

The floristic heterogeneity of the Pantanal and the occurrence of species with different adaptive strategies to water stress

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Received October 14, 2010 – Accepted December 13, 2010 – Distributed April 30, 2011

Abstract

The Pantanal is characterised by a diversity of environments with areas ranging from periodic or permanent heavy flooding to areas with low flood levels, and even environments that never flood. Plant species which inhabit the floodplain are distributed in specific niches, with influence of various phytogeographic domains, including the Seasonal Semi-deciduous Forest, Amazon Rainforest, *Cerrado* and *Chaco*, as well rocky remnants, with a wide ecological span in their components. In intensely flooded areas, aquatic macrophytes are widely distributed, with their dynamics closely linked to time, depth and extent of flooding. Although the term “Pantanal” suggests a huge swamp-type wetland, water level variation during a seasonal cycle does not directly reach the root system of many plants. The landscape diversity of the Pantanal wetland is molded by the flood pulse, which interferes with the dynamics of plant communities. Therefore, the retraction and expansion of populations or communities is reflected in important ecological characteristics, considering the variety of morphological, anatomical and ecophysiological features of the species, whose phenotype is the result of a particular genotype. The present study discusses peculiar issues in the adaptation of species distributed in the Pantanal biome and underscores the importance of multidisciplinary approaches to obtain conclusive data on adaptive studies.

Keywords: flood pulse, ecophysiological features, adaptation of species.

A heterogeneidade florística do Pantanal e a ocorrência de espécies com diferentes estratégias adaptativas ao estresse hídrico

Resumo

O Pantanal caracteriza-se pela diversidade de ambientes com áreas que variam desde intenso alagamento, periódico ou permanente, a áreas com baixo índice de alagamento até ambientes nunca alagados. Espécies vegetais que habitam a planície distribuem-se em nichos específicos, com influência de vários domínios fitogeográficos, entre eles a Floresta Estacional Semidecidual, Floresta Amazônica, Chaco e Cerrado, além de remanescentes rochosos, prevalecendo grande amplitude ecológica de seus componentes. Nas áreas de intenso alagamento, macrófitas aquáticas se distribuem amplamente, com dinâmica intimamente ligada ao tempo, intensidade e amplitude de alagamento. Apesar de o termo Pantanal induzir a ideia de ambiente de alagamento intenso, para muitas espécies, as variações do nível da água num ciclo sazonal não atingem o sistema radical diretamente. A diversidade de paisagens na planície é moldada pelo pulso de inundação que interfere diretamente na dinâmica das comunidades de plantas. Assim, retração ou expansão de populações ou comunidades, reflete características ecológicas importantes, a exemplo do aparato morfológico, anatômico e ecofisiológico das espécies, cujo fenótipo é resultante de genótipo particular. Neste trabalho, são discutidas questões peculiares sobre a adaptação das espécies distribuídas no bioma Pantanal e ressaltada a importância de abordagens multidisciplinares para obtenção de dados conclusivos em estudos adaptativos.

Palavras-chave: pulso de inundação, aparatos ecofisiológicos, adaptação de espécies.

1. Diversity of Environments of the Pantanal Wetlands

The Pantanal is characterised by the heterogeneity of vegetation units, which occupy distinct environments created by fluvial morphogenesis (Adámoli and Pott, 1996; Oliveira, 2007). Several plant families inhabit typical floodable fields, widely distributed in the Pantanal wetland depressions, as well as the *cordilheiras* (strands of elevated soil with unflooded woody vegetation) and *capão* (circular or elliptical forest distributed on periodically flooded natural grassland matrix) (Damasceno-Junior et al., 1999). In the Pantanal wetlands, which constitute about 35% of the Upper Paraguay River Basin (*Bacia do Alto Paraguai*) area, several minor watersheds drain large headwater areas, which are responsible for the vast flood area of the plain. Although the Pantanal is associated with the Paraguay River floodplain and its tributaries, along the wetland occur microbasins arising from the residual relief hills throughout the entire western edge of the Pantanal (Abdon and Silva, 2006).

