

The roles of rainfall, soil properties, and species traits in flowering phenology along a savanna-seasonally dry tropical forest gradient

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Received: 2 September 2016 / Accepted: 7 February 2017 / Published online: 29 March 2017
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Abstract We investigated flowering phenology in a semiarid macroclimate along an environmental gradient encompassing neotropical savanna, transition, and seasonally dry tropical forest (SDTF) areas in the Chapada Diamantina Mountains, northeastern Brazil. We expected to find divergence in flowering patterns between the plant communities studied that would be explained by distinct functional traits selected by differences in rainfall volumes and soil properties. Bud and flower productions were monitored in 809 individuals between January 2010 and March 2012. The savanna exhibited a continuous flowering pattern, while the transition and SDTF areas showed seasonal flowering associated with rainfall. Environmental variables and plant traits (wood densities, water potentials, and water storage capacities) were related to the observed flowering strategies of woody species. The high diversity of functional groups in the savanna was determined by higher plant water potentials that were related to low wood densities and the availability of soil water. The role of rainfall, especially the rainfall volumes during the dry season, is critical in defining different flowering patterns at the community level. The physical properties of the soil

selected the presence of species with distinct water-use strategies (low wood density species in savanna areas, and high wood density species in the transition zone and forest), which in turn affected their flowering.

Keywords Functional groups · Heterogeneity · Seasonality · Water potentials · Wood density

Introduction

Savannas and seasonally dry tropical forests tend to occur in close association with environmental gradients in neotropical regions, especially under seasonal climates (Pennington et al. 2009). Savannas are seasonal ecosystems (with 2–3 dry months) that grow on diverse, but normally deep, soils in regions subject to frequent fires while showing high arboreal and herbaceous species richness and diversity (Oliveira Filho and Ratter 2002). Seasonally deciduous forests, on the other hand, are mainly comprised of arboreal species exposed to longer periods of water shortage (3–5 dry months), growing on a diversity of soil types that are normally shallower than savanna soils (and relatively rich in clay and nutrients). In these systems, the degree of canopy deciduousness is proportional to rainfall levels and soil water availability (Pennington et al. 2009; Coelho et al. 2013; Sánchez-Azofeifa et al. 2013).

Patches of savanna and seasonally dry forests often occur side by side in the Chapada Diamantina Mountains in northeastern Brazil (Juncá et al. 2005; Funch et al. 2009; Neves et al. 2016). These vegetation types experience different levels of water availability, created by differences in the physical properties and depths of their soils, although subject to a similar highly seasonal and semiarid condition (rainfall 688 mm year⁻¹) (Harley et al. 2005). As such, soil

Electronic supplementary material The online version of this article (doi:10.1007/s40415-017-0368-1) contains supplementary material, which is available to authorized users.

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has been considered one of the main conditioning factors selecting for functional adaptations and determining the floristic composition and the spectrum of life forms that define the transition of savannas to seasonally dry forests over reasonably short distances (Neves et al. 2016).

Studies of functional plant traits allow us to better understand plant survival strategies and distribution patterns (Violle et al. 2007) in relation to their environments (Reich 2014). Understanding the link between environmental heterogeneity and plant persistence based on observational studies remains a challenge due to the difficulties encountered in quantifying the many attributes involved, variable sampling effort among species, and the arbitrary choice of the investigative scale (Carmo et al. 2016; Violle et al. 2015). In tropical semiarid regions, environmental seasonality, the water regime, and the heterogeneity of habitat conditions have great influence on the selection of functional aspects, especially those related to phenology, wood density, and leaf water potential (Lima et al. 2012; Mason et al. 2013; Méndez-Alonzo et al. 2013; Rossatto et al. 2013a; Worbes et al. 2003).

The flowering patterns of tropical plant communities are mainly associated with the degree of regional seasonality (Borchert 1994, 1996; Pirani et al. 2009; Lima et al. 2012), but species compositions and their associated functional aspects can have significant effects on community phenological responses (Ramirez 2002; Oliveira et al. 2014). A considerable fraction of woody savanna species bloom at the beginning of the rainy season, while others produce flowers during periods of high water stress (Monasterio and Sarmiento 1976; Batalha and Mantovani 2000; Ramirez 2002; Gottsberger and Silberbauer-Gottsberger 2006; Pirani et al. 2009). It is well established that woody species growing in seasonally dry forests tend to flower at the end of the dry season and/or beginning of the rainy season (Amorim et al. 2009; Neves et al. 2010; Lima et al. 2012; Souza et al. 2014) because most species are essentially dependent on water availability for flowering (Méndez-Alonzo et al. 2013), although water stress can act as a trigger for this phenophase in some species (Sakai et al. 2006; Larcher 2010). Plant water storage capacity, related to wood density, can also have a strong influence on plant phenology (Borchert 1994; Lima and Rodal 2010).

Those phenological responses suggest important interactions between physical factors and species traits in structuring the phenological responses of savanna and dry forest communities in the tropics. Wood density and the values of leaf water potential are important parameters in understanding the phenological responses of communities growing in seasonal and semiarid regions (Tobin et al. 1999; Swenson and Enquist 2007; Lima et al. 2012), especially those under very similar macroclimatic conditions but very divergent in terms of soil water storage

capacities. Savanna plants have developed a wide range of water-use strategies and have distinct wood densities (light to high) (Bucci et al. 2005; Goldstein et al. 2008). Seasonally deciduous tropical forests, by contrast, are usually composed by plants with high wood densities and variable water potentials but more resistant to embolism—an important capacity in environments subject to water deficits (Méndez-Alonzo et al. 2013).

In order to better understand plant flowering phenologies along an environmental gradient encompassing savanna, a transition zone, and a seasonally dry tropical forest (SDTF) in the Chapada Diamantina mountain range, we examined environmental variables (rainfall, temperature, photoperiod, daily insolation, and soil properties) and plant species traits (wood density, water potential, and water storage capacity). We expected to find divergence in flowering behavior between the different plant communities, which will be related to distinct functional traits selected by differences in environmental variables (rainfall volume and soil properties). As such, we expected to find the savanna community with continuous flowering events throughout the year while the flowering pattern in the SDTF and savanna-SDTF transition would be concentrated in times of greatest water availability. Such behavior would imply that functional strategies to deal with water availability are more diverse in savanna environments than in SDTF. Based on this assumption, we hypothesized that the number of functional strategies (groups) would be higher in savanna than in SDTF, and that SDTF and savanna-SDTF would delineate fewer functional groups that would be functionally equivalent in the water use and storage.

Materials and methods

Study area – The Chapada Diamantina mountain range (11°36'–13°56'S and 40°40'–43°56'W) is located in the northern section of the Serra do Espinhaço Range in northeastern Brazil. It covers approximately 50,600 km² several hundred kilometers inland from the coast in a general N–S direction (Franca-Rocha et al. 2005) at altitudes between 400 and 2030 m asl (CEI 1994). The region is characterized by a mosaic of savannas, humid and dry forests, and open rocky field vegetation (Harley 1995; Funch et al. 2009). Extensive rocky outcrops and litholic neosols (shallow, rocky, and of low-fertility) are found in the mountain range, while latosols (deep, well-drained, of low-fertility, and acidic) are more common on plateaus (Juncá et al. 2005). The mesothermic climate defines a rainy period between November and April and a 5-month dry period generally between June and October (Nimer 1989). Mean monthly temperatures vary between 18 and 25 °C, and the mean annual rainfall (between 1961 and

2011) was 1218 mm (data provided by the Brazilian Meteorological Institute; Fig. 1a).

