

Lessons from a tropical deciduous shrub species: leaf fall can play a more important role than rain in leaf budding

Nathália Ribeiro Henriques¹, Cássio Cardoso Pereira¹

¹ Universidade Federal de Minas Gerais, Departamento de Genética, Ecologia e Evolução, Programa de Pós Graduação em Ecologia, Conservação e Manejo da Vida Silvestre, Belo Horizonte, MG, Brazil

Corresponding author: Cássio Cardoso Pereira (cassiocardosopereira@gmail.com)

Academic editor: Anurag Dhyani | Received 29 August 2022 | Accepted 19 October 2022 | Published 11 November 2022

Citation: Henriques NR, Pereira CC (2022) Lessons from a tropical deciduous shrub species: leaf fall can play a more important role than rain in leaf budding. *Neotropical Biology and Conservation* 17(4): 239–251. <https://doi.org/10.3897/neotropical.17.e93846>

Abstract

In the Cerrado, the sequential chaining of phenological events during the dry season is a pattern observed in many plant species. In this season, many plants completely lose their leaves, and soon after deciduous, there is an expressive production of leaf buds. In this study, we investigated the effect of irrigation and early defoliation on the triggering of leaf budding of the deciduous species *Peixotoa tomentosa* A.Juss. in the dry season of a seasonal environment with water restrictions. Therefore, we set up an experiment with three groups of plants: control (n = 15), irrigation treatment (n = 15), and removal treatment (n = 15), and after the complete deciduousness of the plants, we carried out phenological monitoring of the development of leaf buds in these plants. From July to August 2022, the leaf budding phenology of the 45 individuals was evaluated twice a week. To test whether there is a difference in the number of leaf buds between treatments, we built generalized linear mixed models (GLMMs). Plants in the removal treatment had a statistically higher number of leaf buds produced than the plants in the irrigation and control groups ($P < 0.05$). However, the control group and the irrigation treatment did not differ from each other ($P > 0.05$). We showed that early defoliation influenced the triggering of leaf buds in *P. tomentosa*, increasing the production of young leaves in their individuals in a seasonal environment with water restrictions. Irrigation was not able to break the dormancy of leaf buds. Our findings contribute to a better understanding of the triggering of vegetative phenophases in deciduous Cerrado plants, showing that leaf fall may play a more important role than rain in the production of leaf buds in the dry season.

Keywords

Cerrado, leaf buds, leaf fall, Malpighiaceae, phenology, savanna, seasonality

Introduction

In the Cerrado, the sequential chaining of phenological events during the dry season is a pattern observed in many plant species (Pereira et al. 2022). In this season, many plants completely lose their leaves, and soon after deciduous, there is an expressive production of leaf buds (Araújo and Haridasan 2007; Pereira et al. 2022).

Water stress is an important physiological trigger for leaf abscission (Kikuzawa 1991). The decrease in the amount of water in the more superficial layers of the soil, at the beginning of the dry season, has been associated with leaf fall due to the decline in water potential, which would induce this phenophase (Santos et al. 2021). With reduced precipitation and humidity, leaf fall can help conserve water, preventing the plant's vital activities from being compromised in the dry season (Goldstein et al. 2008). Thus, as a result of leaf fall, rehydration promotes adjustments in plant water demand and supply, which are regulated by reducing leaf area, transpiration, increasing root system depth, and internal water reservoir (Scholz et al. 2002), which guarantees the subsequent opening of leaf buds and flower buds (Pereira et al. 2022).

Leaf bud production is linked to a wide range of adaptive responses to seasonal stresses (Pereira et al. 2022). The development of young leaves in the dry season minimizes photosynthetic losses in this period of low light, showing higher efficiency at the beginning of the rainy season of high light, when mature leaves will have their photosynthetic apparatus developed, providing the energy needed for the subsequent peak flowering and fruiting (Goldstein et al. 2008). In addition, predation on young leaves is lower due to adverse conditions for insect populations (Murali and Sukumar 1993), which may increase the chances of leaf development due to the lower abundance of chewing insects at this time (Silva et al. 2020).

Knowledge of seasonal plant variations has been considered essential for the study of the ecology and evolution of the Cerrado and for understanding the spatio-temporal organization of available resources (Pereira et al. 2022). In the tropics, climate change has been causing variations in the intensity of abiotic factors (for example, changes in the amount of rainfall, Mendoza et al. 2017), changing the seasonal rhythms of species by affecting the sequential triggering of phenological events and, consequently, the plant development (Vilela et al. 2017) and community dynamics (Fourcade et al. 2021). Thus, the investigation of the vegetative phenology of Cerrado deciduous plants helps us to better understand how these abiotic events interfere with the development of typical plants in tropical communities subjected to seasonality.

In this study, we investigated the effect of irrigation and early defoliation on the triggering of leaf budding of the deciduous species *Peixotoa tomentosa* A.Juss. in the dry season amidst a seasonal environment with water restrictions. We tested the following hypotheses: (i) The irrigation of plants in the water deficit period increases the production of leaf buds; and (ii) The early removal of senescent leaves accelerates the production of leaf buds. In light of these hypotheses, we made the following

predictions: (i) Irrigation reduces water stress and serves as a stimulus to break the dormancy of leaf buds; (ii) Early leaf removal promotes the rehydration of branches due to reduced transpiration and a reallocation of nutrients that are transferred to the growth of young leaves. To test the hypotheses above, we set up an experiment with three groups of plants: control, irrigation treatment, and removal treatment, and after the complete deciduity of the plants, we carried out the phenological monitoring of the development of leaf buds in these plants.