Among the landscape units the Urucum Residual Plateau (*Planalto Residual do Urucum*) stands out, a formation which holds the *Maciço do Urucum*, a priority area for conservation, because of its composition and richness of plant species (Brasil, 1999) and endemism. It presents isolated hills located in low areas, with altitudes between 300 and 1000 m, entisols and podzol and low humic gley, covered by submontane seasonal semi-deciduous forest and lowland forests (Alho and Gonçalves, 2005). Damasceno-Junior et al. (2005) cite the rocky vegetation formations, shrubby grassland (*campo sujo*), *cerrado*, closed woodland (*cerradão*) and semi-deciduous and deciduous forests, as the phytophysionomies of this formation.

The remnants of rock formations of limestone, sandstone, iron and manganese distributed singly or in North-South axis ridges in the wetland, currently suffer major anthropogenic pressure to extract ore. These areas hold grasslands with particular flora along an altitudinal gradient and, although the floristic inventories are still insufficient to determine the species richness, there is apparently a considerable degree of endemism, with the occurrence of *Aspilia graziellae*, *Gomphrena centrotata* (Pott et al., 2000) and *Vernonia pottii* (Esteves, 2005) being reported on these rock formations. In the low altitude areas the endemic species *Arachis diogoi*, *A. vallsii*, *Maranta pantanensis*, *Stilpnopappus pantanalensis* and *Xanthosoma pottii* stand out (Pott and Pott, 2009). It is suggested that the low level of endemism found in the Pantanal is a consequence of its recent emergence (Quaternary), with insufficient time for the speciation processes (Junk et al., 2006).

Although the term “Pantanal” refers to a region with essentially hydrophyte vegetation, common in swamps, xerophytic and mesophytic species are also distributed in various landscape units, with floristic composition influenced by phytogeographic provinces of *Cerrado*, Amazon Rainforest, Semi-deciduous Forest and *Chaco* (Damasceno-Junior et al., 2005; Oliveira, 2008). The

phytophysionomies of these provinces are mixed in the Pantanal wetlands, in floodable and flood-free areas, in edge areas and on the plateaus.

Alho (2008a,b) emphasises the remarkable combination of xerophytic and mesophytic vegetation growing side by side in seasonally flooded areas in the Pantanal. Tree and shrub species occur at periodically flooded spots, or in areas not subjected to the flood pulse effect of the annual cycle. However, many herbaceous plants and aquatic macrophytes occur in areas with particular water variation or those permanently flooded. Thus, the Pantanal landscape is shaped by water regime, and its dynamics reflect the local rainfall and, mainly, changes in water level corresponding to rainfall in the headwaters of Paraguay River tributaries.

The floristic composition of a certain region is dynamic and probably continues to change over time. On a local scale, this can be exemplified by the seasonal cycle of the Pantanal, where, due to its multiannual period of flood and drought with distinct intensity and duration (Pott and Adámoli, 1996), the species succession and composition in flooded fields is peculiar, and therefore the population dynamics is markedly affected by water regime. The retraction or expansion of the populations or communities are reflected by important ecological characteristics, considering the variety of morphological, anatomical and ecophysiological features of the species, whose phenotypes are the result of a particular genotype (Fahn and Cutler, 1992).

When analysing the morphoanatomical adaptations of Pantanal plants, it is possible to classify them according to their habitats: species that inhabit regions strongly influenced by flood pulse – Pantanal sensu stricto –, and those regions which are not influenced by periodic flood – Pantanal sensu lato (which comprise all species distributed in the biome). Plant species or communities that naturally grow in a given environment share morphoanatomical characteristics and compatible physiological balances (Larcher, 2004; Fahn and Cutler, 1992), which make them adapted to that particular condition. For Fahn and Cutler (1992), adaptation results from the interrelationships of living organisms and the environment they inhabit and from the evolutionary changes throughout the life history of several classes of organisms in their particular environment.

Thus, understanding the structure of plant organs and tissues in relation to the environment for which they were selected during their evolutionary course, involves studies of ecological anatomy, and these must be conducted in a multidisciplinary way, complemented by genetic and ecophysiological studies. With these studies, it is possible to answer more precisely whether the characteristics described are merely phenotypic plasticity or if they are the reflection of genetic changes.

Extensive Pantanal floodable areas consist of monodominant formations of tree populations. Among them can be mentioned the areas of *Tabebuia aurea* (Manso) Benth. et Hook., locally known as *paratudal*, areas with *Tabebuia heptaphylla* (Vell.) Tol., known as *piaval*, the formation known as *cambarazal* comprised of

Vochysia divergens Pohl, the *lixerial* comprised of *Curatella americana* L. and *carandazal* of *Copernicia alba* Morong (Pott, 1994). It is noteworthy that these species are also distributed in plant communities of other biomes, but it is only in the Pantanal that they form large monodominant populations of varying size and shape, reaching an area of 1,000 hectares or more. These species maintain part of the shoot and root system in the anoxic environment for periods ranging from 1 to 4 months.