The present study was conducted in neighboring vegetation types: savanna (centered at 12°26′08″S and 41°31′04″W; 884 m asl), savanna-SDTF transition (12°26′04″S and 41°32′01″W; 736 m asl), and SDTF (12°27′06″S and 41°35′52″W; 697 m asl; Neves et al. 2016). These three environments were located along a single 1-hectare transect in the vicinity of the Chapada Diamantina National Park, Bahia State, Brazil. We established 10 continuous plots (10 × 10 m) in each vegetation type, and all living shrub–arborescent individuals in these plots measuring ≥ 2 cm in diameter at soil level were counted and their basal areas at soil level were calculated. The savanna site presented some rock outcrops and was composed of a continuous herbaceous stratum, with shrub and tree cover varying between 5 and 50%. The plants were ≤ 8 m tall and did not form a continuous or dense canopy. Neither the savanna-SDTF transition nor the SDTF had a continuous herbaceous stratum, and formed discontinuous canopies with shrub and tree individuals up to 10 m tall.

Environment variables – Rainfall data were obtained using pluviometers installed in each vegetation type (Fig. 1b), while relative humidity and temperature data were acquired from a weather station located 8 km away from the savanna, 10 km from the transition area, and 16 km from the SDTF site (Fig. 1c). Day length was calculated using the Solar Photoperiod Calculator (<http://sci.fi/~benefon/sol.html>). Daily insolation was obtained from the NASA Web site (<http://aom.giss.nasa.gov/srlocat.html>) using the Ocean–Atmosphere Model (Fig. 1d). The geographical coordinates of the study areas were used to determine photoperiod and insolation. The physicochemical properties of the soils were presented by Neves et al. (2016) from samples obtained in each vegetation type at depths between 0 and 20 cm; each pooled sample was formed by three 330-g subsamples collected every 50 m in each area.

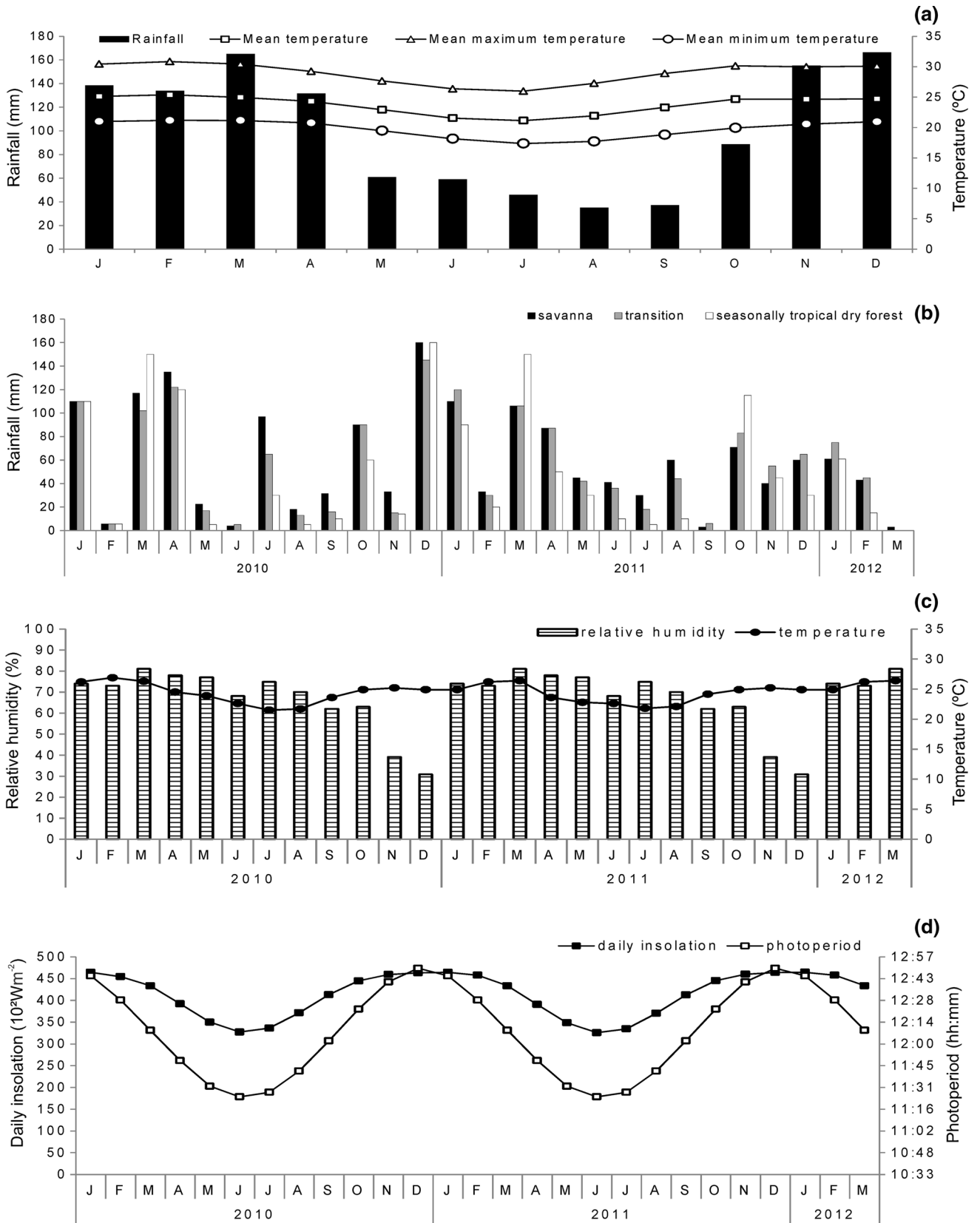
Flowering phenology – Ninety-six species were monitored monthly between January 2010 and March 2012: 41 species in the savanna vegetation area (495 individuals); 21 species in the transition zone (135 individuals); and 48 species in the SDTF (179 individuals) (Appendix S1), corresponding to 84, 83, and 66% of the total numbers of species in each vegetation type, respectively (Neves 2013). The semiquantitative method developed by Fournier (1974) was used to assess the phenological intensities of the phenophases (flower budding and flowering) in each monitored individual. Classifications of the duration, frequency, and regularity of the flowering in each vegetation type were made following Newstrom et al. (1994). Flowering patterns were identified for the species in the

vegetation types based on the timing and frequency of flowering, together with the relative density of species (Neves 2013). The interspecific synchrony was calculated using the percentage activity index of Bencke and Morelato (2002).

