

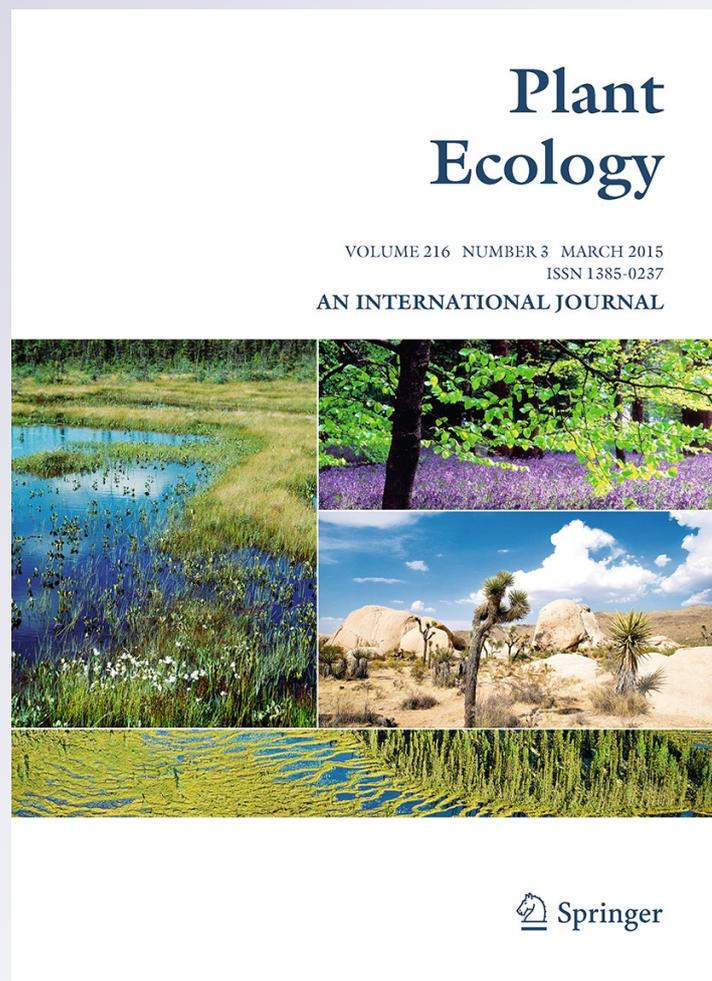
Is the dry season an important driver of phenology and growth for two Brazilian savanna tree species with contrasting leaf habits?

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Is the dry season an important driver of phenology and growth for two Brazilian savanna tree species with contrasting leaf habits?

Ândrea Carla Dalmolin · Francisco de Almeida Lobo · George Vourlitis · Priscila Russani Silva · Higo José Dalmagro · Mario Zortéa Antunes Jr. · Carmen Eugenia Rodriguez Ortíz

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Abstract Brazilian savanna (known as cerrado) has highly seasonal variation in rainfall yet trees have widely different phenological strategies ranging from evergreen to fully deciduous. While qualitative patterns of canopy phenology are well-known, few studies have quantitatively measured schedules of leaf and branch phenology. We measured the leaf and vegetative phenology of two widely distributed cerrado tree species *Vochysia divergens* Pohl., an evergreen species, and *Curatella americana* L., a semi-deciduous species, over a 1-year period and hypothesized that the dry season would represent a trigger for leaf abscission and leaf and branch growth. Leaf and branch emergence and leaf abscission for the semi-deciduous species were coincident with the end and beginning of the dry season, respectively, and were significantly correlated with dry season meteorology, but with time lags that varied

depending on the meteorological variable. Leaf and branch emergence and leaf abscission for the evergreen species were also coincident with the dry season, but correlations with meteorological variables were weaker and seasonal patterns were more subtle. *V. divergens* leaves also suffered more from herbivory than *C. americana*, and there is evidence that herbivory may have altered patterns of leaf emergence for *V. divergens*. *V. divergens* leaves survived longer than *C. americana* leaves, and relative branch growth rates were significantly higher for *C. americana*. While our study was limited to only two tree species and 1 year, we demonstrated quantitatively that patterns of leaf and branch phenology were highly correlated with climatic variations. A strategy of leaf emergence and branch growth initiation during the dry season likely maximizes carbon gain by increasing rates of C assimilation by plants at the onset of the rainy season.