The physical environmental characteristics are very distinct, when comparing the Pantanal, *Cerrado* and Semi-deciduous Forest. This makes the evaluation of species with wide distribution an interesting target for research. A recent work by Holsback-Menegucci et al. (2008) evaluated young plants of *Guazuma ulmifolia* Lam. (Malvaceae) that were artificially flooded for 100 days. These were from two populations, one from the Paraná River Basin and the other from the Pantanal. Higher growth and biomass of aerial portions were observed in the Pantanal plant population, while hypertrophied lenticels were seen in the seedlings of the Paraná River Basin population, indicating distinct ecophysiological and morphoanatomical responses in both populations.

This may indicate that populations of the same species occurring in vegetation formations with different abiotic selection pressure express distinct phenotypes in ecophysiological terms, unaccompanied by differentiation of the reproductive organ morphology, which is usually used to characterise the species. This may be merely phenotypic plasticity or may be already genetically established. Santiago and Paoli (2007) pointed out that large morphology variations in response to flood do not determine the ecophysiological tolerance of the species to it, indicating that within a population, some individuals express morphological changes and others apparently do not express any modification.

The visible changes in global climate have altered the frequency and intensity of drought and flooding events, bringing important consequences for growth and survival of cultivated and native plants. Understanding what adaptations allow plants to respond drought stress is crucial for predicting the impacts of these climate changes in crop production and environmental dynamics (Atkin and Macherel, 2009). Since almost all plant species that comprise the Pantanal occur in other biomes whose physical environmental characteristics are distinct, populations of this biome are excellent models for studies of adaptations to stress.

2. Adaptations of the Plants of the Pantanal

The plant communities of the Pantanal are annually exposed to restrictions in obtaining resources. Thus, plants growing in low areas of Pantanal wetlands, which are called Pantanal *sensu stricto* areas in this study, go through the annual cycle of excess and lack of water. Typical plants from flooded fields, riparian forests, shrubs, palustrine plants and aquatic macrophytes are part of this community. Some of these species are terrestrial, and flooding is an

adverse condition for them. Palustrine species, aquatic macrophytes and, among these, amphibious species, are exposed to favourable environmental conditions during the rainy season, while they face environmental constraints during the dry season.

The Pantanal *sensu lato* areas, with less influence of flood pulse, have flora temporarily subjected to environmental constraint, in this case, a lack of water. In high grassland areas, the excess of light and shortage of water are extreme, especially in low rainfall months. During the annual cycle, the plants located in floodable areas, such as those on flood-free soils, are subjected to a significant deviation from optimal conditions, and forced to change and respond at various functional levels of the organism, which can characterise stress (Larcher, 2004). This condition is reversible in principle, but it can become permanent and irreversible. Stress implies a loss of vitality that worsens with the duration of the event.

A lack or excess of water in the environment leads to different kinds of situations. For example, plants subjected to a process of flooding are immediately exposed to a decreased gas exchange, leading to anoxia or hypoxia conditions. This condition provokes restriction in breathing in the root system, leading to inhibition of metabolic activity and ATP production, restricting the supply of energy for root growth and causing a reduction in plant development, which leads to morphological and/or physiological changes in the organisms, in order to obtain oxygen and energy (Liao and Lin, 2001; Larcher, 2004).

On the other hand, water is also the most common limiting factor for plant growth and its lack affects the opening of the stomata, leading to reduction in photosynthetic capacity and growth rate, due to the restriction of gas exchange. Additionally, as a drought tolerance mechanism, the stomata close during the period of highest water loss, coupled with reduced internal water potential of cells through the accumulation of solutes that promote water absorption from the soil. These mechanisms allow the vegetation to survive in areas where fluid restriction is common (Larcher, 2004).

In this region, water stress suffered by different types of vegetation can be exemplified by *paratudaís*, which are subjected to water deficit during the drought period and anoxia of the root system during flood. This species has different strategies to cope with hydrological variation (Soares and Oliveira, 2009), but not all groups found in the Pantanal are capable of withstanding such water variations, leading to a sequence of colonisation processes.