Water potential and wood density – The water potentials (Ψ) of 20 savanna species (40% of the total species sampled in this vegetation type), 14 savanna-SDTF transition species (47%), and 14 SDTF species (17%) were measured in March and September 2010 using a Scholander-type pressure chamber (PMS, Model 1000, PMS Instrument Co., Corvallis, OR, USA). These species were chosen considering their importance value indices in the investigated vegetation types (Neves 2013). Water potentials at predawn (Ψ_{PD}) (04:30 h) and at midday (Ψ_{MD}) (12:00 h) were measured in the field to determine the highest and the lowest values. Measurements were taken on three terminal branches that were removed from each individual (per species) and stored in sealed plastic bags for a maximum period of 90 min (to prevent water loss) before measuring their water potentials. Ψ_{PD} reflects the nocturnal capacity to recuperate water lost during the day, and is a good indicator of moisture availability in the rhizosphere (Wright and Cornejo 1990; Hernández et al. 2009). The mean water potential of each vegetation type was calculated considering 20 replicates for savanna, 14 for the savanna-SDTF transition, and 14 for the SDTF.

The wood densities of 35 savanna species (74% of the species sampled in this vegetation type), 11 savanna-SDTF transition species (37%), and 43 SDTF species (37%) were determined from samples collected from three individuals of each species, in each vegetation type (Neves 2013). Mean values were calculated for each species in each vegetation type. Wood densities (g cm^{-3}) were calculated by collecting branches 10 cm long (including bark, sapwood, and heartwood) and immersing them in distilled water for 3 days. Their saturated masses were then determined using a precision balance and their volumes determined by water displacement in a 50-mL graduated cylinder. The material was then dried at 60 °C to a constant weight. These values were then used to calculate wood density ($D = Ms V^{-1}$) and the quantity of saturated water [$QWS = 100 (D = Msat - Md) Md^{-1}$]. Species with densities below 0.5 g cm^{-3} were considered low density (Borchert 1994).

Data analysis – The occurrence and intensity of flowering phenophase seasonality in each vegetation type and for each year was evaluated using circular statistics. The frequency of each phenophase was calculated for the total number of species in each year. Months were converted into angles at 30° intervals (0° representing January, 30° representing February, and so forth, until 330° representing December). The mean angles, angular standard deviations,



◀ **Fig. 1** Monthly means of environmental variables. **a** Rainfall and temperature, 1961–2011 (National Institute of Meteorology [INMET], Lençóis), **b** rainfall in each vegetation type, **c** relative humidity and mean temperature (INMET, Lençóis), **d** daily insolation (NASA Web site <http://aom.giss.nasa.gov/srlocat.html> using the Ocean–Atmosphere Model). Day length was calculated using the Solar Photoperiod Calculator (<http://sci.fi/~benefon/sol.html>)

and r vector lengths were calculated. Angle significance was tested using the Rayleigh test (z) for circular distributions (Zar 2010). The flowering phenological events with significant mean angles ($P < 0.05$) were transformed into mean data. Statistical calculations were carried out using Oriana software (demonstration version 4.02, Kovach Computing Services, Anglesey, UK) (Kovach 2004). The Watson–Williams F test was used to compare mean dates for each phenophase (Zar 2010) in each vegetation type. Flowering phenophases whose vector (r) lengths were >0.5 and for which the Rayleigh test indicated as significant were considered seasonal (Morellato et al. 2010).

The normality of the distribution of phenological data was evaluated using the Shapiro and Wilk test (Zar 2010). The Spearman's correlation coefficient (r_s) between flowering phenophases and the monthly variables of rainfall, mean temperature, relative humidity, photoperiod, and insolation were calculated using Statistica software (trial version 13.0, Statsoft, São Paulo, Brazil).

Water potential data for each vegetation type were submitted to analysis of variance (ANOVA) and the means compared using the Tukey's test ($P < 0.05$) using Sisvar (version 5.3, Lavras, Minas Gerais, Brazil) (Ferreira 2011). Each data collection period (dry and rainy seasons) was considered one treatment. We inserted the attributes collected from the functional traits of the species (flowering patterns, predawn water potential, wood density, and quantity of saturated water) into a matrix, with species in rows and traits in columns. We applied the Euclidian distance coefficient to the matrix and performed cluster analysis using Past ver. 2.17c software (Hammer et al. 2001). Principal component analysis (PCA) was performed to determine which of the functional traits analyzed were grouping the species using Past software. To standardize the measured traits, the average values of each trait were subtracted from the observed values and divided by their respective standard deviation (Kröber et al. 2012). The Euclidean distance coefficient was applied to the matrix and cluster analysis performed using UPGMA, using Past ver. 2.17b software (Hammer et al. 2001). Multidimensional scaling (NMDS) was performed to rank the attributes of the species according to their functional similarities. This method produces a graphical representation of the similarity between samples in a small number of dimensions (Henderson and Seaby 2008).

The values of the physical and chemical soil analyses of each vegetation type were submitted to analysis of variance (ANOVA) and the means compared using the Tukey's test ($P < 0.05$), using Sisvar software (version 5.3, Lavras, Minas Gerais, Brazil) (Ferreira 2011). The Chi-square test was used to compare the rainfall at each vegetation type, it was calculated between the rainfall volume of the dry (June to October) and wet (November to April) seasons in each vegetation type, using data from November 2010 to April 2012.

Results

Flowering patterns and environmental seasonality – Flowering patterns in the savanna area were continuous, while flowering patterns in the transition and SDTF vegetation types were seasonal (intermediate and regular, without variation in different years, with the phenophase occurring only during the rainy season) (Fig. 2; Table 1; the complete list of species is presented in Appendix S1). The flowering phenophases were related to day length and daily insolation in all vegetation types, and to rain only in transition and SDTF sites (Table 2). At the population level, we identified five patterns considering the timing and frequency of flowering: continuous, biannual (events in the dry and rainy seasons), annual in the rainy season, annual in the dry season, and annual in the dry–rainy season transition and extending into rainy season. Flowering in the rainy season and in dry–rainy season transition with extension into the rainy season were the two most important patterns in terms of relative density (Table 3).

Water status of the plants and wood density – The Ψ_{PD} in the rainy season differed from that of the dry season in all of the monitored vegetation types (Fig. 3). The Ψ_{MD} differed between the seasons in the SDTF and transition zone but not in the savanna area. The Ψ_{PD} differed from Ψ_{MD} in the savanna and transition sites in both seasons, and in SDTF only during the rainy season. The Ψ_{PD} did not differ from the Ψ_{MD} in the SDTF during the dry season. The mean wood densities of savanna, transition, and SDTF species were 0.55, 0.71, and 0.68 g/cm³, respectively; the proportions of species with high wood densities in the savanna, transition, and SDTF vegetations were above 87%.