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Pantanal · *Vochysia divergens* Pohl

Introduction

Phenological studies attempt to determine the possible consequences of environmental factors on the functional aspects of a species (Lieth 1974; Talora and Morellato 2000; Silvério and Lenza 2010). Studies of leaf phenology describe properties such as the degree of deciduousness, timing of leaf emergence, expansion, and mortality, and leaf longevity (Kikuzawa 1995). Variations in leaf phenology can be regarded as strategies to maximize survival and productivity (Rossato and Kolb 2009), since plant carbon balance and growth are closely related to patterns of leaf emergence and abscission and leaf longevity (Reich 1995). Similarly, vegetative phenology studies focus on patterns of branch expansion and mortality, and are essential for the understanding patterns of tree growth, water transport, and net primary productivity (Reich 1995; Negi 2006; Rossato and Franco 2008).

In Brazilian savanna (also known as cerrado), for example, numerous studies have qualitatively assessed leaf phenological patterns with visual assessments of the overall change in the crown appearance (Mantovani and Martins 1988; Batalha et al. 1997; Batalha and Mantovani 2000; Bulhão and Figueiredo 2002; Lenza and Klink 2006; Munhoz and Felfili 2007; Conceição et al. 2007; Rossato and Franco 2008; Pirani et al. 2009; Silvério and Lenza 2010). However, there is limited information about the average lifespan of leaves and how leaf emergence and abscission are related to environmental characteristics (Damascos et al. 2005; Lenza 2005). These studies are important since they can identify phenophases, or developmental phases associated with the seasonal dynamics of a given species, that are critical for understanding plant ecophysiological responses to changing environmental conditions.

We quantified the leaf and branch phenological patterns of two widespread tree species of the Brazilian cerrado, *Vochysia divergens* Pohl and *Curatella americana* L. (Pott and Pott 1994; Lorenzi 2002; Sano et al. 2008). Both species have been found in widely different hydrological regimes ranging from seasonal flooding to severe soil water deficit, highlighting their

physiological plasticity (Parolin et al. 2010; Dalmolin et al. 2012; 2013; Dalmagro et al. 2013; 2014); however, there are no studies that address the quantitative phenology of these species. Given the importance of phenological traits in plant growth and survival (Negi 2006; Rossato and Franco 2008), it is important to determine how these traits vary in response to seasonal variations in climate. Thus, the objectives of this study were to quantify patterns of leaf and branch phenology of *V. divergens* and *C. americana* and determine how these patterns vary in response to seasonal variations in climate. Seasonal variations in climate, photoperiod, and/or resource availability have been found to be important triggers for leaf and branch phenology in a wide variety of tree species (Reich and Borchert 1984; Borchert 1996; Gordo and Sanz 2009; Silvério and Lenza 2010; Nanda et al. 2014). In Brazilian savanna and tropical dry forest, soil water deficits and/or high evaporative demand that develop during the dry season may stimulate litter production, reproduction, and leaf development and growth (Borchert 1996; Sanches et al. 2008; Nanda et al. 2014). Thus, we hypothesized that seasonal reductions in rainfall would represent a trigger for leaf emergence and abscission and branch growth as has been qualitatively described for other cerrado woodlands (Mantovani and Martins 1988; Lenza and Klink 2006; Silvério and Lenza 2010).

Materials and methods

Site and species descriptions

The study was conducted in *campo sujo* (dirty field) cerrado located at the Miranda Farm (15°43'53"S and 56°04'18"W) near the city of Cuiabá, Mato Grosso, Brazil. *Campo sujo* cerrado vegetation consists of a relatively continuous layer of perennial grasses and a discontinuous layer of small trees and shrubs (Eiten 1972). The study site is on flat terrain with an average elevation of 157 m. The climate, according to Köppen classification, is Aw (Antunes-Junior et al. 2011), and the long-term (30 year average) mean annual temperature and rainfall are 26.5 °C and 1,420 mm, respectively (Vourelitis and da Rocha 2011). There is a period of extensive and prolonged seasonal drought that begins in May and ends in September, when monthly evapotranspiration exceeds rainfall by on average a

factor of 10 (Antunes-Junior et al. 2011; Vourlitis and da Rocha 2011). The regional soil type is a rocky, dystrophic red–yellow latosol locally known as a Solo Concrecionário Distrófico (Radambrasil 1982) with low pH, extractable cations and P, and soil organic matter content (Vourlitis et al. 2013).

Curatella americana L. (commonly known as Lixeira) is a tree that is native to cerrado (Lorenzi 2002). It has an upright growth habit that typically reaches a height of 6–10 m, and is described as semi-deciduous, with large leathery leaves (Pott and Pott 1994). *Vochysia divergens* Pohl. (commonly known as Cambara) is an evergreen tree that is native to flooded lowland regions of the Amazon Basin. Cambara has an upright growth habit that can reach a height of 15–20 m (Pott and Pott 1994). Both species have a wide distribution throughout the savanna region of Mato Grosso, and can be found in a variety of cerrado types, including woodlands (cerrado sensu stricto), upland forests (cerradão), riparian forests, and grasslands (Santos et al. 2006; Vourlitis et al. 2011, 2013; Dalmagro et al. 2014).