For example, areas previously occupied by species adapted to high water supply conditions are occupied during periods of low rainfall by pioneer woody species that colonise previously flooded grassland. According to Pott (1994), species such as *Curatella americana* L. become dominant in sandy soils, while in clayey soil *Tabebuia aurea* takes over. However, when there is a series of rainy years, tree species like *Vochysia divergens* Pohl, *Licania parvifolia* Huber and *Couepia uti* Benth.,

which are more tolerant to flooding, expand from patches of riparian vegetation (Pott and Pott, 2009).

Many species do not have the ability to adapt to the soil flooding process, which in turn subjects their roots to anoxic conditions, so they are indicators of the boundary between floodable and dry areas. An example is the *Caraguatá* (*Bromelia balansae* Mez), which defines areas that the flood waters reach during the rainy season. This condition is easily observed on the forest edge, where this species can survive and grow, because it is flood free.

Another interesting example can be observed in years of low flood, when *Byrsonima orbignyana* A. Juss. (Malpighiaceae), which composes the monodominant formations known as *canjiqueirais*, proliferates and colonises periodically floodable grasslands. This species has all the morphoanatomical features of xerophytes: cuticle on leaf epidermis, hypodermis aquifer, vascular bundle hem, hem extension lignified, and little intercellular space in chlorenchyma. The alternation of aquatic and terrestrial phases exposes the root system of this plant to complete anoxia or hypoxia in a given period, which may mean deviation from the ecological optimum, and results in responses that suggest the existence of an adaptive traits complex, not only structural but also physiological. This deviation is temporary, but for *B. orbignyana*, flooding exposure for prolonged periods, much higher than the annual seasonal pulse, implies a permanent injury, with the death of the individuals. Thus, even in its natural environment, this species is subject to optimum deviation, and according to Larcher (2004), this can be interpreted as a condition of stress, which is initially reversible, but can become irreversible with the prolonged duration of a flood.

The flood pulse is an annual characteristic of the Pantanal, and presents alternated multi-annual cycles, some years with predominantly high inundation and others with predominantly low inundation. This cycle shapes the landscape, “vanishing” the pioneer species that are established in the floodable grasslands in low water years. However, this condition – death of species that are intolerant to extended flood periods – is also well exemplified in Pantanal areas known as “*arrombados* of the Taquari River”. In this region, extensive areas of native vegetation have been destroyed by permanent flooding, resulting in riparian forest death, caused by livestock and agriculture advancing into the high portion of this watershed in recent decades. These activities have accelerated the natural silting of the Taquari River, changing the riverbed and resulting in great losses of native vegetation areas (ANA, 2004). Interestingly, in the *arrombados* areas, terrestrial species intolerant of prolonged flooding have given way to hydrophytes, which colonise the extensive wetlands permanently.

3. Dynamics of Aquatic Plants in Relation to Seasonality

One effect of the flood is to limit the number of species per environment (Rebellato and Cunha, 2005); duration, levels and frequency of flooding are determining factors

for species composition, and may act as a filter for species group. This relationship is barely known in the Pantanal; in addition, the soil fertility also contributes to species distribution. For Wang et al. (2002), intermediate levels of soil fertility tend to provide higher species richness in grasslands.

The relation between flooding and species distribution in Pantanal grasslands is poorly known, few studies have shown the species richness of these formations (Zeilhofer and Schessl, 1998; Pott and Adámoli, 1999). Periodic and pulse-type flooding of the Pantanal’s low areas influences the morphological, anatomical and physiological responses (Scremin-Dias, 1999, 2000), and phenological and/or ethological adaptations, producing characteristic community structures that are not well known (Junk, 1999).

In low areas – Pantanal sensu stricto – where flooding is likely to be permanent, there is a predominance of aquatic species, which often turn into floating islands of vegetation (*baceiros*). Pivari et al. (2008) conducted a study on the dynamics of the floating islands formed by substrate histosol with variable thickness, in the Pantanal sub-regions of Miranda and Abobral. The species composition on these *baceiros* is diverse and, depending on successional stage, shrubs and small trees can grow and reproduce on them.