Environmental variables – Chi-square tests performed to rainfall volume in the dry (June to October) and wet (November to April) seasons in each vegetation type, measured between January 2010 and April 2012, showed that rainfall volumes in the vegetation types differed only during the dry season: savanna \times transition 6.18 ($p < 0.05$), savanna \times SDTF 53.14 ($p < 0.05$), and transition \times SDTF 24.00 ($p < 0.05$). The savanna soils

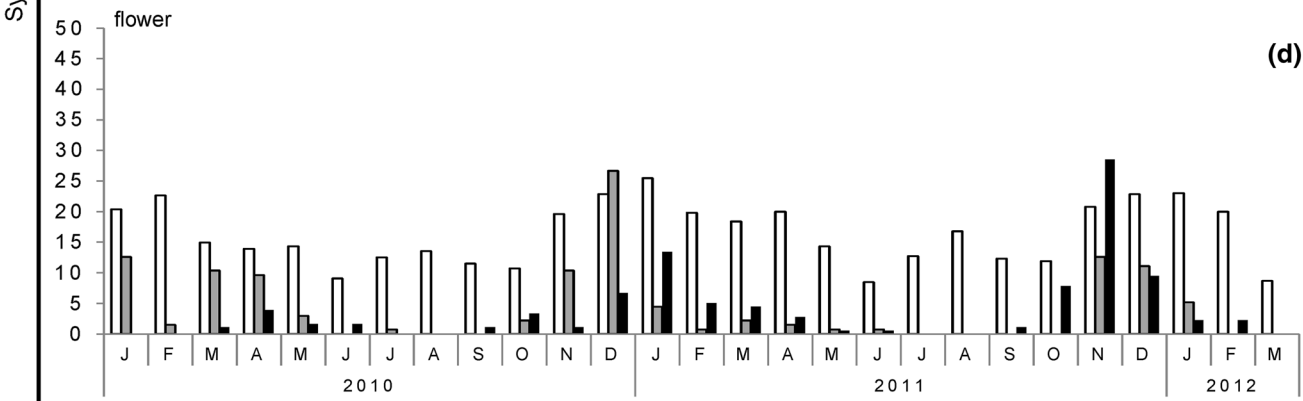
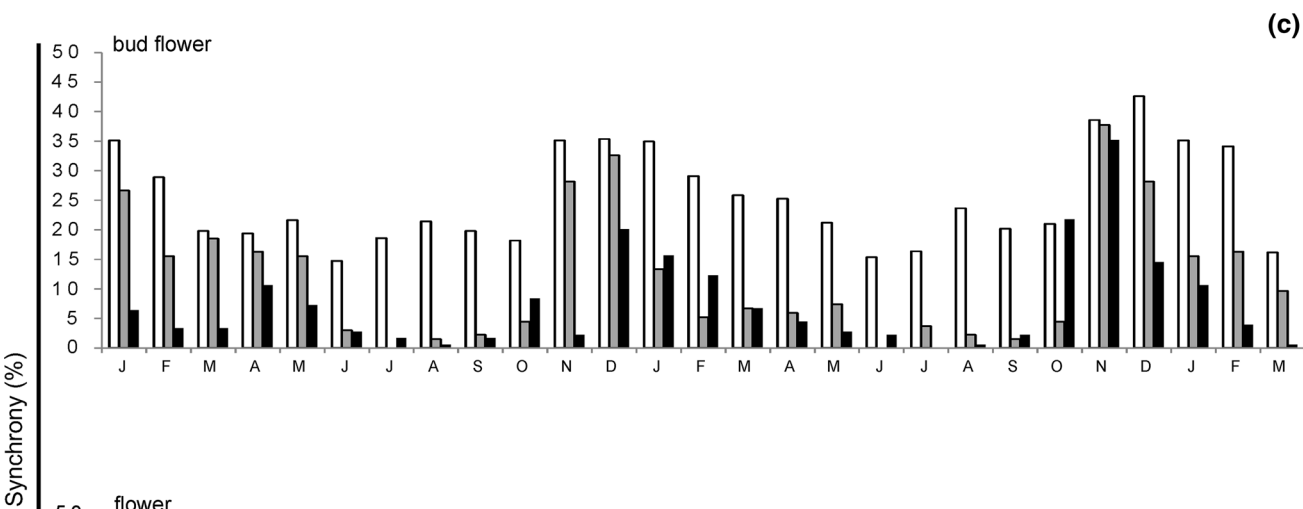
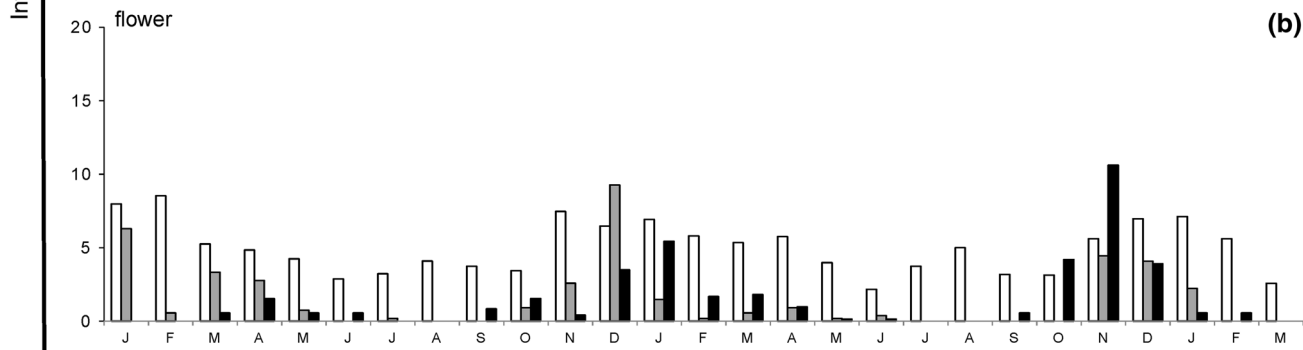
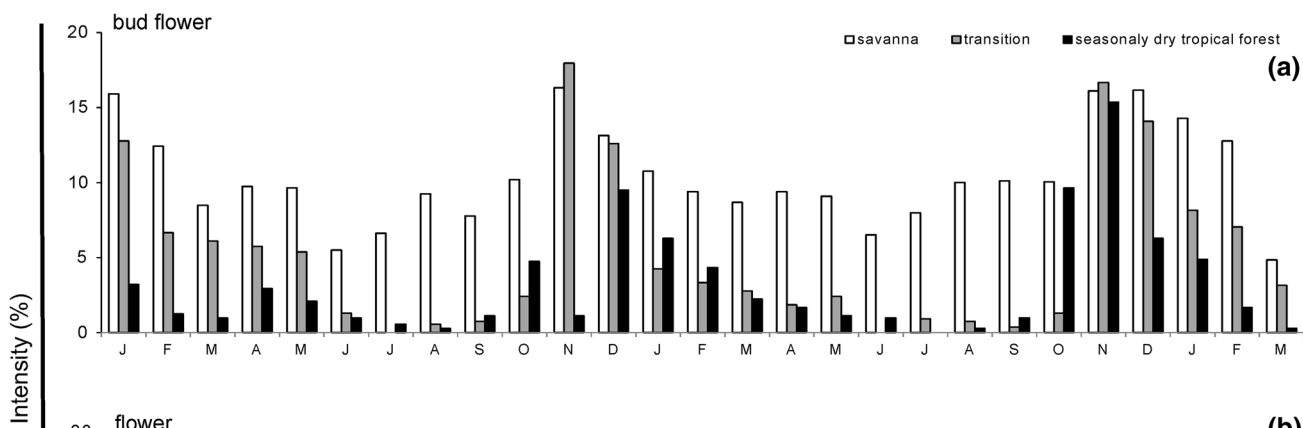


Fig. 2 Production of buds and flowers between January 2010 and March 2012. **a, b** Fournier intensity, **c, d** synchrony of individuals. *Horizontal bars* indicate the dry season. Savanna-transition-seasonally dry tropical forest continuum (SDTF) in the Chapada Diamantina mountain range, northeastern Brazil

examined were classified as sandy, while the transition and SDTF vegetations grew in clayey loam soils. The soils were dystrophic (alkali saturation < 50%), acidic (pH < 5), non-aluminous (Al < 1.3 cmol/dm³, except in

the transition area), and had low cation exchange capacities (CEC < 13).