Methods

Study site

The study was carried out in the municipality of Congonhas, Minas Gerais, south-eastern Brazil (Fig. 1). The study area has approximately 10 ha and is located at the geographic coordinates of 20°32'16"S and 43°48'30"W, with altitude of approximately 950 m (Personal observation). The vegetation is classified as Cerrado Típico, a subdivision of the Cerrado *sensu stricto* (Fig. 2A), with a tree cover of 20 to 50% and trees with an average height of 3 to 6 m (Ribeiro and Walter 2008). The soil in this area is deep and classified as red latosol (Ribeiro and Walter 2008, see Fig. 2B), and the climate is subtropical in altitude (Cwb) according to the Köppen classification, with dry winters between May and September and mild summers between October and April (Alvares et al. 2013).

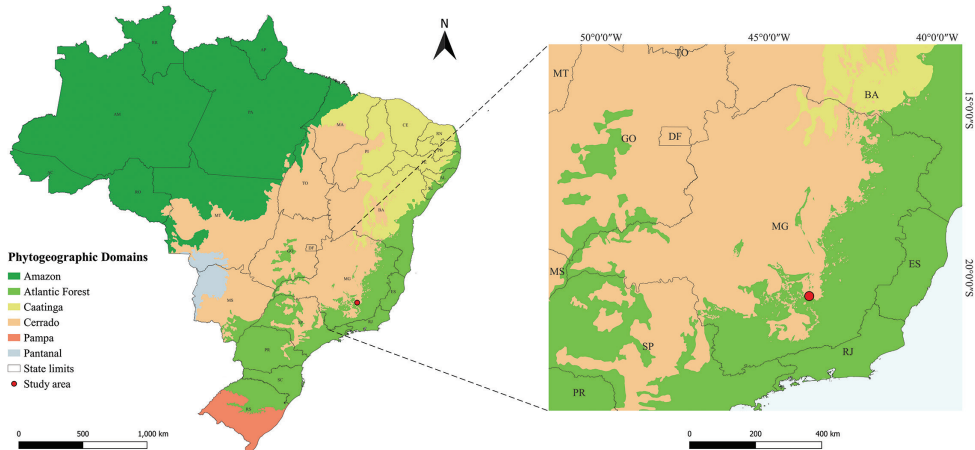


Figure 1. Map of the geographic location of the study area in Congonhas, Minas Gerais, Brazil. The boundaries of Brazilian phytogeographic domains were adapted from shapefiles available from the Instituto Brasileiro de Geografia e Estatística (2022), from the global ecoregions of Dinerstein et al. (2017), and from the map of vegetations on rocky outcrops of the Cerrado domain by Newton Barbosa. Map design: Cássio Cardoso Pereira.

Study system

P. tomentosa is a shrub species of the Malpighiaceae family, reaching up to 3 m in height (Fig. 2C). The leaves have tomentose indument on both sides. It has a pair of extrafloral nectaries at the base of the leaf blade on the abaxial surface (Pereira et al. 2020). Its flowers are yellow and have ten elaiophores at the base of five sepals, distributed in pairs. The petals are unguiculated and fimbriate, and the dorsal banner petal is smaller and thicker. The flowers produce up to four-winged samara seeds (Mamede 1987). This species is classified as brevideciduous, losing all its leaves in the dry season for a period of up to 21 days (Pereira et al. 2022).

Data sampling

Leaf budding

Before the experiment, we marked 45 plants in May 2022 and divided them into 3 groups, the control group ($n = 15$), removal treatment ($n = 15$) and irrigation treatment ($n = 15$). We randomly marked mature individuals with an average height of 1.5 m, separated by a minimum distance of 10 m between them, to avoid possible sampling of leaf buds from the same individual. All individuals were marked with biodegradable tape, and the chosen area was close to a water source, necessary for one of the treatments.

At the end of June, when we observed that the leaves of the individuals were starting to fall, the plants of the removal treatment had all the leaves manually removed early. In the irrigation treatment, the individuals were watered with a watering can at regular intervals of five days, with approximately 2.5 L of water, between July 4th (after the plants lost their leaves and before the beginning of leaf budding) and August 23th (the last week of the experiment). The amount of water used did not soak the soil. We chose to use a smaller volume of water, as the excess could hinder the oxygenation of the roots, rotting them and harming the development of the plants.



Figure 2. **A** Overview of the Cerrado Típico, a subdivision of the Cerrado *sensu stricto* phytophysiology that occurs in the study area. **B** Exposed soil by the action of termites and armadillos, evidencing the red latosol under the study area. **C** *Peixotoa tomentosa* A.Juss. shrub marked with biodegradable tape. Photo credits: Cássio Cardoso Pereira.

From July 4th to August 25th, the phenology of the 45 individuals was evaluated twice a week. To assess leaf budding, we counted all leaf buds of all individuals in this period. Finally, we collected daily precipitation data at the Instituto Nacional de Meteorologia (2022), from July 1st to August 25th, to cover the entire experiment period, at the Ouro Branco automatic station, which is approximately 8 km from the study area.

