Reproductive phenology of aquatic macrophytes in the Cerrado-Pantanal ecotone

Crisley Helena Simão* 1, Flavio Macedo Alves1, Adriana de Barros2, Polyana Milena Simão2, Arnildo Pott1 and Camila Aoki1, 2

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;
Batalha & Mantovani 2000; Batalha & Martins 2004; Tannus et al. 2006), Caatinga (Barbosa et al. 2003; Araújo et al. 2011), Atlantic Forest (Morello & Haddad 2000; Morello 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 (Felfifi 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 (Péel 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 salzmannii (Benth.) Wettst. ex Edwall, Hydrocleys 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 [Elodea azuarea (Sw.) Kunth, Ludwigia sedoides (Humb. & Bonpl.) H.Hara and Nymphoides homboldtiana (Kunth) Kunzte] 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 exsiccate incorporated into the collection of the Herbarium CGMS of the Universidade Federal do Mato Grosso do
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      |
| Total phosphorous           | mgL⁻¹           | Valderrama1981                     |
| Total nitrogen              | mgL⁻¹           | Valderrama1981                     |
| Electric conductivity       | µScm⁻¹          |                                    |
| Dissolved oxygen            | DO Mg           | Multiparameter sampler             |
| pH                          |                 | (Hanna HI9826 or YSI 556MPS)       |
| Physicochemical water variables |             |                                    |
| Total phosphorous           | mgL⁻¹           |                                    |
| Total nitrogen              | mgL⁻¹           |                                    |
| Electric conductivity       | µScm⁻¹          |                                    |
| 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 H0 hypothesis that the data are uniformly distributed along the circumference (year) was rejected with a chance of error lower than 5 %.

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 Criterium (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 salzmannii (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 intermediate 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. salzmannii, 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 |
|-----------------|----------------------------------------------|---------------------|---------|
| Fabaceae        | Aeschynomene fluminensis Vell.               | Ext (12)            | 78486   |
| Hydrocharitaceae| Egeria najas Planch.                         | Ext (6)             | 78498   |
| Hydroloaceae    | Hydroloa spinosa L.                          | Int (3)             | 78499   |
| Melastomataceae | Desmoscelia villosa (Aubl.) Naudin           | Int (4)             | 78495   |
| Menyanthaceae   | Nymphoides humboldtiana (Kunth) Kuntze       | Ext (12)            | 78485   |
| Onagraceae      | Ludwigia decurrens Walter                    | Ext (6)             | 78498   |
| Onagraceae      | Ludwigia lagunae (Morong) H. Hara            | Ext (12)            | 78490   |
| Onagraceae      | Ludwigia nervosa (Foix.) H. Hara             | Ext (8)             | 78491   |
| Onagraceae      | Ludwigia sedoides (Humb. & Bonpl.) H. Harra  | Ext (12)            | 78492   |
| Onagraceae      | Ludwigia tomentosa (Cambess.) H. Hara        | Ext (12)            | 78493   |
| Onagraceae      | Ludwigia rupulosa (Arn.) H. Harra            | Ext (8)             | 78494   |
| Plantaginaceae  | Bacopa myriophylloides (Benth.) Wettst.       | Int (5)             | 78487   |
| Plantaginaceae  | Bacopa salzmannii (Benth.) Wettst. ex Edwall | Int (5)             | 78488   |
| Pontederiaceae  | Eichornia azurea (Sw.) ex Wettst.             | Ext (6)             | 78497   |
| Xyridaceae      | Xyris jupicai Rich.                          | Int (3)             | 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.
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).
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 (Irgan 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.
Figure 5. Circular histogram 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 & Kielpinski 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; Balatalha et al. 1997; Balatalha & Mantovani 2000; Balatalha & 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 & Leuen 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 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;
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. 1993).

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 Guadryan Barônio for the figures.

**References**

Abernethy K, Bush ER, Forget PM, Mendoza I, Morellato LPC. 2018. Current issues in tropical phenology: a synthesis. Biotropica 50: 477-482.

Adler GH, Kielbinski KA. 2000. Reproductive phenology of a tropical canopy tree, *Spondias mombim*. Biotropica 32: 686-692.