Functional groups – The cluster analysis, PCA, and NMDS (final stress of 0.07 in SDTF and 0.12 in savanna and transition) showed that the strongest factor for the formation of groups in the vegetation types studied here was their water potential (Figs. 4, 5).

The savanna cluster analysis identified four functional groups: (1) The first group contained all of the species showing annual flowering; with two subgroups: A—species flowering in the rainy and dry-rainy transition; B—

Table 1 Results of circular statistics of frequency of individuals

Frequency of individuals												
Statistical parameters	Bud						Flower					
	Savanna		Transition		SDTF		Savanna		Transition		SDTF	
	2010	2011	2010	2011	2010	2011	2010	2011	2010	2011	2010	2011
Mean angle	355.82°	358.28°	21.26°	344.39°	17.16°	337.52°	11.18°	16.91°	11.93°	344.36°	5.60°	340.20°
Mean date	25 Dec	28 Dec	22 Jan	14 Dec	18 Jan	7 Dec	12 Jan	17 Jan	12 Jan	14 Dec	6 Jan	10 Dec
R	0.17	0.20	0.50	0.56	0.28	0.59	0.17	0.17	0.59	0.71	0.18	0.66
Z	8.70	12.61	40.64	35.48	5.13	41.72	5.40	5.86	26.69	17.13	0.73	32.04
P	1.66e-04	3.34e-06	<1e-12	<1e-12	0.01	<1e-12	0.00	0.00	2.58e-12	1.42e-08	0.485	<1e-12
F (P)	0.43 (0.52)	0.73 (0.40)	1.46 (0.24)	0.55 (0.47)	1.85 (0.19)	3.27 (0.08)						
Watson-Williams test												
	Bud				Flower							
	F	P	F	P	F	P	F	P				
Savanna × transition	2010	6.80	0.02		11.57	0.00						
	2011	15.67	6.68e-04		53.04	2.71e-07						
Savanna × SDTF	2010	46.48	7.54e-07		87.29	4.10e-09						
	2011	17.19	4.33e-04		15.08	8.02e-04						
Transition × SDTF	2010	4.77	0.04		3.91	0.06						
	2011	2.00e-03	0.97		1.50	0.23						

Savanna-transition-seasonally dry tropical forest continuum (SDTF), Chapada Diamantina mountain range, northeastern Brazil (P < 0.05)

Table 2 Spearman (rs) correlation between environmental variables and the proportion of budding species (b), flowering species (fl), of species carrying immature fruit (if) and mature fruit (mf), between January 2010 and March 2012

	Month of the event					
	Savanna		Transition		Seasonally dry tropical forest	
	b	fl	b	fl	b	fl
Rainfall	–	–	0.40	0.72	0.74	0.58
Photoperiod	0.75	0.56	0.73	0.54	0.69	0.48
Temperature	–	–	0.64	0.39	0.38	–
Relative humidity	–0.44	–	–	–	–	–
Daily insolation	0.76	0.54	0.73	0.51	0.68	0.48

Savanna-transition-seasonally dry tropical forest continuum, Chapada Diamantina mountain range, northeastern Brazil (P < 0.05)

species flowering in the dry season; (2) the second functional group contained species with continuous and biannual flowering, and high Ψ_{PD} ; (3) the third group contained species with continuous flowering, and high wood density and low water saturation; (4) the fourth group contained species showing continuous flowering and low Ψ_{PD} . *Annona coriacea* was set apart from the other groups as it showed low wood density (0.33 g cm^{-3}) and high water saturation (236%) (Fig. 4a). The savanna-SDTF transition cluster analysis showed only one large functional group (with species flowering in the rainy

Fig. 4 Cluster analysis (Euclidian distances) of the functional attributes of woody species in a savanna-transition-seasonally dry tropical forest continuum (SDTF) in the Chapada Diamantina mountain range, northeastern Brazil. **a** Savanna, **b** transition, **c** seasonally dry tropical forest

season and dry extending for rainy season, which formed two subgroups, respectively (Fig. 4b). Three species remained isolated from this group: *Cordia rufescens*, due its low wood density (0.42 g cm^{-3}), and *Bignoniaceae* sp.1 and *Thyrsacanthus ramosissimus*, due their low water

Table 3 Flowering patterns, considering flowering timing

	Savanna	Transition	SDTF	Savanna	Transition	SDTF	Savanna	Transition	SDTF
Flowering timing	Continuous			Rainy			Biannual		
Number									
Species	11 (27%)	1 (5%)	–	11 (27%)	8 (38%)	11 (23%)	2 (5%)	1 (5%)	–
Genera	9	1	–	10	8	10	2	1	–
Families	9	1	–	6	4	7	2	1	–
Relative density	29.75	5.16	–	11.42	47.28	26.23	2.21	4.34	–
Flowering timing	Dry			Dry–rainy			Did not flower		
Number									
Species	2 (5%)	1 (5%)	3 (6%)	13 (32%)	9 (43%)	17 (35%)	2 (5%)	1 (5%)	17 (35%)
Genera	2	1	3	13	6	14	2	1	15
Families	2	1	3	10	4	9	1	1	8
Relative density	3.67	2.72	8.28	52.41	30.71	31.60	0.54	8.69	9.36

Savanna-transition-seasonally dry tropical forest continuum, Chapada Diamantina mountain range, northeastern Brazil