Aquatic plants have different life forms (Pott and Pott, 2000; Scremin-Dias, 1999, 2009), distributed along the moisture gradient. These life forms range from free floating through fixed floating, free submerged, fixed submerged, emergent, amphibious and emergent (Pott and Pott, 2000; Scremin-Dias, 2009). They correspond to the plant habit, reflecting the species’ tolerance to submergence or desiccation (Scremin-Dias, 2000), and are independent of the phylogenetic correlations between groups (Scremin-Dias, 2009).

A wide inventory conducted by Pott and Pott (2000) found about 250 species of aquatic macrophytes in the Pantanal floodable areas, distributed among the phanerogams and cryptogams. Some aquatic macrophytes also form extensive monodominant areas, highlighting *pirizal* formed by *Cyperus giganteus* Vahl, the *caetezal* with prevalence of *Thalia geniculata* L. and two species of native rice, *Oryza glumaepatula* Steud. and *O. latifolia* Desv., forming extensive rice fields along the Paraguay River.

Among these monodominant formations, *Cyperus giganteus* and *Thalia geniculata* grow preferably in areas with water level ranging up to 1.80 m at the flood peak, with water remaining in general for a short time at this level, subsequently decreasing gradually. These species tolerate palustrine soils and flood-free areas, being denominated as amphibious. The amphibious way of life is the most peculiar one, because of the ecological amplitude of the species, which grow and can reproduce in both aquatic and flood-free (aerated soils) environments.

Species with fixed floating, emergent and amphibious habits generally have stems and roots attached to the substrate. These underground parts may remain as resistance structures during the dry season (Scremin-Dias, 2009), and display contractile roots that pull the apical buds

below the soil surface, protecting them during the dry season (Sculthorpe, 1967). This feature has already been described by Raunkiaer (1934) as acquired by higher plants during the evolutionary process, with the aim of hiding and protecting buds, allowing the survival of plants in unfavourable environmental conditions.

Under these conditions, various plant species express large phenotypic plasticity, an adaptation which, for Santiago and Paoli (2007), cannot be mistaken for a mere character expression in response to environmental pressures, but should be considered as a process, which is not restricted only to the individual. According to these authors, the organisms under these conditions may or may not express morphological, physiological or both traits, through gene activation or suppression, and these traits may or may not have an adaptive component.

For amphibian species, established in flood-free soil during the ebb, emergence of new stems, leaves and roots may occur, and these characteristics of the tissues are very different from those observed in individuals of the same species developed in water. Among the changes, is important to highlight the significant decrease in the leaf sheet, the petiole, the stem internodes, differential distribution of stomata and increased lignification in the vascular tissues as observed for various aquatic macrophytes in the Pantanal, accompanied by a seasonal cycle of flood and drought (Scremin-Dias, 2000, 2009).

For some species that occur in periodically flooded areas, with intensely fluctuating water levels, ecophysiological adaptations allow their "accommodation" to depth variations. This process, described by Ridge (1987), affords the elongation of petioles, leaves, stem internodes, and floral scapes, shortly after the submersion of these organisms. This, in response to anoxia, produces metabolites that act on their cells, stretching or stimulating their division, resulting in an increase in length. Thus, the distribution of species in areas with intense changes in water level favours the establishment of species that possess this adaptive mechanism.

In the Pantanal, the vast native rice fields exemplify this process. Bertazzoni (2008) measured individuals of *Oryza latifolia* with up to 5 m of stem elongation, after rising waters. According to the author, the vegetative propagation of this species is effective, because the branches drop on to the moist soil at the ebb period, allowing regrowth on the stem nodes, which stretch after the rainy season and form new individuals by budding or by seed germination. *Oryza glumaepatula* also follows the water level by elongation of stem internodes, as observed by Silva (2010) over seasonal cycles monitored in floodable fields of the Paraguay River.

4. The Evolutionary Significance of Differential Adaptations

Molecular studies have been increasingly used to evaluate adaptive differences of populations, distinguishing genetic lineages and assessing whether or not they are associated with different environments. When comparing populations

that have distinct morphoanatomical characteristics, linked to their adaptation to different habitats, taxonomic and evolutionary questions arise concerning the delimitation of species. Molecular phylogenies using DNA sequences may clarify aspects of the evolution of morphological and ecological traits, and the use of multiple genes describes these processes more accurately. The comparison of homologous DNA sequences may be important in defining species of certain groups, because the observed coalescence pattern and mutational events represent the genealogical relationships, tracing the history of the ancient DNA molecule (Hewitt, 2001). Several types of molecular markers have been used, making it possible to obtain a large amount of data collected from small samples of biological material, using non-destructive methods (Petit et al., 2001).