Field measurements

Microclimatic variables were measured using an automatic weather station that was installed on a 15-m-tall micrometeorological tower. Air temperature and relative humidity were measured using a thermo-hygrometer (HMP 45AC; Vaisala, Inc., Helsinki, Finland). Incident photosynthetic active radiation (PAR) was measured using quantum sensor (LI-190SB-L; LI-COR Biosciences, Inc., Lincoln, NE, USA). Precipitation was measured using a tipping-bucket rainfall gage (TR-525 M; Texas Electronics, Inc., Dallas, TX, USA). Measurements were made every 30 s and stored as 30 min averages using a datalogger (CR1000, Campbell Scientific, Inc., Logan, UT, USA). The vapor pressure deficit of air (VPD) was calculated as the difference between the saturated vapor pressure (e_s) and the actual vapor pressure (e) estimated from the air temperature and relative humidity data (Antunes-Junior et al. 2011).

Ten adult trees, five of *C. americana* and five of *V. divergens*, were randomly selected in June 2010 for the analysis of leaf phenology. On each individual, 16 branches were randomly selected and tagged, and on each branch, all of the leaves were marked with colored tape. Between July 2010 and June 2011, each tree was visited on a weekly basis, and on each branch,

the number of new leaves or leaf buds that emerged was counted and marked with colored tape, and all of the previously marked leaves that were still attached to the branch or fallen were counted. These measurements allowed for the determination of leaf emergence, abscission, and lifespan.

Leaf and branch growth rates were determined weekly on ten of the marked branches on each individual. All new leaves on these branches were measured weekly for length and width using a digital caliper. Branch growth rates were quantified by measuring the change in branch length each week.

Data analysis

The one-sided leaf area (LA) was calculated as the product of leaf length and maximum leaf width, which were measured weekly for each species. Estimates of LA derived from the leaf length and width measurements were calibrated with direct measurements of LA made with a portable leaf area meter (CI-202, CID, Inc., Camas, WA, USA). Linear regression analyses revealed that estimates of LA derived from leaf width and length measurements were highly correlated with the direct measurements of LA (*V. divergens*: $LA_{\text{measured}} = 1.34 \times LA_{\text{estimated}} + 0.709$, $R^2 = 0.99$; *C. americana*: $LA_{\text{measured}} = 1.29 \times LA_{\text{estimated}} + 2.243$, $R^2 = 0.92$; $n = 250$ measurements for both species).

Variations in leaf area over time were modeled using a simple logistic equation (Radford 1967),

$$LA = \alpha / 1 + \beta \exp^{-kt}, \quad (1) \leftarrow$$

where t is the leaf age and α , β , and k are model coefficients calculated using the Solver function for Microsoft Excel. Coefficients derived from this model were used to calculate leaf absolute (AGR_L) growth rates;

$$AGR_L = \alpha \beta k \exp^{-kt} / 1 + \beta \exp^{-kt}. \quad (2) \leftarrow$$

Leaf relative growth rates (RGR_L) = AGR_L/LA (Radford 1967). AGR_L and RGR_L were analyzed only for the sigmoidal LA growth curves that had adjustment R^2 values > 0.89 .

The absolute growth rate of branches (AGR_B) was calculated each week as $(L_1 - L_0)/(t_1 - t_0)$, where L_1 is the current branch length and L_0 is the branch length measured during the previous week (both in cm)

divided by elapsed time ($t_1 - t_0$). Branch relative (RGR_B) growth rates were calculated as $[\text{LN}(L_1) - \text{LN}(L_0)]/(t_1 - t_0)$, where $\text{LN}(L_1)$ and $\text{LN}(L_0)$ are the natural log of the branch length of the current and previous week, respectively and ($t_1 - t_0$) is the elapsed time.

The leaf phenology and growth of the branches were analyzed using circular statistics, which are used to analyze time series for peaks in activity by transforming each month of the year into 30° angular increments, with the month of January represented as 0° and 30°, February as 31° and 60°, and each month increasing by a 30° interval thereafter (Rossatto et al. 2009). Rayleigh's (z) test was used to test the null hypothesis that leaf and branch phenology were evenly distributed throughout the year. The life span of leaves not consumed by herbivores was quantified for each species as the time from leaf emergence to abscission.