Values in brackets represent the percentage of species accompanied

SDTF seasonally dry tropical forest

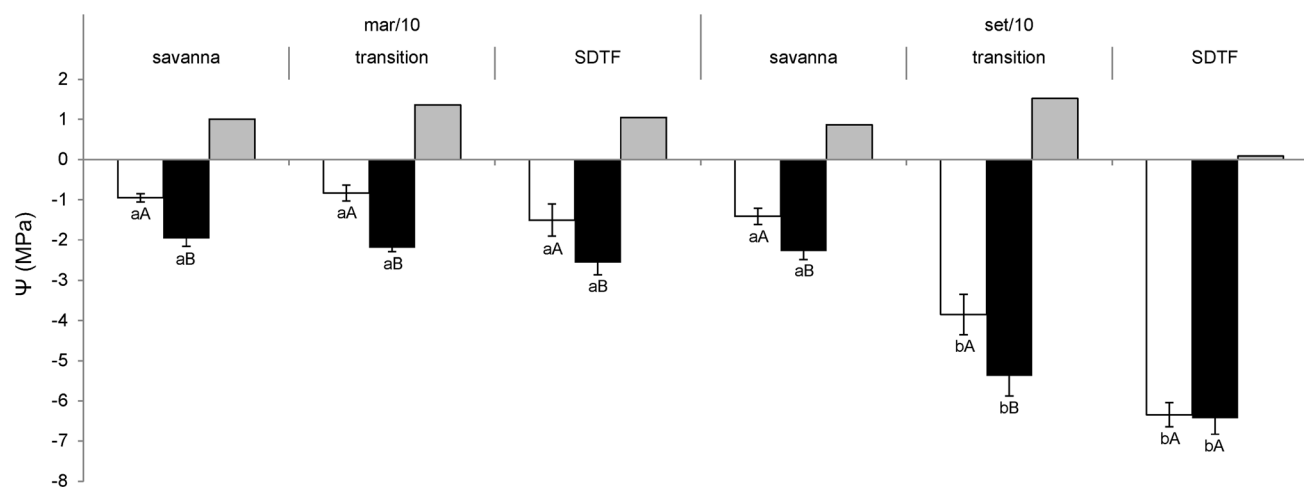
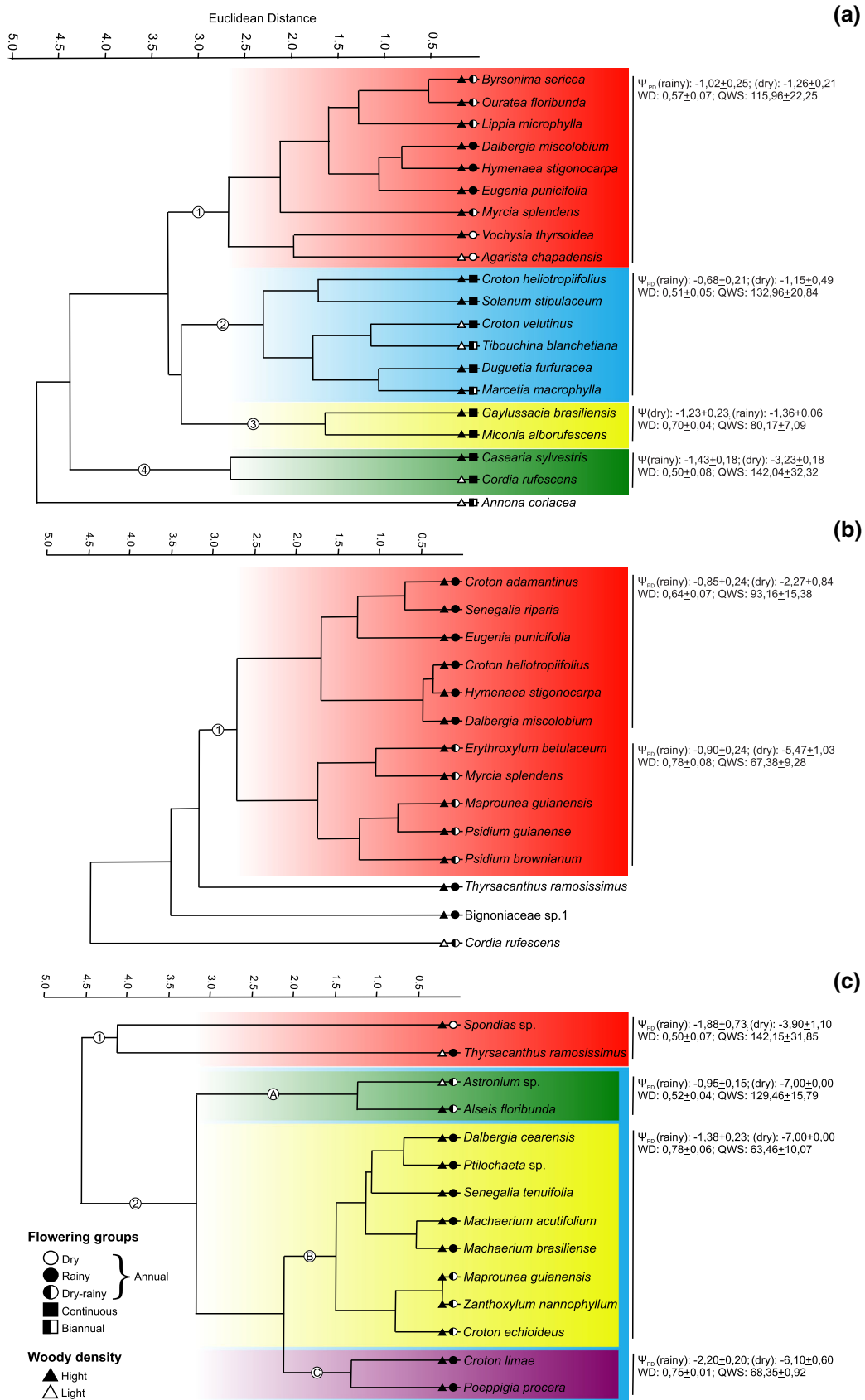


Fig. 3 Means (\pm standard deviation, SD) of predawn (Ψ_{PD}) and midday (Ψ_{MD}) water potentials in a savanna-transition-seasonally dry tropical forest continuum (SDTF) in the Chapada Diamantina mountain range, northeastern Brazil. Lowercase letters indicate comparisons of Ψ between the wet (March) and dry (September) season in each vegetation type. Uppercase letters indicate comparisons between the Ψ_{PD} and Ψ_{MD} of the vegetation types in each season. Values followed by the same letter indicate no statistically significant differences ($P < 0.05$)