Soil collection

To verify if the irrigation treatment provided a different environmental condition for the plants, a soil collection was carried out on August 12 (four days after the plants were watered this week). On that date, 15 soil samples were collected close to the root of individuals from the irrigation treatment and the control treatment.

Sampling was performed with PVC tubes, approximately 4.5 cm in diameter, which penetrated about 20 cm into the soil. After removal from the soil, the samples were transferred to paper bags and taken to the laboratory for verification of the wet weight, with the aid of a precision digital balance. After weighing, the samples were placed in an oven for 48h at approximately 70 °C and then weighed to verify the dry weight.

Data analysis

To evaluate the behavior of the population at each phenological follow-up date, we constructed time series plots with the mean of leaf buds of all 15 individuals for each of the 12 evaluated dates (Table 1).

To test whether there is a difference in the mean number of leaf buds between treatments, we built generalized linear mixed models (GLMMs). The mean values of the number of leaf buds of the 15 individuals of each treatment were calculated along with the eight phenological observation dates (Table 2). In this way, differences between the mean values of the number of leaf buds of the individuals of each treatment were tested, using the mean number of leaf buds per individual as dependent variables, each treatment as the fixed factor, and individual plants as random factors. Error distribution was checked through restricted maximum likelihood (REML). Treatment means were compared using a post hoc Tukey test ($\alpha = 0.05$).

The estimation of the relative water content (RWC) of each soil sample was made according to the formula: $RWC = (Ww - Dw) / Ww \times 100$, where Ww = wet weight and Dw = dry weight (Table 3). The average values of the relative water content (RWC) of the 15 samples of the control soil and the irrigated soil were calculated and, to test if there was a difference between the treatments, we built generalized linear mixed models (GLMMs). For this, we considered the values of the relative water content (RWC) of the individuals as dependent variables, each treatment as a fixed factor, and individual plants as random factors. Error distribution was checked through restricted maximum likelihood (REML). All analyzes were performed using the “lme4” package (Bates et al. 2011) in the R software (R Core Team 2021).

Table 1. Time series data showing the number and mean (\pm SE) of leaf buds found in each of the 12 phenological monitoring dates for the 15 individuals of *Peixotoa tomentosa* A.Juss. in the control, irrigation, and removal treatments. SE = Standard Error.

Treatments	Phenology Dates	Plant Individuals															Mean of Leaf Buds	SE
		1	2	3	4	5	6	7	8	9	10	11	12	13	14	15		
Control	Jul 18 th	2	3	7	6	5	7	2	7	3	6	4	7	7	7	3	5.07	0.52
Control	Jul 21 th	4	5	6	6	7	7	5	6	8	5	4	8	7	6	7	6.07	0.33
Control	Jul 25 th	3	5	5	7	8	6	6	5	7	5	5	7	5	4	10	5.87	0.45
Control	Jul 28 th	4	5	5	8	7	4	8	5	8	7	7	7	7	6	8	6.40	0.38
Control	Aug 1 st	3	4	6	6	8	5	5	6	7	5	5	6	5	6	5	5.47	0.31
Control	Aug 4 th	4	4	4	6	6	6	6	6	7	5	5	8	5	4	5	5.40	0.31
Control	Aug 8 th	2	4	2	4	5	5	5	6	4	5	3	4	6	5	5	4.33	0.32
Control	Aug 11 th	2	2	2	3	3	3	3	1	5	0	2	2	3	2	4	2.40	0.31
Control	Aug 15 th	1	2	2	0	1	1	1	0	2	0	4	1	3	1	3	1.47	0.31
Control	Aug 18 th	0	0	2	0	0	0	0	0	0	0	2	1	1	0	2	0.53	0.22
Control	Aug 22 th	0	0	2	0	0	0	0	0	0	0	1	1	1	1	1	0.47	0.17
Control	Aug 25 th	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.00	0.00
Irrigation	Jul 18 th	5	7	2	7	3	7	2	7	3	6	7	3	5	7	2	4.87	0.55
Irrigation	Jul 21 th	7	7	5	6	8	6	5	6	8	6	7	7	7	7	5	6.47	0.26
Irrigation	Jul 25 th	8	6	6	5	9	7	6	5	11	5	5	5	8	6	6	6.53	0.46
Irrigation	Jul 28 th	7	8	5	5	8	6	8	5	8	5	6	8	8	8	8	6.87	0.35
Irrigation	Aug 1 st	5	5	5	6	7	5	5	6	7	4	5	5	6	5	5	5.40	0.21
Irrigation	Aug 4 th	6	7	6	6	7	6	6	6	7	4	6	5	6	6	6	6.00	0.20
Irrigation	Aug 8 th	5	5	5	6	7	5	5	6	4	4	4	5	5	5	5	5.07	0.21
Irrigation	Aug 11 th	3	3	3	1	2	3	3	1	4	2	6	4	3	3	3	2.93	0.32
Irrigation	Aug 15 th	1	1	1	0	2	1	1	2	2	2	3	3	1	1	1	1.47	0.22
Irrigation	Aug 18 th	0	0	0	0	0	2	0	0	0	0	1	2	0	0	0	0.33	0.19
Irrigation	Aug 22 th	2	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0.27	0.15
Irrigation	Aug 25 th	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.00	0.00
Removal	Jul 18 th	9	3	4	6	8	6	9	6	4	11	8	9	7	5	12	7.13	0.68
Removal	Jul 21 th	10	8	4	6	9	13	11	8	9	12	11	14	11	5	14	9.67	0.80
Removal	Jul 25 th	7	11	4	4	13	9	12	12	11	8	10	11	5	5	8	8.67	0.80
Removal	Jul 28 th	8	9	2	4	9	9	10	8	10	10	8	12	9	6	6	8.00	0.66
Removal	Aug 1 st	8	8	3	4	5	7	10	10	5	8	10	7	10	8	7	7.33	0.58
Removal	Aug 4 th	4	7	2	3	9	5	8	9	9	1	6	7	8	7	6	6.07	0.67
Removal	Aug 8 th	3	7	2	3	4	7	5	9	8	2	6	7	10	7	5	5.67	0.65
Removal	Aug 11 th	3	3	2	2	5	3	2	5	8	0	3	1	3	4	7	3.40	0.55
Removal	Aug 15 th	5	2	2	1	2	2	2	1	4	0	4	1	2	3	6	2.47	0.42
Removal	Aug 18 th	0	1	2	1	3	1	1	0	3	0	2	0	0	0	2	1.07	0.28
Removal	Aug 22 th	0	1	2	0	0	1	0	0	0	1	0	0	0	0	0	0.33	0.16
Removal	Aug 25 th	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0.00	0.00