Mean values of leaf life span, leaf expansion time, AGR_L and AGR_B , and RGR_L and RGR_B for species were statistically compared using bootstrap resampling techniques. This technique calculates the mean $\pm 95\%$ confidence intervals (95% CI) by resampling the measured values (with replacement) for 1,000 iterations, and means with $\pm 95\%$ confidence intervals that do not overlap are considered to be statistically significant at a $p < 0.05$ (Efron and Tibshirani 1993). Cross-correlation analysis was used to assess for correlations, and the potential for lagged correlations, between leaf or branch phenology and meteorological variables such as mean monthly rainfall, PAR, air temperature and the VPD.

Results

Seasonal variations in microclimate

Accumulated rainfall over the study period was 1,259 mm, which is approximately 160 mm lower than the long-term (30 year) average for this area (Vourlitis and da Rocha 2011). The distribution of rainfall was not uniform over the year, and nearly all of the annual rainfall (ca. 77%) occurred during the months of January–March (Fig. 1). The climatological dry season, defined as the consecutive months with rainfall < 100 mm/month (Hutyra et al. 2005), occurred between the months of July–October 2010

and April–June 2011. Average monthly values of PAR were generally lower during the dry season months of July–September and increased during the wet season to a peak of $213.6 \mu\text{mol m}^{-2} \text{s}^{-1}$ in December (Fig. 1). The vapor pressure deficit (VPD) had its highest average in September (2.4 kPa) and its lowest average in March (0.6 kPa) (Fig. 1). Average air temperature increased from a minimum of 23.2°C in July 2010 to a maximum of 29.8°C in September 2010 and declined thereafter (Fig. 1).

Leaf phenology

Leaf abscission and emergence occurred during every month for *V. divergens* and *C. americana*, but both emergence (Fig. 2a) and abscission (Fig. 2b) were not evenly distributed throughout the year. Leaf emergence for *V. divergens* reached two peaks, one during the dry–wet season transition in October 2010 and another larger peak during the wet–dry season transition in April 2011 ($\mu = 90.25^\circ$, $z = 98.98$; $p < 0.001$; Fig. 2a). These dynamics were positively correlated with PAR (Maximum $r = 0.61$) and temperature ($r = 0.64$), but with a lag of 5 and 7 months, respectively. For *C. americana*, leaf emergence also began during the dry season but was concentrated during the month of October ($\mu = 255^\circ$, $z = 130.89$; $p < 0.001$; Fig. 2a). Peaks in leaf emergence occurred 5 months prior to the peak in precipitation ($r = 0.63$) and 1 month after the peak in VPD ($r = 0.79$) but were negatively correlated with PAR ($r = -0.72$) and temperature ($r = -0.63$) with a lag of 1 and 3 months, respectively (Table 1).

Leaf abscission for *V. divergens* increased during the dry–wet season transition until February, declined slightly in March and April, and reached a peak in May 2011 ($\mu = 149.30^\circ$, $z = 97.39$; $p < 0.001$; Fig. 2b), and these temporal trends were positively correlated ($r = 0.59$) with rainfall with a lag of 3 months (Table 1). Leaf abscission for *C. americana* increased during the wet season in January–March and reached a peak in April ($\mu = 106.77^\circ$, $z = 192.35$; $p < 0.001$) during the wet–dry season transition (Fig. 2b). These trends were positively correlated with peaks in rainfall ($r = 0.65$), PAR ($r = 0.61$), and VPD ($r = 0.68$) but with a lag of 1, 4, and 7 months, respectively (Table 1).

Branch emergence showed a distinctive seasonal trend for *C. americana* but not for *V. divergens*

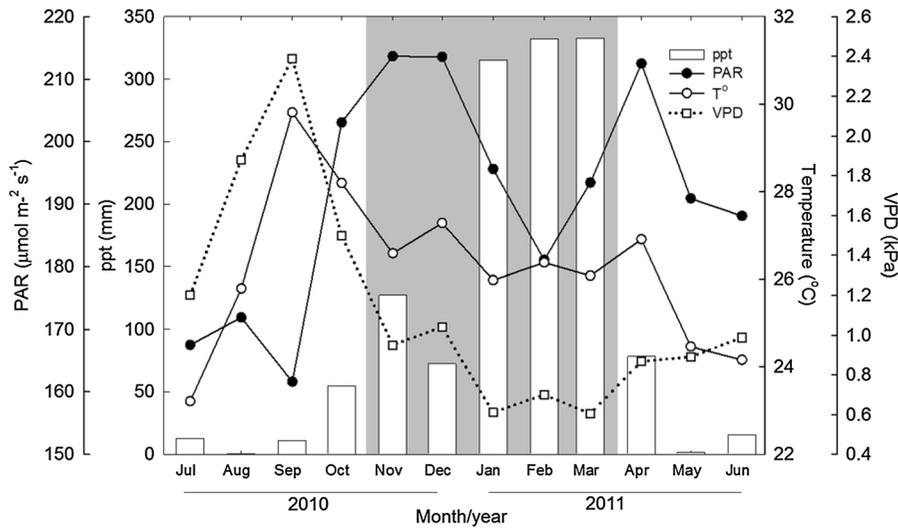


Fig. 1 Total monthly rainfall (white bars) and average monthly photosynthetically active radiation (PAR; black circles, solid line), atmospheric vapor pressure deficit (VPD; white squares, dotted line), and temperature (white circles; solid line) for the study site between July 2010 and June 2011. The scales for

