resulting in ecological and economic losses. Long term studies, investigating how such environmental alterations can modify such species' phenology are necessary for the Pantanal and other wetlands.

Acknowledgements

This work had support from the Universidade Federal de Mato Grosso do Sul (UFMS/MEC) and Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES). We thank FUNDECT for support to the projects developed by the research group "Integrated studies on Biodiversity of Cerrado and Pantanal". A. Pott thanks CNPq for the productivity grant (Process 303191/2017-1). We thank Joelder Murilo for assistance in field work and Gudryan Barônio for the figures.

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