Results

There were no rainfall records during the evaluation period (0 mm of rainfall between July 1st and August 25th).

Leaf budding

The mean leaf buds ranged from 9.67 (\pm 0.80 SE) in the removal treatment on July 21th to zero in all groups from August 25th onwards. The evaluated individuals of *P. tomentosa* presented leaf buds from July 18th. Subsequently, as these leaf buds developed into young leaves, the number of leaf buds dropped throughout August (Fig. 3, Table 1). Thus, from the last fortnight of August, the leaves began to mature,

Table 2. Number and mean of leaf buds found in each individual of *Peixotoa tomentosa* A.Juss. from the control, irrigation, and removal treatments along the 12 phenological monitoring dates.

Treatments	Plant Individuals	July 2022						August 2022						Mean of Leaf Buds
		18 th	21 th	25 th	28 th	1 st	4 th	8 th	11 th	15 th	18 th	22 th	25 th	
Control	1	2	4	3	4	3	4	2	2	1	0	0	0	2.08
Control	2	3	5	5	5	4	4	4	2	2	0	0	0	2.83
Control	3	7	6	5	5	6	4	2	2	2	2	2	0	3.58
Control	4	6	6	7	8	6	6	4	2	0	0	0	0	3.75
Control	5	5	7	8	7	8	6	5	3	1	0	0	0	4.17
Control	6	7	7	6	4	5	6	5	3	1	0	0	0	3.67
Control	7	2	5	6	8	5	6	5	3	1	0	0	0	3.42
Control	8	7	6	5	5	6	6	6	1	0	0	0	0	3.50
Control	9	3	8	7	8	7	7	4	5	2	0	0	0	4.25
Control	10	6	5	5	7	5	5	5	0	0	0	0	0	3.17
Control	11	4	4	5	7	5	5	3	2	4	2	1	0	3.50
Control	12	7	8	7	7	6	8	4	2	1	1	1	0	4.33
Control	13	7	7	5	7	5	5	6	3	3	1	1	0	4.17
Control	14	7	6	4	6	6	4	5	2	1	0	1	0	3.50
Control	15	3	7	10	8	5	5	5	4	3	2	1	0	4.42
irrigation	1	5	7	8	7	5	6	5	3	1	0	2	0	4.08
irrigation	2	7	7	6	8	5	7	5	3	1	0	0	0	4.08
irrigation	3	2	5	6	5	5	6	5	3	1	0	0	0	3.17
irrigation	4	7	6	5	5	6	6	6	1	0	0	0	0	3.50
irrigation	5	3	8	9	8	7	7	7	2	2	0	0	0	4.42
irrigation	6	7	6	7	6	5	6	5	3	1	2	0	0	4.00
irrigation	7	2	5	6	8	5	6	5	3	1	0	0	0	3.42
irrigation	8	7	6	5	5	6	6	6	1	2	0	0	0	3.67
irrigation	9	3	8	11	8	7	7	4	4	2	0	0	0	4.50
irrigation	10	6	6	5	5	4	4	4	2	2	0	0	0	3.17
irrigation	11	7	7	5	6	5	6	4	6	3	1	1	0	4.25
irrigation	12	3	7	5	8	5	5	5	4	3	2	1	0	4.00
irrigation	13	5	7	8	8	6	6	5	3	1	0	0	0	4.08
irrigation	14	7	7	6	8	5	6	5	3	1	0	0	0	4.00
irrigation	15	2	5	6	8	5	6	5	3	1	0	0	0	3.42
removal	1	9	10	7	8	8	4	3	3	5	0	0	0	4.75
removal	2	3	8	11	9	8	7	7	3	2	1	1	0	5.00
removal	3	4	4	4	2	3	2	2	2	2	2	2	0	2.42
removal	4	6	6	4	4	4	3	3	2	1	1	0	0	2.83
removal	5	8	9	13	9	5	9	4	5	2	3	0	0	5.58
removal	6	6	13	9	9	7	5	7	3	2	1	1	0	5.25
removal	7	9	11	12	10	10	8	5	2	2	1	0	0	5.83
removal	8	6	8	12	8	10	9	9	5	1	0	0	0	5.67
removal	9	4	9	11	10	5	9	8	8	4	3	0	0	5.92
removal	10	11	12	8	10	8	1	2	0	0	0	1	0	4.42
removal	11	8	11	10	8	10	6	6	3	4	2	0	0	5.67
removal	12	9	14	11	12	7	7	7	1	1	0	0	0	5.75
removal	13	7	11	5	9	10	8	10	3	2	0	0	0	5.42
removal	14	5	5	5	6	8	7	7	4	3	0	0	0	4.17
removal	15	12	14	8	6	7	6	5	7	6	2	0	0	6.08

with great speed and synchrony: the evaluated population changed from young leaves to mature, hairy and green leaves.