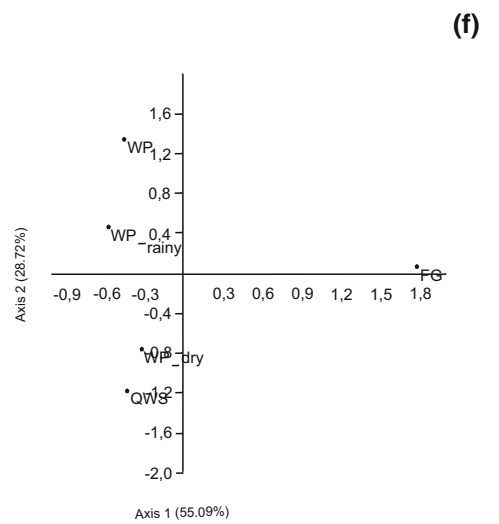
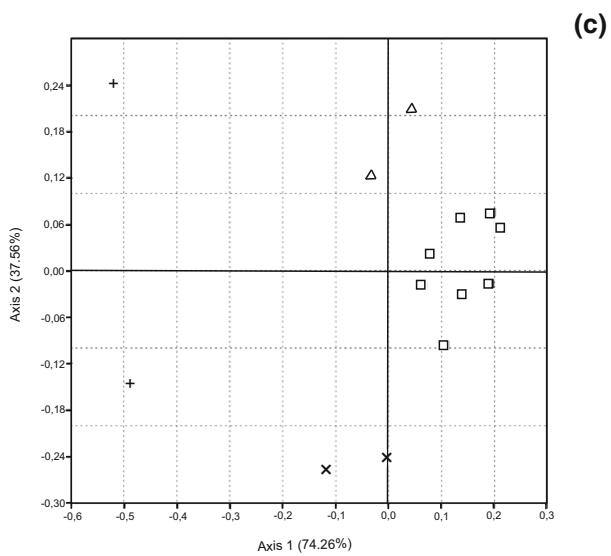
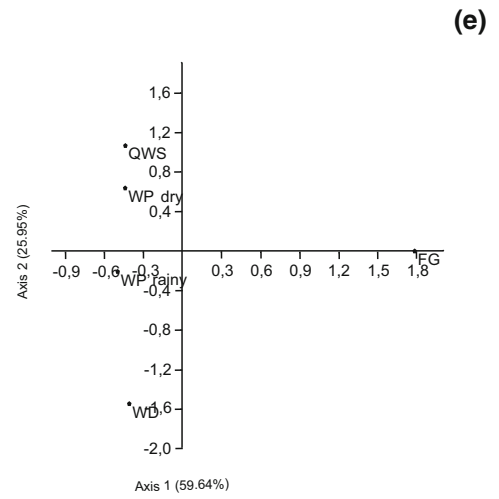
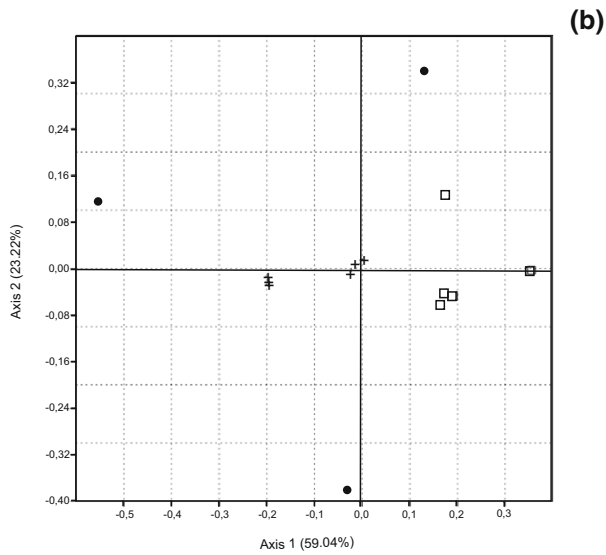
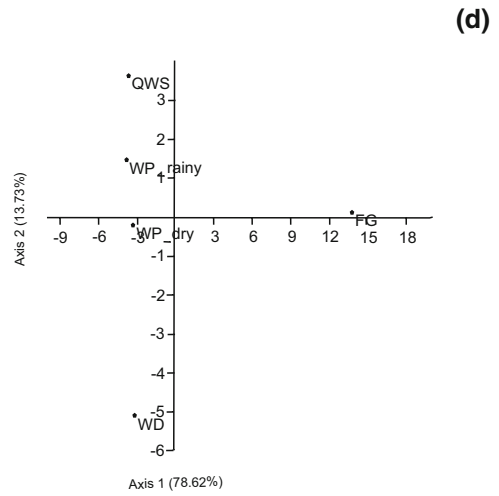
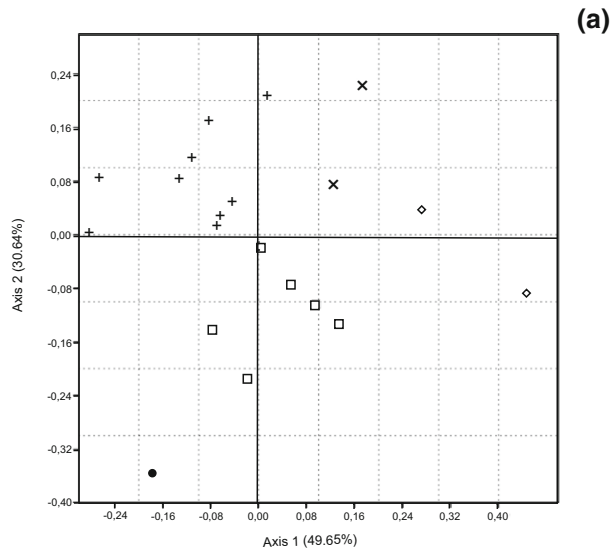


Fig. 5 Multidimensional scaling (NMDS) analyses of the sampled species. **a** *plus* (species with annual flowering), *square* (species with continuous and biannual flowering, and higher Ψ_{PD}), *times* (species with continuous flowering, high wood density, and low water saturation), *diamond* (species with continuous flowering, and low Ψ_{PD}), *circle* (*Annona coriaceae*), **b** *plus* (species flowering in the rainy season), *square* (species flowering in the dry season and extending into the rainy season), *circle* (*Cordia rufescens*, *Bignoniaceae* sp.1, and *Thrysanthus ramosissimus*, *c plus* (species with high Ψ_{PD} [dry season]), *times* (species with high Ψ_{PD} [rainy season]), *square* (the species with high wood density and low water saturation), *triangle* (species with low Ψ_{PD} [rainy season]), **d, e, f** Principal component analyses (PCA) of the attributes of the sampled species. (*FG* flowering group, *QWS* quantity of saturated water, *WD* wood density, *WP rainy season* mean of maximum water potential in the rainy season, *WP dry* mean of minimum water potential in the dry season) in a savanna-transition-seasonally dry tropical forest continuum (SDTF) in the Chapada Diamantina mountain range, northeast Brazil

potential values in the dry season and rainy season, respectively (Fig. 4b). The SDTF cluster analysis showed two functional groups: The first group contained the species with high Ψ_{PD} (dry season). The second group contained species with low Ψ_{PD} (dry season), with three subgroups: A—species with high Ψ_{PD} in the rainy season; B—species with high wood densities and low water saturations; C—species with low Ψ_{PD} in the rainy season (Fig. 4c).

We identified the most similar characteristics between the species that strengthened the formation of the groups using the spatial configurations of the cerrado species generated by the NMDS and the PCA (Fig. 5a). We found that the clustering of species with annual flowering was driven principally by water potential and water storage capacity. The formation of species groups with continuous and biannual flowering was principally driven by wood density and water potential in the dry season. The formation of species groups with continuous flowering was principally driven by the combination of flowering group, wood density, and water potential. The formation of species groups with continuous flowering and low water potentials was strongly influenced by water potential in the dry season. Using the spatial configurations of the species of the transition zone generated by the NMDS and the PCA (Fig. 5b), we found that clustering of species with dry-rainy transition flowering was driven principally by the flowering group, and the species showing flowering during the rainy season was driven by water potential in the rainy season. Using the spatial configurations of the species of the caatinga zone generated by the NMDS and the PCA (Fig. 5c), we found that clustering of the species was driven by water potential during the rainy season, another group was driven by the flowering group, and a third group was driven by wood density and water saturation.