Aoki C, Faria RR, Damasceno-Junior GA, Pott A. In press. Synthesis of the present knowledge on plant phenology of the Pantanal. In: Damasceno-Junior GA, Pott A. (eds.) Flora and Vegetation of the Pantanal wetland. Berlin, Série: Plant and Vegetation, Springer.

Aoki C, Teixeira-Gamarra MC, Gamarra RM, et al. 2017. Abiotic factors drive the structure of aquatic plant assemblages in riverine habitats of the Brazilian “Pantanal”. Brazilian Journal of Botany 40: 405-415.

APG IV - Angiosperm Phylology Group. 2016. An update of the Angiosperm Phylology Group classification for the orders and families of flowering plants: APG IV. Botanical Journal of the Linnean Society 181: 1-20.

Araújo LDA, Quirino ZGM, Machado IC. 2011. Fenologia reprodutiva, biologia floral e polinização de *Allanamanda blanchetti*, uma Apocynaceae endémica da Caatinga. Revista Brasileira de Botânica 34: 211-222.

Arts GHP, Leuven RSEW. 1988. Floristic changes in shallow soft waters in relation to underlying environmental factors. Freshwater Biology 20: 97-111.

Barbosa DCA, Barbosa MCA, Lima LCM. 2003. Fenologia de espécies lenhosas da caatinga. In: Leal IR, Tabarelli M, Silva JMC. (eds.) Ecologia e conservação da caatinga. Recife, Universitária UFPE. p. 657-693.

Barbón JW, Gunnison D, Carpenter SR. 1991. Sediment interactions with submerged macrophyte growth and community dynamics. Aquatic Botany 41: 41-65.

Batalha MA, Aragaki S, Mantovani W. 1997. Florística do cerrado em Emas, Pirassununga, SP. Boletim de Botânica da Universidade de São Paulo 16: 49-64.

Batalha MA, Mantovani W. 2000. Reproductive phenological patterns of Cerrado plant species at the Pê-de-Gigante reserve (Santa Rita do Passo Quatro, SP, Brazil): a comparison between the herbaceous and wood floras. Revista Brasileira Biologia 60: 129-145.

Batalha MA, Martins FR. 2004. Reproductive phenology of the Cerrado plant community in Emas National Park (Central Brazil). Australian Journal of Botany 52: 140-161.

Batista TL, Freire MA, Margalhães UAS, Colares IG. 2013. Efeitos de fatores de ambientais sobre a germinação de sementes de *Nymphoides indica* (L.). O. Kuntze (Menyanthaceae). Estudos de Biologia - Ambiente e Diversidade 85: 143-152.

Bertazzioni EC, Damasceno-Júnior GA. 2011. Aspectos da Biologia e Fenologia de *Oryza latifolia* Desv. (Poaceae) no Pantanal sul-mato-grossense. Acta Botanica Brasílica 25: 476-486.

Bhat DM, Murali KS. 2001. Phenology of understorey species of tropical moist forest of Western Ghats region of Uttara Kannada district in South India. Current Science 81: 799-805.

Biudes JFV, Camargo AFM. 2006. Changes in biomass, chemical composition and nutritive value of *Sparrtina alterniflora* due to organic pollution in the Itanhâem River Basin (SP, Brazil). Brazilian Journal of Biology 66: 781-789.

Borges HEN. 1991. Biologia reprodutiva de quatro espécies de Melastomataceae. MsC Thesis, Universidade Estadual de Campinas, Campinas.

Brasil MS, Matos AT, Soares AA. 2007. Plantio e desempenho fenológico da taboa (*Typha sp.*) utilizada no tratamento de esgoto doméstico em sistema alagado construído. Engenharia Sanitária e Ambiental 12: 266-272.

Bulhão CF, Figueiredo PS. 2002. Fenologia de espécies arbróreas em uma área de cerrado marginal no nordeste do Maranhão. Revista Brasileira de Botânica 25: 361-369.

Burnham KP, Anderson DR. 2002. Model selection and multimodel inference - A practical-theoretic approach. 2nd. edn. New York, Springer-Verlag.