Plants in the removal treatment (4.98 ± 0.29 SE) had a statistically higher number of leaf buds produced than the plants in the control group (3.62 ± 0.16 SE) and in the irrigation treatment (3.85 ± 0.11 SE) ($F_{2,41} = 14.995$, $P = 0.0001$). The control group and the irrigation treatment did not differ from each other ($P > 0.05$) (Fig. 4, Table 4).

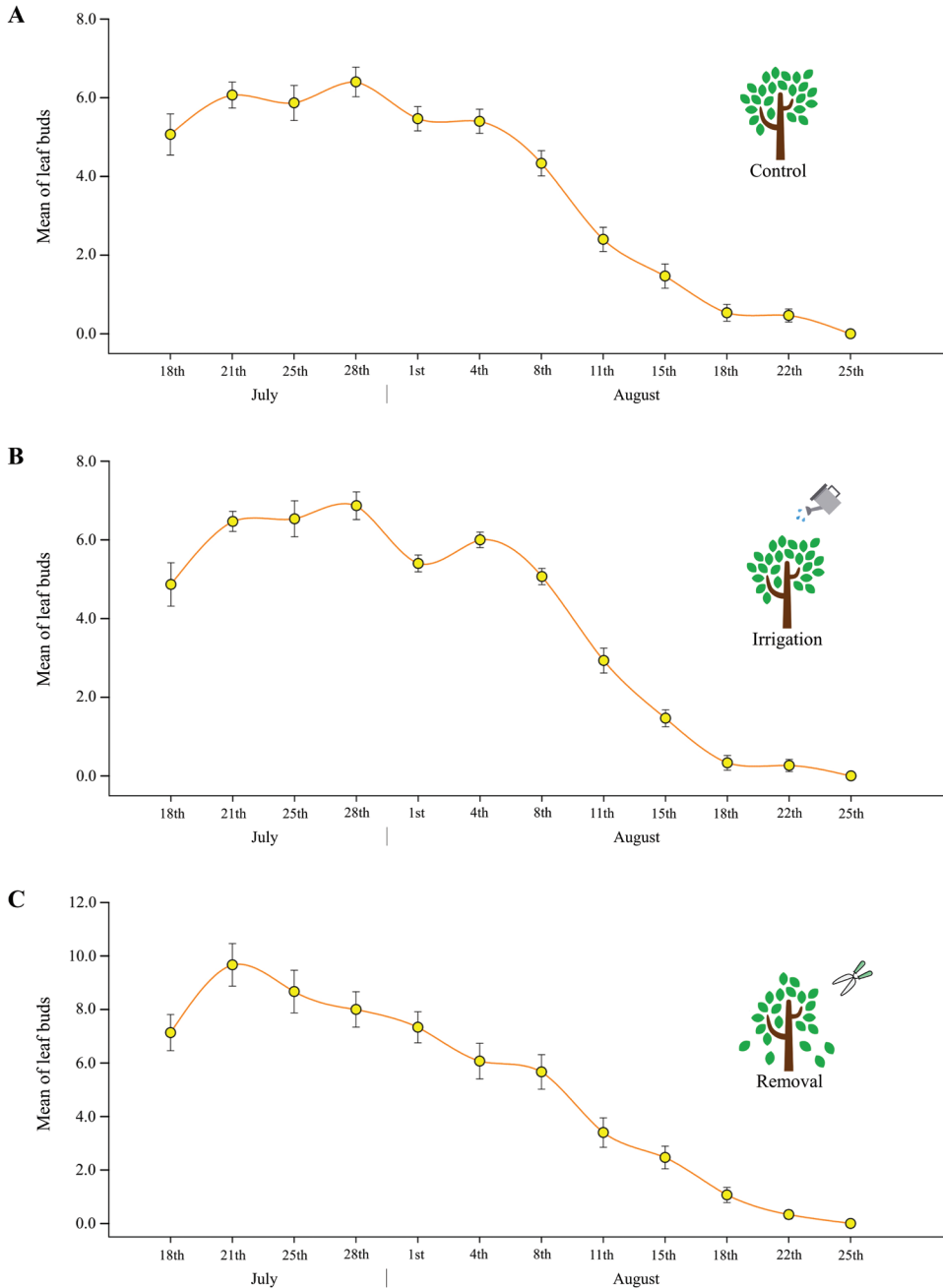


Figure 3. Time series analysis showing the mean of leaf buds (points) and the standard error (vertical limits) of the 15 individuals of *Peixotoa tomentosa* A.Juss. in each of the 12 observation dates between July and August 2022. Control group (A), irrigation treatment (B), and removal treatment (C).