rainfall and PAR are displayed on the left-hand axis, and the scales for VPD and temperature are displayed in the right-hand axis. The shaded portion displays the duration of the wet season, defined as the number of consecutive months with a rainfall > 100 mm/month

(Fig. 2c). For *C. americana*, branch emergence increased markedly in August, reached a peak in October, and declined thereafter with consistently low branch emergence during the wet season (Fig. 2b). These temporal trends were significantly positively correlated with the temperature of the current month ($r = 0.62$) and the VPD of the previous month ($r = 0.92$) and negatively correlated with the PAR of the previous month ($r = -0.68$; Table 1). For *V. divergens*, branch emergence reached a peak in July–August and a secondary peak in February, but these trends were not significantly correlated with any of the measured meteorological variables (Table 1).

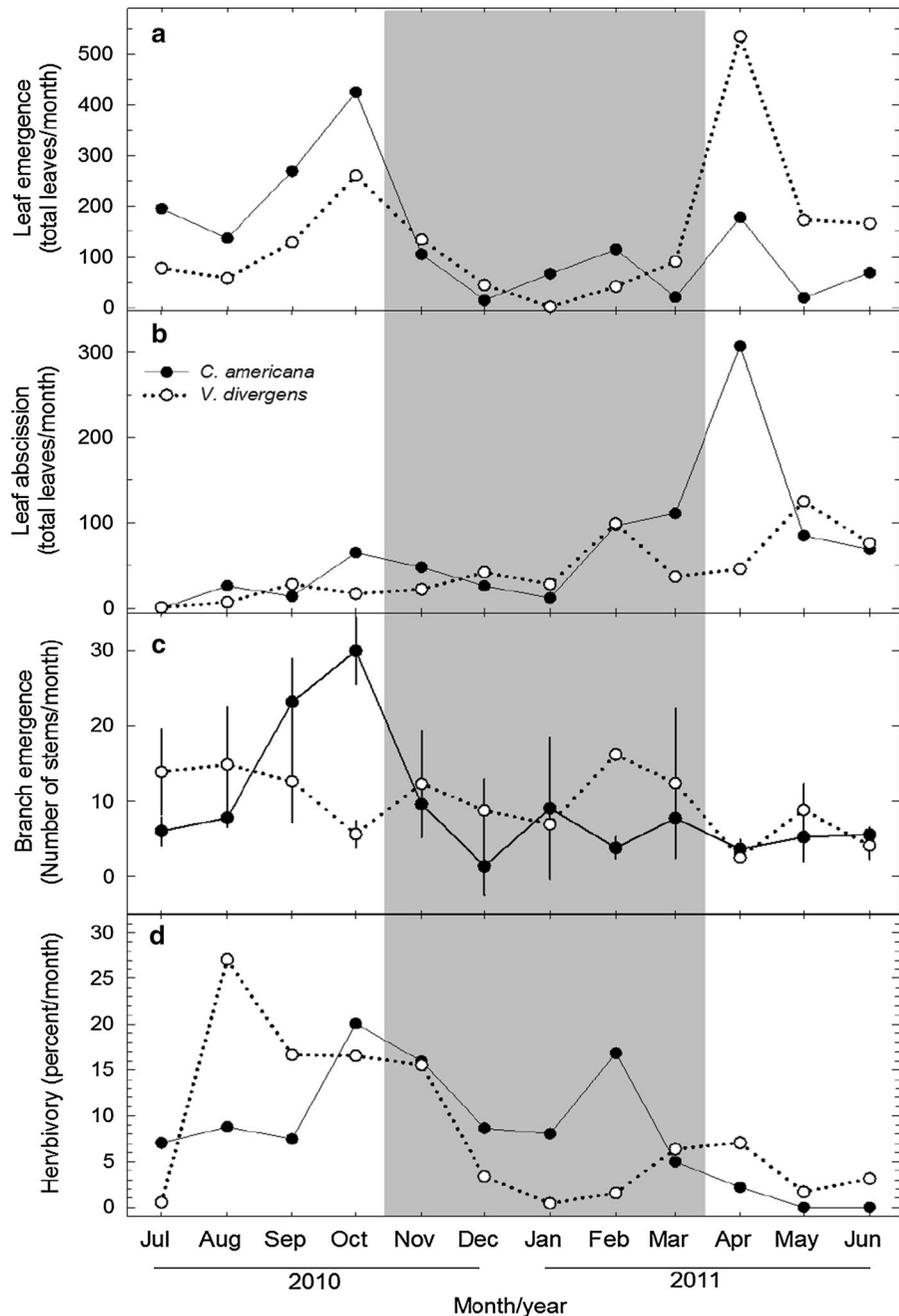
Nearly all of the tagged leaves for both species (ca. 85 %) exhibited signs of herbivore damage (Table 2), primarily from grasshoppers, and there were distinct seasonal patterns in herbivory for both species (Fig. 2d). Herbivore damage of *V. divergens* leaves was intense, with over 70 % of all tagged leaves experiencing severe leaf damage (Table 2). Herbivory increased during the dry season and reached a peak in August, but rates remained high (>18 %) throughout the dry–wet season transition until November. Interestingly, herbivory was not significantly correlated with leaf abscission; however, leaf emergence was positively correlated with herbivory ($r = 0.61$; $p < 0.05$) but with an 8-month

