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Relationships between leaf deciduousness and flowering traits of woody species in the Brazilian neotropical savanna

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ABSTRACT

The relationships between foliage permanence and flowering throughout the year were analyzed in 92 woody species of Cerrado vegetation categorized as either deciduous (DE), semideciduous (SD) or evergreen (EV). Flowering of DE, SD and EV species was investigated via three variables, measured over the course of the year: flowering duration (FLD), calculated as the number of months in flower in each species; flowering distribution (FDI), calculated as the number of species in flower per month; and flowering peak (FPE), defined as the four consecutive months yielding the highest number of species in flower. The months with the highest numbers of species in flower were October (52 species), September (50) and August (49). These months correspond to the period of transition from the dry season to the wet season. In the majority of species studied, seasonal climatic factors were strong enough to induce fruit formation in the dry season and seed dispersal in the following wet season, when sufficient water was available to support germination and plantlet growth. However, significant differences in FLD, FDI and FPE were found among the leaf phenological groups. High FLD in EV species is likely favored by the continuous input of resources from the year-round foliage. In contrast, DE species employ reserves of carbon, water and nutrients to form new leaves and flowers on a crown free of foliage at the end of the dry season. In DE species, their low FLD may reduce the impact of flowering on reserve consumption. SD species showed an intermediate level of foliage persistence, resulting in intermediate FLD values. In addition, SD species exhibited a different pattern of flowering distribution from those of DE and EV species. Many SD species have two flowering periods per year. The first period occurs when the crowns are full of leaves, in the middle of the dry season in June, similar to EV species. The second occurs when only half of the original foliage area is present, near the peak of the dry season in September, similar to DE species. Therefore, despite a strong influence of seasonal climatic conditions on the flowering behavior of DE, SD and EV woody species of Cerrado vegetation, these leaf phenological groups differ significantly in FLD, FDI and FPE.

Introduction

Tropical savannas are a widespread biome throughout the world and consist of a discontinuous stratum of trees over a largely continuous layer of grasses (Huntley and Walker, 1985; Williams et al., 1997). The climate of tropical savanna regions is marked by seasonality, with a wet season followed by a dry season; during the latter, little to no rain falls (Huntley and Walker, 1985; Tothill and Mott, 1985). The Brazilian Cerrado is a neotropical savanna with multiple physiognomies and is found primarily in the central region of Brazil. In the Cerrado, the wet season occurs between October and March and the dry season between April and September (Damascos et al., 2005; Monteiro and Prado, 2006; Prado et al., 2004). The main factors that affect plant growth and development in Cerrado vegetation are the availability of water and nutrients in the soil, irradiance and the corresponding evaporative demand in the atmosphere, herbivory and fire (Medina and Silva, 1990; Prado et al., 2004; Santos et al., 2012).

The woody species of tropical savannas show varying levels of leaf deciduousness that allow them to cope with water stress in both the soil and atmosphere during the dry season (Oliveira, 2008; Prado et al., 2004; Santos et al., 2012; Williams et al., 1997). Deciduous (DE) woody species in Cerrado vegetation shed their leaves when the dry season approaches its end, remaining leafless for nearly 30 days. They undergo leaf production during a short period at the end of the dry season (Damascos et al., 2005). Semideciduous (SD) woody species in Cerrado vegetation shed approximately half of their leaves during the dry season and can rapidly regain their original foliage area during the same season (Lenza and Klink,

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2006). In contrast, evergreen (EV) woody species of the Cerrado retain a near-constant foliage area throughout the year and have continuous leaf production (Damascos et al., 2005; Lenza and Klink, 2006). The three different deciduousness groups (DE, SD and EV) also differ significantly in the patterns of leaf and branch growth (Damascos et al., 2005), crown structure (Souza et al., 2009b, 2011) and in the mass or surface area relationships between shoots and foliage (Souza et al., 2009a).

Foliage maintenance in DE, SD and EV Cerrado woody species is expected to influence the relationships between photosynthetic production in autotrophic tissues and the consumption of photosynthates in heterotrophic tissues. At the end of the dry season, Cerrado DE species likely mobilize their reserves of carbohydrates, water and nutrients from the roots, stems and branches for flushing the new foliage on a crown free of leaves, as do temperate DE species (Koslowski and Pallardy, 1996; Larcher, 2003; Luxmoore, 1991). As EV Cerrado woody species have a permanent foliage area, they may use the ongoing net photosynthesis as a source of carbohydrates and the xylem mass flow as source of water and nutrients throughout the year. In addition, Cerrado EV species can mobilize reserves stored in heterotrophic tissues, as do EV species in temperate climates (Koslowski and Pallardy, 1996; Larcher, 2003). In contrast, SD Cerrado species may function similarly to either DE or EV species with respect to carbohydrate, nutrient and water use, as they retain a large photosynthetically active area throughout the year but only half of their full foliage area at the peak of the dry season. Despite these large behavioral differences among DE, SV and EV species, the relationships between heterotrophic and autotrophic phenological events, such as flowering and foliage persistence, have not yet been studied in Cerrado woody species.