Table 3. Values of wet weight, dry weight, and relative water content (RWC) for the 15 soil samples from the irrigation treatment and the control group.

Treatments	Plant Individuals	Wet Weight (g)	Dry Weight (g)	Relative Water Content (%)
control	1	303.19	294.53	2.86
control	2	282.50	273.91	3.04
control	3	247.36	238.35	3.64
control	4	279.59	267.13	4.46
control	5	281.69	272.78	3.16
control	6	290.60	278.81	4.06
control	7	286.83	273.62	4.61
control	8	228.65	218.78	4.32
control	9	269.47	261.61	2.92
control	10	284.83	277.70	2.50
control	11	262.87	255.17	2.93
control	12	280.67	275.82	1.73
control	13	266.75	259.92	2.56
control	14	281.11	273.49	2.71
control	15	273.76	268.67	1.86
irrigation	1	293.87	275.59	6.22
irrigation	2	317.14	299.24	5.64
irrigation	3	290.02	273.51	5.69
irrigation	4	292.22	277.07	5.18
irrigation	5	335.14	312.45	6.77
irrigation	6	327.33	308.57	5.73
irrigation	7	295.60	289.56	2.04
irrigation	8	336.13	324.28	3.53
irrigation	9	285.25	278.57	2.34
irrigation	10	281.86	271.54	3.66
irrigation	11	285.57	277.93	2.68
irrigation	12	311.72	302.27	3.03
irrigation	13	296.40	287.05	3.15
irrigation	14	239.22	232.21	2.93
irrigation	15	293.86	282.80	3.76

Table 4. Pairwise comparisons ($P < 0.05$; GLMM/Tuckey's post hoc test. $\alpha = 0.05$) showing the differences between the control group, irrigation, and removal treatments. * = Significant difference between treatments.

Treatments	Control	Irrigation	Removal
Control	-	0.671	0.0001*
Irrigation	0.671	-	0.0001*
Removal	0.0001*	0.0001*	-

Soil collection

The soil of the plants in the irrigation treatment presented a statistically higher relative water content ($4.16\% \pm 0.40$ SE) than that found in the soil of the plants in the control group ($3.16\% \pm 0.23$ SE, $F_{1,27} = 7.670$, $P = 0.01$).

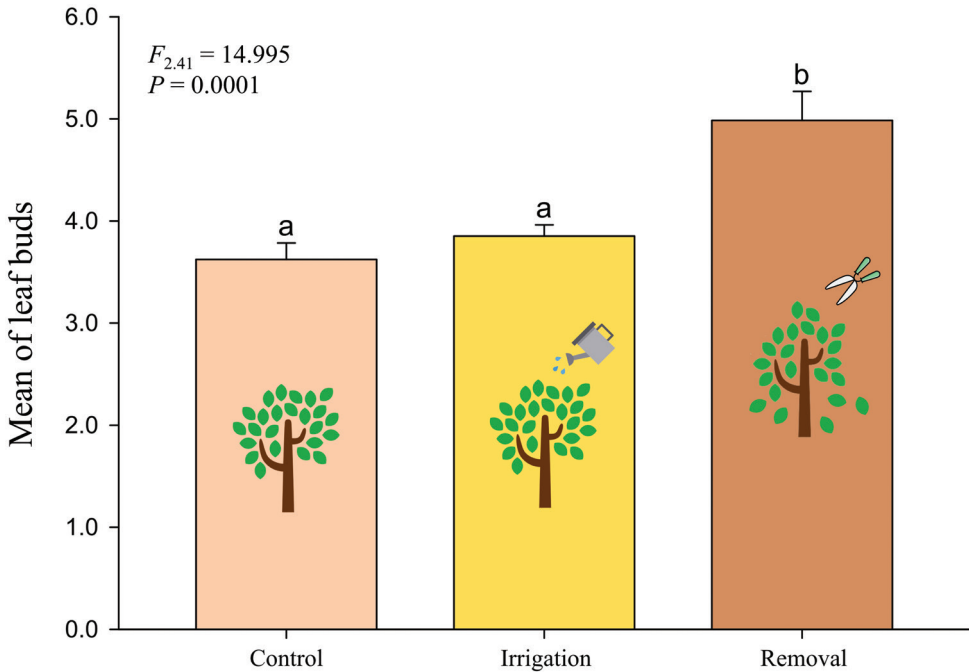


Figure 4. Mean leaf buds in individuals of *Peixotoa tomentosa* A.Juss. from the control, irrigation treatment, and removal treatment. Error bars represent \pm SE. Means followed by the same letters do not differ statistically from each other ($P < 0.05$; GLMM/Tuckey's post hoc test. $\alpha = 0.05$).

Discussion

Our findings showed that early defoliation influenced the triggering of leaf buds on *P. tomentosa*, increasing the production of young leaves in its individuals in a seasonal tropical environment with water restrictions. However, irrigation was not able to break the dormancy of leaf buds.

Many Cerrado woody plants have an extensive root system that, in many cases, penetrates deeper into the soil, reaching the water table. These roots, by remaining humid throughout the year, ensure a stable water source for plants, minimizing the effects of seasonal water deficit (Nardoto et al. 1998; Scholz et al. 2002). Thus, we suggest that despite the irrigation treatment having provided a more humid soil for the plants, the depth, and extension of the root system of *P. tomentosa* allow these plants to capture enough water to minimize the effects of the water deficit, not interfering with the production of leaves in the dry season (Scholz et al. 2002).