lag between the period of peak herbivory and peak leaf emergence. Herbivore damage was less intense for *C. americana* leaves, with slightly more than half of the tagged leaves experiencing mild damage and approximately 25 % of leaves experiencing severe damage (Table 2). Herbivory increased during the dry–wet season transition and reached peaks in October and in February (Fig. 2d). Herbivory was not significantly correlated with leaf emergence or abscission for *C. americana*.

Leaf and branch growth rates

Although differences between species were observed for the periods of peak leaf emergence and abscission, both species exhibited a similar elapsed time in the emergence of two consecutive leaves, referred to here as the leaf emergence interval (Table 3). Leaf emergence intervals were on average of 29 days over the study period; however, significant differences were observed between the dry and wet period for both species. During the dry season, *V. divergens* and *C. americana* put out a new leaf on average every 19 and 13 days, respectively, while during the wet season, the average leaf emergence interval was 39 and 53 days for *V. divergens* and *C. americana*, respectively. Leaf area for *C. americana* was 3 times higher than *V.*

Fig. 2 Total number of leaves emerging **a** and abscising **b** for all marked trees and/or branches per month, **c** mean (± 1 sd; $n = 5$ trees/species) number of branches emerging each month, and **d** the percent leaves damaged by herbivores each month between July 2010 and June 2011 for *Vochysia divergens* (white circles, dotted line) and *Curatella americana* (black circles, solid line). The shaded portion displays the duration of the wet season as defined in Fig. 1



divergens, but *V. divergens* leaves had a significantly longer life span than *C. americana* leaves (Table 3).

The leaf growth dynamics for both species were well described by the sigmoidal growth model (Eq. 1), with a coefficient of variation (r^2) of 0.90–0.99 for both *V. divergens* and *C. americana*. Despite differences in leaf area and longevity, both

species had similar absolute (AGR_L) and relative (RGR_L) leaf growth rates (Table 3). Absolute rates of branch growth (AGR_B) were also similar for both species, and ranged between 0.046 and 0.052 cm d^{-1} ; however, relative branch growth rates (RGR_B) were significantly higher for *C. americana* (Table 3).

Table 1 Results from cross-correlation analysis of monthly leaf emergence, abscission, and branch growth as a function of total monthly precipitation and average monthly photosynthetically active radiation (PAR), vapor pressure deficit (VPD), and air temperature

| | Precipitation | | PAR | | VPD | | Temperature | |
|---------------------|---------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|
| | Max <i>r</i> | Lag (months) | Max <i>r</i> | Lag (months) | Max <i>r</i> | Lag (months) | Max <i>r</i> | Lag (months) |
| <i>C. americana</i> | | | | | | | | |
| Leaf abscission | 0.65 | 1 | 0.61 | 4 | 0.68 | 7 | – | – |
| Leaf emergence | 0.63 | –5 | –0.72 | 1 | 0.79 | 1 | –0.63 | 3 |
| Branch growth | 0.66 | –4 | –0.68 | 1 | 0.92 | 1 | 0.62 | 0 |
| <i>V. divergens</i> | | | | | | | | |
| Leaf abscission | 0.59 | 3 | – | – | – | – | – | – |
| Leaf emergence | – | – | 0.61 | 5 | – | – | 0.64 | 7 |
| Branch growth | – | – | – | – | – | – | – | – |

Shown are the maximum cross-correlation coefficient (Max *r*) and the number of months that a phenology variable preceded (negative lag) or followed (positive lag) a given meteorological variable. Cross-correlation coefficients displayed in the table are statistically significant ($p < 0.05$)–($p > 0.05$)