Discussion

Based on a temporal set (27 months) of phenological flowering data from 96 woody plant species (809 individuals), we examined the broad variety of flowering patterns from savanna, transition, and seasonally dry tropical forest species, and their associated drivers. We show here that the regional austral summer climate in the study area, with high rainfall, long day lengths, and high daily insolation, favored flower production in all of the vegetation types. The analyses of the frequencies and durations of the phenophases of savanna, transition, and SDTF plant species confirmed our hypothesis and showed that their flowering patterns differed and that precipitation plays a key role in flowering, especially in the transition and SDTF areas. The differences in the rainfall volumes during the dry season and the physical properties of soils were found to be the main determining factors of the differences in the frequencies of the flowering phenophases of savanna (continuous), transition, and SDTF (annual) species. The distinct soil properties of each site selected for specific plant traits linked to maintain their water status, with the SDTF and savanna-SDTF communities exhibiting similar flowering patterns and appearing functionally similar in terms of their use and storage of water thus delineating similar functional groups.

The continuous flowering pattern observed in the savanna vegetation area, with a discrete increase in flowering soon after the beginning of the first rains, has been reported for other Brazilian savannas by Silva et al. (2011) and by Moraes (2011). This pattern results from the predominance of annual species flowering in sequence, and this continuous phenological pattern appears to be mainly related to edaphic factors. Savanna soils contain high percentages of sand, which allows easier root penetration and aeration; this sandy soil, however, is not able to retain high amounts of water (Grohmann and Medina 1962; Beutler et al. 2002). The availability of these deeper soils to plant roots provides varied niches and strategies to be explored by a great diversity of species (Rossatto et al. 2012) in distinct seasons (Rossatto et al. 2013a), which helps to explain the continuous flowering patterns in savanna areas. The flowering of a significant number of savanna species during the dry season may be related to specific adaptations to the physical properties of those sandy soils. Savanna species showed less dense wood (0.55 g cm^{-3}), which is normally associated with the high water storage capacity of their trunk parenchyma (Hacke and Sperry 2001; Diniz 2009). In this way, some savanna species can flower during the dry season due to the significant amounts of water stored in their trunks (Bucci et al. 2005; Scholz et al. 2007; Meinzer et al. 2008), allowing

them to regulate their water potentials and provide water to the buds (Goldstein et al. 2008). This strategy can be confirmed in this study since predawn and midday water potentials were similar between seasons, and always less negative than plants growing in transition and SDFD vegetation sites.

The transition region and SDFD area investigated in the present study were very similar in terms of their floristic, physiognomic, and pedological characteristics (Neves et al. 2016), which was reflected in the frequencies and durations of their phenological patterns. Flowering was almost completely restricted to the rainy season in both sites, characterizing an opportunistic phenological response to temporal variations in water availability (Dyer et al. 2012). Several approaches have been used to explain seasonal variations in the reproductive phenophases of dry forest species. Parente et al. (2012) reported that the most frequent species flowered only after the beginning of the rainy season. Lima et al. (2012) found that species with low wood densities and greater water storage capacities flowered between the dry and rainy seasons, while high wood density species flowered only in the rainy season. A number of studies have demonstrated the role of wood density in drought resistance, and its importance in modulating leaf behavior in dry forests (Worbes et al. 2003; Méndez-Alonzo et al. 2013).

In the present study, the SDFD species that flowered only during the rainy season had the highest relative population densities, and had elevated wood density values. These results indicate the degree to which these species depend on water availability and the important influence of wood density on their flowering strategies. This importance can clearly be seen in terms of their water potential values, which were very variable between the different seasons (Fig. 3). The transition and SDFD vegetations grow on clayey soils, which have a high water retention capacities (Hall et al. 1977). This, and the fact that transition and SDFD species have elevated wood densities, appears to be the cause of the restriction of flowering to the rainy season or the dry–rainy transition.

Changes in the water conductivity of roots, and in the longitudinal water pressure gradient between the roots and the aerial portions, may interfere with the physiological activities of those aerial organs (Tyree 1997). The higher densities of shrub–arboreal individuals in the transition and SDFD areas as compared to the savanna site indicate greater root masses in those soils that should intensify water stress in plants growing in the first two areas, especially during the dry season (Gerhardt 1996). Thus, as rainfall volumes were significant during the dry season across the three sites, water stress scenarios in the transition and SDFD areas would be more severe due to the high competition for soil water resources. The absence of a

continuous herbaceous stratum (as seen in the savanna site) that can retain humidity and lessen evaporation presumably also aggravates water stress (Giambelluca et al. 2009), and the lack of a continuous canopy in the transition and SDFD sites diminishes the capacity to retain humidity. The seasonal variations in rainfall and soil water availability appear to be the main causes of the seasonal characters of the flowering observed in the SDFD and transition areas. In savannas, the vertical partitioning of soil water (i.e., the use of ground water at different depths by grasses, herbs, and trees growing side by side) results in a more complex pattern of soil water extraction (Rossatto et al. 2013b) which, together with the availability of soil water throughout the year, would favor the continuous flowering observed in our study.

The greater diversity of functional groups in the savanna area was determined by plant water potentials, reflecting the variability in wood densities of the species and the availability of soil water, unlike the transition and SDFD areas where the plants had lower water potentials and flowering occurring only in the rainy season. The diversity of phenological strategies observed in the savanna, SDFD, and transition areas reflects factors such as species composition, soil characteristics, and wood density that promote adjustments in flowering patterns based on resource allocation and the influence of community structure (Arbeláez and Parrado-Rosselli 2005; Oliveira 2008) and SDFD (Jara-Guerrero et al. 2011).

We have shown that the role of rainfall, especially the rainfall volumes during the dry season, is critical in defining different flowering patterns at the community level. The physical properties of the soil select for the presence of species with distinct water-use strategies (low wood density species in savanna areas and high wood density species in the transition zone and forest) which in turn affected their flowering phenophases. The specific physical characteristics of the savanna soil and subsoil water reserves favored strategies based on the retention of large quantities of water in the plant body that could be used throughout the year, in contrast to the elevated root competition in the soils in the transition and SDFD areas. Therefore, the water potential of plants, which is affected by both water availability in the soil and by wood density, plays an important role in the continuous phenological patterns observed in savanna vegetation and in the seasonal patterns seen in the transition and SDFD sites. Lastly, this study advances our understanding of the link between environmental heterogeneity and plant persistence in communities under semiarid climate.

Acknowledgements The authors would like to thank the specialists who helped identify the plant species, the undergraduate students of Universidade Estadual de Feira de Santana, and the Graduate Program

in Botany for their assistance with the field work, and the Brazilian Meteorological Institute for kindly providing the climate data used to calculate the 50-year rainfall mean. This study was funded by Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq 480508/2008) and by Fundação de Amparo a Pesquisa do Estado da Bahia (FAPESB 5303/2009). S.P.S.N. received FAPESB and CAPES Grants, and L.S.F. received CNPq Grants.

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