Campos CF de, Souza GSF, Martins D, Pereira MRR, Bagatta MVB. 2012. Influência da chuva após aplicação de Imazamox sobre o controle de plantas daninhas aquáticas. Bioscience Journal 28: 413-419.
Crisley Helena Simão, Flavio Macedo Alves, Adriana de Barros, Polyana Milena Simão, Arnildo Pott and Camila Aoki

Catian G, Schemer-Dias E, Pott A. 2017. Reproductive phenology of Polygonum hispidum Kunth and P. punctatum Elliott (Polygonaceae), in response to the flooding cycle in the Pantanal, Brazil. Boletim do Museu Paraense Emílio Goeldi - Ciências Naturais 12: 197-207.

Catian G, Schemer-Dias E, Pott A. 2019. Reproductive phenology of macrophyte community in response to wetland flooding cycle. Oecologia Australis 23: 856-873.

Catling PM, Freedman B, Stewart C, Kerekes JI, Lefkovich LP. 1995. Aquatic plants of acid lakes in Kejimkujik National Park, Nova Scotia; floristic composition and relation to water chemistry. Canadian Journal of Botany 73: 724-729.

Colares IG, Batista TL, Magalhães UAS, Santos LC, Schlee MBB. 2007. Efeitos da temperatura e do fotoperíodo no crescimento e nas respostas fotossintéticas de Potamogeton pectinatus L. (Potamogetonaceae), em cultivo experimental. Estudos de Biologia 29: 297-306.

Esteves FA. 1998. Fundamentos de Limnologia. 2nd edn. Rio de Janeiro, Interciência.

Fava WS, Covre WS, Sigrist MR. 2011. Atalâa phareata and Bacillus glaucescens (Arecaceae, Arecidoideae): Phenology and pollination ecology in the Pantanal, Brazil. Flora 206: 575-584.

Felfili JM, Silva Junior MC, Dias BJ, Resende AV. 1999. Estudo fenológico de Strychnos odoradens (Mart.) Coville no cerrado sensu stricto da Fazenda Água Limpa, no Distrito Federal, Brasil. Revista Brasileira de Botânica 22: 83-90.

Fernandes GW, Oki Y, Sanchez-Azofeifa A, Faccion G., Amaro-Arruda HC. 2011. Hall impact on leaves and endophytes of the endemic threatened Coccoloba cerefera (Polygonaceae). Plant Ecology 212: 1687-1697.

Flora do Brasil 2020. 2020. Jardim Botânico do Rio de Janeiro. Rio de Janeiro. http://floradobrasil.jbrj.gov.br/. 30 Jan. 2020.

Foster RB. 1985. The seasonal rhythm of fruitfall on Barro Colorado Island. In: Lieth Jr. EG, Rand AS, Windsor DM. (eds.) The ecology of a tropical forest: seasonal rhythms and long-term changes. Washington, Smithsonian Institution Press. p. 151-172.

Frankie GW, Baker HG, Opler PA. 1974. Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. Journal of Ecology 62: 881-913.

Fraser O, Morton JK. 1983. Aquatic plants in Lake Superior Provincial Park in relation to water chemistry. Canadian Field Naturalist 97: 181-186.

Freire JM, Azevedo MC, Cunha CF, Silva TF, Resende AS. 2013. Fenologia e frutificação de Myrtaceae de Floresta Atlântica: Roessleria 6: 395-404.

Gressler E. 2005. Floração e frutificação de Myrtaceae da Floresta Atlântica: limitações ecológicas e filogenéticas. MSc Thesis, Universidade Estadual Paulista, Rio Claro.

Irgang BE, Pedralli G, Waechter JI. 1984. Macrófitos aquáticos da Estação Ecológica do Tatin, Rio Grande do Sul, Brasil. Roesleria 6: 395-404. JANZEN DF. 1967. Synchronization of sexual reproduction of trees within the dry season in Central America. Evolution 21: 620-37.

Johnson JB, Omland KS. 2004. Model selection in ecology and evolution. Trends in Ecology & Evolution 19: 101-108.

Johnson SD. 1992. Climatic and phylogenetic determinants of flowering seasonality in the Cape flora. Journal of Ecology 80: 567-572.

Kissmann KG. 1997. Plantas infestantes e nocivas. 2nd edn. São Paulo, Lammi J. 2001. Online photoperiod calculator. Computation of daylengths, sunrise/sunset times, twilight and local noon. Version 1.9 L http://www.sci.fi/~benefon/sol.html. 25 Oct. 2015.

Larcher W. 2006. Ecosistemas vegetal. São Carlos, SP, Editora e Livraria Rima.