Table 2 Estimates of leaf herbivory for *Vochysia divergens* and *Curatella americana* over the 1-year field study

| Herbivory category | Severity of leaf damage | Number of leaves (% of total) | |
|--------------------|---------------------------------------------------------------|-------------------------------|---------------------|
| | | <i>V. divergens</i> | <i>C. americana</i> |
| Undamaged | | 141 (15) | 116 (16) |
| Mild | <50 % of the leaf damaged, leaf remained attached to the stem | 94 (10) | 366 (51) |
| Moderate | >50 % of the leaf damaged, leaf remains attached to the stem | 41 (4) | 48 (7) |
| Severe | >50 % of the leaf damaged, leaf abscised | 663 (71) | 182 (26) |
| Total | | 939 | 712 |

Herbivory was classified into three different groups depending on severity of leaf damage. Shown are the total number of leaves and the percent of all leaves of each species as a function of each herbivory damage category

Table 3 Mean (± 95 % confidence interval (CI)) leaf emergence interval, lifespan and area, and absolute (AGR) and relative (RGR) growth rates for leaves and branches of *V. divergens* and *C. americana* from July 2010 to June 2011

| Variable | Species | |
|-------------------------------------------------------|-----------------------------------------------|-----------------------------------------------|
| | <i>V. divergens</i> | <i>C. americana</i> |
| Leaf emergence interval (days) | 28.8 \pm 5.5 ($n = 122$) ^a | 29.5 \pm 4.9 ($n = 248$) ^a |
| Leaf lifetime (days) | 244.6 \pm 8.7 ($n = 113$) ^a | 199.6 \pm 6.8 ($n = 208$) ^b |
| Leaf area (cm ²) | 30.2 \pm 10.9 ($n = 388$) ^a | 109.2 \pm 6.1 ($n = 396$) ^b |
| AGR _L (cm ² day ^{–1}) | 0.029 \pm 0.016 ($n = 19$) ^a | 0.030 \pm 0.014 ($n = 19$) ^a |
| RGR _L (day ^{–1}) | 0.0023 \pm 0.0008 ($n = 19$) ^a | 0.0011 \pm 0.0004 ($n = 19$) ^a |
| AGR _B (cm day ^{–1}) | 0.046 \pm 0.016 ($n = 20$) ^a | 0.052 \pm 0.010 ($n = 20$) ^a |
| RGR _B (day ^{–1}) | 0.059 \pm 0.017 ($n = 20$) ^a | 0.105 \pm 0.018 ($n = 20$) ^b |

Values with different letters for a given variable indicate a statistically significant ($p < 0.05$) difference between species based on the ± 95 % CI

n number of leaves or shoots

Discussion

Our results support the hypothesis that the dry season is an important trigger for leaf abscission and leaf and branch emergence in *V. divergens* and *C. americana*, which is consistent with previous observations made in seasonal tropical forest and savanna (Reich and Borchert 1984; Franco 2002; Franco et al. 2005; Rossatto et al. 2009; Silvério and Lenza 2010). However, there were substantially different leaf and branch phenology patterns in the two cerrado tree species, *V. divergens* and *C. americana*, studied here.

For *C. americana*, a semi-deciduous tree species, definitive peaks in leaf emergence and abscission were observed, which were closely tied to the onset and end of the dry season. These dynamics are broadly consistent with many semi-deciduous cerrado tree species (Mantovani and Martins 1988; Oliveira and Gibbs 2000; Lenza and Klink 2006; Silvério and Lenza 2010), trees in seasonal tropical forests (Reich and Borchert 1984; Borchert 1996; Nanda et al. 2014), trees in African savanna (de Bie et al. 1998), and plants in extra-tropical areas such as the Mediterranean Basin (Peñuelas et al. 2004) and deserts (Abd El-Ghani 1997; Ghazanfar 1997) where seasonal variations in climate are large. Leaf abscission at the beginning of the dry season is thought to be an adaptation against eventual water loss (Rizzini 1979) that occurs when soil moisture becomes limiting and evaporative demand increases (Jackson et al. 1999; Franco 2002; Bucci et al. 2004), and allows branches without leaves to be rehydrated from water acquired from both internal water reserves and deeper in the soil profile (Reich and Borchert 1984; Rossatto et al. 2012). Thus, branch growth and budding can occur during the dry season even under soil water deficit (Reich and Borchert 1984), and allow the establishment of a new cohort of leaves before and during the onset of the rainy season (Franco 2002; Lenza and Klink 2006; Rossatto et al. 2009). In turn, establishing a new cohort of leaves before the wet season can maximize carbon gain by increasing rates of C assimilation when the first rains begin (Franco et al. 2005; Rossatto et al. 2009). Furthermore, leaf N and P concentrations have been found to increase during the dry season for *C. americana* and *V. divergens* (Dalmagro et al. 2013) and other cerrado tree species (Leitão and Silva 2004), as N and P from senescent leaves are translocated to new, expanding leaves (Reyes-Arribas et al. 2001). An

increase in internal water and nutrient reserves presumably accounted for the higher rates of leaf emergence and branch emergence observed during the dry season.