Although irrigation was not related to leaf budding, the removal of senescent leaves proved to be an important factor in triggering young leaves. The reduction in transpiration appears to be a key factor in triggering the leaf buds of *P. tomentosa* (Pereira et al. 2022). Studies have shown that the leaf fall can avoid water stress in tropical deciduous species, as it reduces the transpiration surface of the foliage and,

therefore, reduces water demand and the risks of xylem embolism and plant desiccation (Goldstein et al. 2008; Lima et al. 2021; Santos et al. 2021). Thus, leaf fall is closely related to leaf senescence in such a way that it can be used as a proxy for leaf budding, as this would reduce water loss by the plant, leading to rehydration of leafless branches and leaf production in *P. tomentosa*, even under severe water stress (John et al. 2018). Furthermore, we suggest that the defoliation of senescent leaves did not prevent the translocation of nutrients, and, since these plants had all their leaves removed at the same time, there was a drastic reduction in the transpiration of these individuals, which produced new leaves in higher numbers than found in the other groups.

Evidence is accumulating that the timing and intensity of the vegetative phenophases of deciduous plants are changing as a result of climate change (Gordo and Sanz 2009; Gunderson et al. 2012; Estiarte and Peñuelas 2015; Liu et al. 2022). On average, climate warming will delay, and drought will advance, leaf senescence, but to varying degrees depending on the species (Gunderson et al. 2012). Warming and drought, therefore, have opposite effects on the phenology of leaf senescence, and the impact of climate change will depend on the relative importance of each factor in specific regions (Estiarte and Peñuelas 2015). Furthermore, the overall effects of climate change on nutrient reabsorption will depend on the contrasting effects of warming and drought, because the construction of new leaves depends almost exclusively on nutrients reabsorbed from the leaves during the previous leaf fall (Estiarte and Peñuelas 2015). Thus, changes in leaf falling and leaf budding phenology will impact carbon uptake, but also nutrient cycling in the ecosystem (Jia et al. 2022).

Conclusion

Our findings contribute to a better understanding of the triggering of vegetative phenophases in Cerrado deciduous plants, showing that leaf fall may play a more important role than rainfall in the production of leaf buds in the dry season.

Acknowledgements

The authors would like to thank CSEC, PPG-ECMVS and CAPES for continuous support. This study was financed in part by the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior – Brasil (CAPES) – Finance Code 001.

References

- Alvares CA, Stape JL, Sentelhas PC, Gonçalves JLM, Sparovek G (2013) Köppen's climate classification map for Brazil. *Meteorologische Zeitschrift* (Berlin) 22(6): 711–728. <https://doi.org/10.1127/0941-2948/2013/0507>
- Araújo JFD, Haridasan M (2007) Relação entre deciduidade e concentrações foliares de nutrientes em espécies lenhosas do cerrado. *Revista Brasileira de Botânica. Brazilian Journal of Botany* 30(3): 533–542. <https://doi.org/10.1590/S0100-84042007000300017>

- Bates D, Maechler M, Bolker B (2011) lme4: Linear Mixed-Effects Models Using Eigen and S4 Classes. R Package Version, Vienna. <http://cran.R-project.org/package=lme4>
- Dinerstein E, Olson D, Joshi A, Vynne C, Burgess ND, Wikramanayake E, Hahn N, Palminteri S, Hedao P, Noss R, Hansen M, Locke H, Ellis EC, Jones B, Barber CV, Hayes R, Kormos C, Martin V, Crist E, Sechrest W, Price L, Baillie JEM, Weeden D, Suckling K, Davis C, Sizer N, Moore R, Thau D, Birch T, Potapov P, Turubanova S, Tyukavina A, Souza N, Pintea L, Brito JC, Llewellyn OA, Miller AG, Patzelt A, Ghazanfar SA, Timberlake J, Klöser H, Shennan-Farpón Y, Kindt R, Lillesø JPB, van Breugel P, Graudal L, Vogt M, Al-Shammari KF, Saleem M (2017) An ecoregion-based approach to protecting half the terrestrial realm. *Bioscience* 67(6): 534–545. <https://doi.org/10.1093/biosci/bix014>
- Estiarte M, Peñuelas J (2015) Alteration of the phenology of leaf senescence and fall in winter deciduous species by climate change: Effects on nutrient proficiency. *Global Change Biology* 21(3): 1005–1017. <https://doi.org/10.1111/gcb.12804>
- Fourcade Y, WallisDeVries MF, Kuussaari M, Swaay CAM, Heliölä J, Öckinger E (2021) Habitat amount and distribution modify community dynamics under climate change. *Ecology Letters* 24(5): 950–957. <https://doi.org/10.1111/ele.13691>
- Goldstein G, Meinzer F, Bucci S, Scholz F, Franco A, Hoffman W (2008) Water economy of Neotropical savanna trees: Six paradigms revisited. *Tree Physiology* 28(3): 395–404. <https://doi.org/10.1093/treephys/28.3.395>
- Gordo O, Sanz JJ (2009) Long-term temporal changes of plant phenology in the Western Mediterranean. *Global Change Biology* 15(8): 1930–1948. <https://doi.org/10.1111/j.1365-2486.2009.01851.x>
- Gunderson CA, Edwards NT, Walker AV, O'Hara KH, Campion CM, Hanson PJ (2012) Forest phenology and a warmer climate-growing season extension in relation to climatic provenance. *Global Change Biology* 18(6): 2008–2025. <https://doi.org/10.1111/j.1365-2486.2011.02632.x>
- Instituto Brasileiro de Geografia e Estatística (2022) Biomas. <https://www.ibge.gov.br>
- Instituto Nacional de Meteorologia (2022) Banco de dados meteorológicos para ensino e Pesquisa. <http://www.inmet.gov.br/portal>
- Jia G, Chen L, Yu X, Liu Z (2022) Soil water stress overrides the benefit of water use efficiency from rising CO₂ and temperature in a cold semi-arid poplar plantation. *Plant, Cell & Environment* 45(4): 1172–1186. <https://doi.org/10.1111/pce.14260>
- John GP, Henry C, Sack L (2018) Leaf rehydration capacity: Associations with other indices of drought tolerance and environment. *Plant, Cell & Environment* 41(11): 2638–2653. <https://doi.org/10.1111/pce.13390>
- Kikuzawa KA (1991) A cost-benefit analysis of leaf habit and leaf longevity of trees and their geographical pattern. *American Naturalist* 138(5): 1250–1263. <https://doi.org/10.1086/285281>
- Lima ALA, Rodal MJN, Castro CC, Antonino ACD, Melo AL, Gonçalves-Souza T, Sampaio EVDSB (2021) Phenology of high- and low-density wood deciduous species responds differently to water supply in tropical semiarid regions. *Journal of Arid Environments* 193: e104594. <https://doi.org/10.1016/j.jaridenv.2021.104594>