Lenza E, Klink CA. 2006. Comportamento fenológico de espécies lenhosas em um cerrado sentido restrito de Brasília, DF. Revista Brasileira de Botânica 29: 627-638.

Lieth H. 1974. Introduction to phenology and the modeling of seasonality. Phenology and seasonality modeling. In: Lieth H. (ed.) Ecological Studies 8. Berlin, Springer-Verlag. p. 3-19.

Lima MS, Damasceno-Junior GA. 2020. Phenology and dispersal syndromes of woody species in deciduous forest fragments of the Pantanal in Mato Grosso do Sul State, Brazil. Acta Botanica Brasiliensis 34: 312-326.

Lobo JA, Quesada M, Stoner KE, et al. 2003. Factors affecting phenological patterns of Bombacaceous trees in seasonal forests in seasonal forests in Costa Rica and Mexico. American Journal of Botany 90:1054-1063.

Mantovani W, Martins FR. 1988. Variações fenológicas das espécies do cerrado da reserva biológica de Moju-Guaçu, Estado de São Paulo. Revista Brasileira de Botânica 11: 101-112.

Marengo JA, Alves LM, Torres RR. 2015. Regional climate change scenarios in the Brazilian Pantanal watershed. Climate Research 68: 201-213.

Marquis RJ, Moraes HC, Diniz IR. 2002. Interactions among Cerrado plants and their herbivores: unique or typical?. In: Oliveira OS, Marquis RJ. (eds.) The cerrados of Brazil. New York, Columbia University Press. p. 306-328.

Martin-Gajardo IS, Morellato LPC. 2003. Fenologia de Rubiaceae do sub-bosque em floresta Atlântica no sudeste do Brasil. Revista Brasileira de Botânica 26: 299-309.

Miranda HS, Sato MN, Andrade SM, Haridasan M, Moraes HC. 2004. Queimadas de Cerrado: caracterização e impactos. In: Aguilar LMS, Camargo AJA. (eds.) Cerrado ecolóxica e caracterización. Planaltina, DF, EMBRAPA Cerrados. p. 69-123.

Morellato LPC. 1991. Estudo da fenologia de árvores, arbustos e lianas do cerrado da reserva biológica de Moji-Guaçu, Estado de São Paulo. Revista Brasileira de Botânica 12: 85-98.

Morellato LPC, Talora DC, Takahasi A, Bencke CC, Romero EC, Zipparro VB. 2000. Phenology of Atlantic rain forest trees: a comparative study. Biotropica 32: 811-823.

Morellato LPC. 1995. As estações do ano na floresta. In: Morellato LPC, Haddad CFB. (eds.) Introduction: The Brazilian Atlantic Forest. Biotropica 32: 786-792.

Morellato LPC, Rodrigues RR, Leitão Filho HF, Joly CA. 1989. Estudo fenológico de árvores e arbustos em um cerrado restrito de Brasília, DF. Revista Brasileira de Botânica 22: 83-90.

Munguía-Rosas MA, Ollerton J, Parra-Tabla V, De-Nova JA. 2011. Meta-análisis de fenología y dispersión de aves, reptiles, anfibios y mamíferos en la Serra do Japi: ecologia e preservación de una área florestal en el sudeste del Brasil. Campinas, Editora da UNICAMP. PAFESP. p.112-140.

Murno A, Sano SM, Almeida SP, Ribeiro JF. (eds.) Cerrado ecologia e caracterização. Planaltina, DF, EMBRAPA Cerrados. p. 37-41.

Necchi Jr. O, Branco LH, Branco CCZ. 1996. Análise nictimeral e sazonal de um cerrado da reserva biológica de Moji-Guaçu, Estado de São Paulo. Revista Brasileira de Botânica 22: 83-90.

Oliveria PEAM. 2008. Fenologia e biologia reprodutiva das espécies de Cerrado. In: Sano SM, Almeida SP, Ribeiro JF. (eds.) Fenologia e biologia da flora. Brasília, DF, EMBRAPA Cerrados. p. 273-290.

Ollerton J, Finlayson BL, McMahon TA. 2007. Updated world map of the Köppen-Geiger climate classification. Hydrology and Earth System Sciences 11: 1633-1644.