Flowering in Cerrado woody species is concentrated during the transition from the dry season to the wet season, indicating that flower production is not strictly limited by soil water availability (Batalha and Mantovani, 2000; Franco et al., 2005; Lenza and Klink, 2006). However, there is a significant reduction in net photosynthesis in DE, SD and EV species during the dry season (Prado et al., 2004). At least some reserves stored in vegetative structures are expected to be mobilized to meet the carbon demand of reproductive structures produced during the dry season. Therefore, leaf deciduousness should be strongly correlated with the onset and duration of flowering in DE, SD and EV woody species in Cerrado vegetation. Adequate amounts of maintained foliage area and carbohydrate reserves are needed to meet the demand of reproductive structures during the dry season in woody species of Cerrado vegetation.

EV species of the Cerrado have more vertical (orthotropic) branches than the other two types of woody species, which promotes foliage self-shading from the apex to the base of the branch (Souza et al., 2009b). Therefore, the flowers of EV species may be less exposed to ambient stress factors, such as irradiance and evaporative air demand, than those of other types of woody species. The orthotropic branches associated with the constant source of carbohydrates yielded from ongoing net photosynthesis can promote flower persistence and increase flowering duration. In contrast, DE species strongly depend on reserve mobilization to meet the demands of reproductive structures in a crown free of foliage or with newly developing leaves, as is present in the transition from the dry to the wet season (Damascos et al., 2005). The exposure of flowers preferably on plagiotropic branches (Santos et al., 2012; Souza et al., 2009b) and the intense consumption of reserves for leaf and flower formation during the dry season may result in a shorter period of flower persistence in DE species than in EV species. SD species show a level of branch inclination intermediate between those of EV and DE species and retain half of their foliage during the dry season. Thus, SD species may exhibit an intermediate level of flower persistence.

Table 1
Published works surveyed in the present study containing data on the floral or foliar phenology of deciduous, semideciduous and evergreen woody species in three Cerrado vegetation physiognomies: *campo sujo* [1], *cerrado sensu stricto* [2] and *cerradão* [3].

Phenology data	Work	Cerrado physiognomy
Floral + foliar	Silvério and Lenza (2010)	1, 2, 3
Floral + foliar	Pirani et al. (2009)	2
Floral + foliar	Lenza and Klink (2006)	2
Floral	Tannus et al. (2006)	1
Floral	Weiser and Godoy (2001)	2
Floral	Batalha and Mantovani (2000)	1, 2, 3
Foliar	Souza et al. (2011)	2
Foliar	Rossatto et al. (2009)	1, 2, 3
Foliar	Goldstein et al. (2008)	1, 2, 3

We aimed to identify the months of flowering in the DE, SD and EV woody species of the Cerrado and to test for temporal correspondence over the course of the year between the amount of foliage maintained and floral characteristics such as flower persistence, the period of flowering and the period during which the most species are in flower in each leaf phenological group. Therefore, we seek to identify associations in Cerrado woody species beyond those already established between foliage maintenance and both canopy structure (Damascos et al., 2005; Souza et al., 2011) and shoot-foliage relationships (Souza et al., 2009a,b). The relationships between foliage maintenance and flowering behavior will reveal other interdependent relationships in DE, SD and EV species and will more clearly define functional groups in Cerrado woody species.

Materials and methods

Literature data

We consulted the literature to classify the woody species of the Cerrado into three leaf phenological groups: deciduous, semideciduous and evergreen. Published papers were found using Web of Science and Google Scholar using the keywords “phenology”, “Cerrado”, “woody species” and “tree species”. For Google Scholar, the same keywords in both English and Portuguese were used. We selected all papers containing data on the flowering period or foliar deciduousness of Cerrado woody species, including species from different Cerrado vegetation physiognomies, such as in *campo cerrado*, *cerrado sensu stricto* or in *cerradão* (cerrado woodland). Nine published works were considered (Table 1). A total of 92 species finally resulted, of which 37 were DE, 21 were SD, and 34 were EV.

The groups “continuous evergreen species” and “seasonal evergreen species” described in Silvério and Lenza (2010), Pirani et al. (2009) and Lenza and Klink (2006) were considered here as one group of “evergreen species” (EV). According to these authors, continuous evergreen species replace their leaves continuously throughout the year, whereas seasonal evergreen species produce young leaves either before or simultaneously with foliage abscission at the end of the dry season. Because there is no period of significant loss of foliage area in either group of species, we pooled them together as evergreen species (EV). Where deciduousness classifications differed among published works, we used the classification of the most recent paper. In cases of disagreement over flowering period, we considered all months during which flowers were reported in all works. Additional information on the pollinator guilds of each species were obtained from published works other than those nine consulted for the relationships between flowering and leaf phenology.