For the evergreen species (*V. divergens*), rates of leaf abscission peaked during the early dry season, while leaf emergence exhibited two peaks, one at the onset of the rainy season and the other immediately after the end of the wet season. Presumably, the leaf emergence at the beginning of the wet season was due in part to the leaf abscission that occurred during the onset of the previous dry season. However, Silvério and Lenza (2010) and Lenza and Klink (2006) found that many evergreen cerrado trees have peaks in leaf emergence during the wet season, a pattern that was reportedly due to drought limitations to leaf expansion during the dry season. It is unclear whether *V. divergens* has similar traits; however, several lines of evidence, such as little seasonal variation in canopy conductance and evapotranspiration (Sanches et al. 2011; Vourlitis and da Rocha 2011) and the ability to redistribute leached nutrients and water from hydraulic redistribution (Vourlitis et al. 2011), indicate that *V. divergens* has a root system that can access deep water reserves during the dry season. Rather, we speculate that the secondary peak in leaf emergence was due to the intense herbivory that occurred on *V. divergens* leaves during the previous August. Leaf emergence was significantly positively correlated with herbivory but with an 8-month lag, and the secondary peak in leaf emergence that occurred in April 2011 was exactly 8 months after the peak in herbivory. Herbivory plays an important role in phenology of leaves, and young leaves are often preferred over mature leaves due to a lower content of structural carbon (Rickfles 2003; Van Asch and Visser 2007). Leaves of *V. divergens* also had relatively higher concentrations of N than *C. americana* (Dalmagro et al. 2013), which was not preyed upon with the same intensity and may make it less palatable than *V. divergens* (Furlan et al. 1999; Peeters 2002).

Leaf area was over 3 times higher for *C. americana* than *V. divergens*, and while species differences in LA are largely genetically controlled, LA can be heavily influenced by environmental conditions such as exposure to sunlight and soil water and nutrient availability (Chapin 1991; Pierce et al. 1994; Reich et al. 1999; Knops and Reinhart 2000; Dalmagro et al. 2014). However, environmental variations in LA were

insufficient to change the relative difference in LA between these species.

The shorter leaf lifespan for the semi-deciduous *C. americana* is consistent with previous studies (Damascos et al. 2005; Lenza 2005, Guimarães 2011). Plants with shorter leaf lifespan typically have higher growth rates than plants with longer leaf lifespan (Reich et al. 1999), and while absolute and relative leaf growth rates were similar for both species, *C. americana* had a significantly higher relative rate of branch growth. Full leaf expansion occurred for both species in about 2 months, which is substantially shorter than *Miconia albicans* (92 days), an evergreen cerrado tree species, and *Leandra lacunosa* (76 days), a semi-deciduous cerrado tree species (Damascos et al. 2005).

In conclusion, we found that the dry season was a key trigger for leaf abscission and leaf and branch emergence of an evergreen and a deciduous tree species of the Brazilian cerrado. A strategy of leaf emergence and branch growth initiation during the dry season likely maximizes carbon gain by increasing rates of C assimilation by plants at the onset of the rainy season. These results have implications for anthropogenic climate change, which is predicted to result in a longer, more intense dry season (Li et al. 2008; Costa and Pires 2010). In turn, a longer dry season would lead to later leaf emergence and earlier abscission for *C. americana*, assuming that leaf longevity is somewhat flexible, and a later peak in emergence for *V. divergens*. Presumably, an intensification of the dry season would affect deciduous species more than evergreen species, which were less tied to the seasonal variations in meteorology. However, a longer dry season would reduce the duration that both growth forms are fully leafed-out, which would likely reduce annual C gain (Franco 2002; Lenza and Klink 2006; Rossatto et al. 2009). In addition, while meteorological variation was an important phenological trigger, other pressures such as herbivory also affected schedules of leaf emergence, especially for *V. divergens*.

Our study was limited to only two tree species and 1 year, and clearly, more data, especially over multiple years, are needed to fully understand how leaf and stem phenology are affected by meteorological variation. Even so, the quantitative approach used here demonstrated that patterns of leaf and branch phenology were related to climatic variations, albeit with lags

depending on the variable of interest. Our data highlight phenological adaptations of cerrado tree species and how these adaptations can potentially affect productivity and survival in seasonally variable environments.

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