Pereira TS, Costa MLNN, Moraes LFD, Luchiari C. 2008. Fenologia de espécies arbóreas em Floresta Atlântica da Reserva Biológica de Poço das Antas, Rio de Janeiro, Brasil. Iheringia, Série Botânica, Porto Alegre 63: 329-339.
Reproductive phenology of aquatic macrophytes in the Cerrado-Pantanal ecotone

Petracco P. 2006. Efeitos das variáveis abióticas na produção primária de Egeria najas e Utricularia breviscarpa da lagoa do Óleo (Estação Ecológica de Jataí, Luiz Antonio-SP). PhD Thesis, Universidade Federal de São Carlos, São Paulo.

Pinto AM, Morellato LPC, Barbosa AP. 2008. Fenologia reprodutiva de Dipteryx odorata (Aubl.) Willd (Fabaceae) em duas áreas de floresta na Amazônia Central. Acta Amazonica 38: 643-649.

Pott VJ, Pott A. 2000. Plantas aquáticas do Pantanal. Brasília, EMBRAPA.

Pulido C, Riera JL, Ballesteros E, Chappuis E, Gacia E. 2015. Predicting aquatic macrophyte occurrence in soft-water oligotrophic lakes (Pyrenees mountain range). Journal of Limnology 74: 143-154.

R Development Core Team. 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. https://www.r-project.org/foundation/. 03 Jul. 2020.

Rathcke B, Lacey EP. 1985. Phenological patterns of terrestrial plants. Annual Review of Ecology and Systematics 16: 179-214.

Rathcke B. 1988. Flowering phenologies in a shrub community: competition and constraints. Journal of Ecology 76: 975-994.

Rathcke B. 1988. Flowering phenologies in a shrub community: competition and constraints. Journal of Ecology 76: 975-994.

Santos SB, Pedralli G, Meyer ST. 2005. Aspectos da fenologia e ecologia de Hedychium coronarium (Zingiberaceae) na Estação Ecológica do Tripuí, Ouro Preto-MG. Planta Daninha 23: 175-180.

Schiavo JA, Pereira MG, Miranda LPM, Neto AHD, Fontana A. 2010. Caracterização e Classificação de solos desenvolvidos de arenitos da formação Aquidauana- MS. Revista Brasileira Ciência do Solo 34: 881-889.

Smits AJM, Avesaath PH, Velde GVD. 1990. Germination requirements and seed bank of some nymphaeid macrophytes: Nymphaea alba L., Nuphar lutea (L.) Sm. and Nymphoides peltata (Gmel.) O. Kuntze. Freshwater Biology 24: 315-326.

Souza EP, Martins SRO. 2010. Conflicts territoriais no entorno do Parque Natural Municipal da Lagoa Comprida em Aquidauana/MS. Percurso: Sociedade, Natureza Cultura 11: 273-289.

Talora DC, Morellato LPC. 2000. Fenologia de espécies arbóreas em floresta de planície litorânea do sudeste do Brasil. Revista Brasileira de Botânica 23: 13-26.

Tannus JLS, Assis MA, Morellato LPC. 2006. Fenologia reprodutiva em campo sujo e campo úmido numa área de Cerrado no sudeste do Brasil. Itirapina - SP: Biota Neotropica 6: 3. doi: 10.1590/S1676-06032006000300008

Thomaz SM, Pagliaro TA, Bini LM, Murphy KJ. 2006. Effect of reservoir drawdown on biomass of three species of aquatic macrophytes in a large sub-tropical reservoir (Itaipu, Brazil). Hydrobiologia 570: 53-59.

Valderrama JC. 1981. The simultaneous analysis of total nitrogen and total phosphorous in natural waters. Marine Chemistry 10: 109-222.

Van TK, Wheeler GS, Center TD. 1999. Competition between Hydrilla verticillata and Vallisneria americana as influenced by soil fertility. Aquatic Botany 62: 225-233.

Vieira AOS. 2002. Biologia reprodutiva e hibridização em espécies sintópicas de Ludwigia (Onagraceae) no sudeste do Brasil. PhD Thesis, Universidade Estadual de Campinas, Campinas.

Wikander T. 1984. Mecanismos de dispersión de diasporas de una selva decídua en Venezuela. Biotropica 16: 276-283.

Wright SJ, Smits CP. 1994. Light and the phenology of tropical trees. American Naturalist 143: 192-199.