- Liu H, Wang H, Li N, Shao J, Zhou X, van Groenigen KJ, Thakur MP (2022) Phenological mismatches between above-and belowground plant responses to climate warming. *Nature Climate Change* 12(1): 97–102. <https://doi.org/10.1038/s41558-021-01244-x>
- Mamede MCH (1987) Flora da Serra do Cipó, Minas Gerais: Malpighiaceae. *Boletim de Botânica da Universidade de São Paulo* 9(0): 157–198. <https://doi.org/10.11606/issn.2316-9052.v9i0p157-198>
- Mendoza I, Peres CA, Morellato LPC (2017) Continental scale patterns and climatic drivers of fruiting phenology: A quantitative neotropical review. *Global and Planetary Change* 148(1): 227–241. <https://doi.org/10.1016/j.gloplacha.2016.12.001>
- Murali KS, Sukumar R (1993) Leaf flushing phenology and herbivory in a tropical dry deciduous forest, southern India. *Oecologia* 94(1): 114–119. <https://doi.org/10.1007/BF00317311>
- Nardoto GB, Souza MP, Franco AC (1998) Estabelecimento e padrões sazonais de produtividade de *Kielmeyera coriacea* (Spr) Mart. nos Cerrados do Planalto Central: Efeitos do estresse hídrico e sombreamento. *Revista Brasileira de Botânica. Brazilian Journal of Botany* 21(3): 1172–1186. <https://doi.org/10.1590/S0100-84041998000300011>
- Pereira CC, Boaventura MG, Castro GC, Cornelissen T (2020) Are extrafloral nectaries efficient against herbivores? Herbivory and plant defenses in contrasting tropical species. *Journal of Plant Ecology* 13(4): 423–430. <https://doi.org/10.1093/jpe/rtaa029>
- Pereira CC, Boaventura MG, Cornelissen T, Nunes YRF, Castro GC (2022) What triggers phenological events in plants under seasonal environments? A study with phylogenetically related plant species in sympatry. *Brazilian Journal of Biology* 84: e257969. <https://doi.org/10.1590/1519-6984.257969>
- R Core Team (2021) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. <https://www.R-project.org/>
- Ribeiro JF, Walter BMT (2008) As principais fitofisionomias do bioma Cerrado. In: Sano SM, Almeida SP, Ribeiro JF (Eds) *Cerrado: Ecologia e Flora*. Embrapa-CPAC, Planaltina, 151–212.
- Santos M, Barros V, Lima L, Frosi G, Santos MG (2021) Whole plant water status and non-structural carbohydrates under progressive drought in a Caatinga deciduous woody species. *Trees (Berlin)* 35(4): 1257–1266. <https://doi.org/10.1007/s00468-021-02113-y>
- Scholz FG, Bucci SJ, Goldstein G, Meinzer FC, Franco AC (2002) Hydraulic redistribution of soil water by neotropical savanna trees. *Tree Physiology* 22(9): 603–612. <https://doi.org/10.1093/treephys/22.9.603>
- Silva JO, Espírito-Santo MM, Santos JC, Rodrigues P (2020) Does leaf flushing in the dry season affect leaf traits and herbivory in a tropical dry forest? *Naturwissenschaften* 107(6): 1–10. <https://doi.org/10.1007/s00114-020-01711-z>
- Vilela AA, Del-Claro VTS, Torezan-Silingardi HM, Del-Claro K (2017) Climate changes affecting biotic interactions, phenology, and reproductive success in a savanna community over a 10-year period. *Arthropod-Plant Interactions* 12(2): 215–227. <https://doi.org/10.1007/s11829-017-9572-y>