Wu (2001) suggests that the most suitable genes to investigate processes of species differentiation are those responsible for adaptive traits. Studies in this area assess phylogenetically related species or populations, in search of different alleles that have opposite effects on adaptive value. Among the investigated genes, we can mention those related to reproduction, such as specific floral traits to different pollinator attraction (corolla color, position of anthers and stigma, odor production) (Stuurman et al., 2004) and those related to adaptation to extreme environments (Brady et al., 2005).

Plants grown under different water regimes are good models for the study of resistance genes to excess and/or scarcity of water. These plants have evolved under strong selective pressure, with leaves emerged at certain times and submerged at others. These changes have a strong impact on photosynthesis efficiency, and the genes linked to this function are strong candidates for differential adaptation. Studying the *rbcl* gene, a chloroplast gene that encodes a catalytic subunit of RuBisCO, in ecologically diverse aquatic plants, Iida et al. (2009) found positive selection in some lines with heterophylly. This increase in the aminoacid substitution rate may imply a continuous adjustment of RuBisCo over variable ecological conditions. To survive and grow under anoxia conditions, some submerged plants have to activate the transcriptional regulation of a range of genes involved in physiological events that also control energy production, pH regulation and cell growth (Harada et al., 2007). Other plants do not increase the expression of genes that optimise photosynthesis under anoxia conditions, but rather the genes related to stem elongation and metabolism of different sugars to sustain this growth (Das and Uchimiya, 2002; Harada et al., 2005). Tolerance of desiccation, as well as of water excess, induces expression of specific genes, especially genes that cause coordinated cellular metabolism suppression.

Except for cultivated plant species, the genes directly responsible for differential adaptation are rarely known. In these cases, molecular markers that represent selectively and adaptively neutral polymorphisms can be used (Durbin et al., 2003). Phylogeography, the study of spatial/temporal distribution of genetic diversity, has been widely used to assess the variability among individuals and between

related species (Avice, 2000). Through this approach it is possible to identify independent evolutionary lineages and associate (or not) them with certain geographic regions, an extremely useful tool to assess whether interpopulation phenotypic differences reflect historical genetic divergence.

DNA sequencing has wide applicability in these studies because different parts of the genome have different rates of evolution, making it possible to evaluate various taxonomic levels on several geographical scales (Avice, 2000). Among the most used markers in plant phylogeography surveys, we can highlight the non-coding regions of plastid DNA (cpDNA) (Alsos et al., 2005), especially those intergenic regions that tolerate mutations and evolve rapidly without affecting the function of adjacent genes (Hamilton et al., 2003). The frequent uniparental inheritance is one of the advantages of these markers in differential assessment of pollen and seed flow (Hamilton and Miller 2002); furthermore, the analysis of cpDNA allows the identification of past hybridisation events that are not detectable morphologically (Bleeker, 2003). As the plastid genome is haploid, the effective population size is smaller than when considering the nuclear genome. This feature speeds up the genetic drift processes; hence, the cpDNA may show faster differentiation between populations or divergent lineages (Hamilton et al., 2003). Among nuclear markers, ribosomal DNA (nrDNA) is widely studied in plants. The higher plants' nrDNA is in one or more chromosomal regions, and each arrangement can display hundreds and even thousands of copies or paralogs (Buckler-IV et al., 1997). Mutations in these tandem repeats are individually homogenised through concerted evolution, in which unequal crossing-over and gene conversion are the main mechanisms involved (Arnheim, 1983). The mode and time of nrDNA concerted evolution varies greatly between different plant groups. Thus, nrDNA can present interspecific, interpopulation, and even intra-individual variation (Mayer and Soltis, 1999).

Populations with different morphoanatomical adaptations may reflect independent evolutionary units and incipient speciation processes. They may be triggered by geographical, ecological, morphological or behavioral changes, with natural selection and genetic drift being the most active evolutionary mechanisms. To understand these processes and to distinguish phenotypic plasticity from genetic differentiation, it is interesting to approach the morphological characteristics in a genetic context, obtained through neutral or adaptive molecular markers. Evaluating these patterns of several Pantanal species, we will be able to outline a more complete overview on the phytoecological evolution of this biome.

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