



Phenological dynamics of four populations of *Handroanthus spongiosus* in seasonally dry tropical forest in Brazil

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ABSTRACT

The scarcity of phenological studies based on different populations of tropical forest trees limits seed management and collection for reforestation efforts. Precipitation is the primary factor driving tropical plant phenology in seasonal environments, although other environmental variables and plant traits may be associated. We examined the seasonality, synchrony, and intensities of the vegetative and reproductive phenophases of four populations of *Handroanthus spongiosus*, an endangered species, under similar climate regimes in a seasonally dry tropical forest, in northeastern Brazil. We expected to observe some divergence in the phenologies of the populations related to distinct functional traits selected for by differences in rainfall and soil properties. Mature trees ($n = 87$) were monitored during a three-year period. Seasonality was examined using circular statistics, and the influences of environmental variables on phenophases were investigated using generalized additive models. Variations in intensities and activity indices were identified among the different populations. Vegetative phenophases were seasonal, driven by precipitation and photoperiod, with leaf longevity of up to 7 months; budding peaked in February-March, while leaf fall peaked in April and October. The reproductive phenophases were found to be seasonal, during the rainy season (November to April), influenced by temperature and photoperiod. The slight divergences noted among the phenological behaviors of the populations were related to distinct functional traits (e.g., tree height, stem diameter) selected for by differences in certain environmental variables (rainfall volumes and soil properties). Given ongoing global climate changes, increases in leaf fall and reductions of flowering intensity, as verified here, will likely be observed.

1. Introduction

Analyses of different populations of the same species can contribute to better understanding their phenological patterns and their relationships with local climatic factors (Duboscq-Carra et al., 2020; Santos et al., 2020; Silva et al., 2022). Flowering and leaf production have been the most studied phenomenon among tropical trees (e.g., Pires et al., 2013; Souza et al., 2019; Wright and Calderón, 2018), followed by fruiting and seed dispersal – which also play very fundamental roles in population ecology (e.g., Chapman et al., 2018; Dunham et al., 2018). Phenological patterns in tropical trees may be affected by a variety of

local factors, such as rainfall, temperature, day length, irradiance, relative humidity (Chapman et al., 2018; Dunham et al., 2018; Mendoza et al., 2017), and species traits (Babweteera et al., 2018; Silva et al., 2022).

The Seasonally Dry Tropical Forests (SDTF) biome, which includes Caatinga vegetation in northeastern Brazil, is among the least studied but most threatened phytophysiognomies in the world, having already lost more than 60% of its original area (Miles et al., 2006). SDTF are found on most continents, although more than half of their total area is found in South America (Pezzini et al., 2014; Pennington et al., 2018). Caatinga vegetation covers approximately 900.000 km², exclusively in

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Brazil, and consists of a mosaic of xerophytic and deciduous vegetation whose physiognomy and floristic composition varies considerably on small spatial scales, from open formations to forest patches (Prado, 2003; Queiroz et al., 2017; Barbosa et al., 2019). The distributions of those vegetation mosaics are mainly linked to reduced rainfall, geological formations, and soil attributes (Prado, 2003; Andrade et al., 2017). Rainfall in the Caatinga evidence wide spatial-temporal variations, with annual means between 400 and 800 mm generally distributed into just four months (Reddy, 1983), marking distinct dry and rainy periods (Andrade et al., 2017). Temperatures and solar radiation, on the other hand, are relatively constant (Pennington et al., 2018; Paloschi et al., 2020).

In general, woody plants growing in arid ecosystems, such as the Caatinga, exhibit highly seasonal vegetative and reproductive events, with the onset of leaf and flower production at the beginning of the rainy period, with fruit set during the late rainy season at times of greatest water availability, followed by leaf fall during the dry season (Lima et al., 2012; 2021; Quirino and Machado, 2014; Neves et al., 2017; 2022). Studies comparing phenological events across populations can reveal much about the survival strategies of species and how abiotic factors influence their phenological variability (Pennington et al., 2006; Apgaua et al., 2014). Some Caatinga species, such as *Ziziphus joazeiro* Mart. and *Croton heliotropifolius* Kunth, for example, exhibit fine adjustments and adaptations to local environmental factors (Nadia et al., 2007; Santos et al., 2015; Costa et al., 2021). In the last ten years, there have been advances in terms of the number of phenological studies undertaken in SDTF areas, although there are still significant gaps in our understanding of the diversity found there and much to be done in terms of their conservation as vital resources in tropical countries (Meave et al., 2012; Oliveira et al., 2017; Pennington et al., 2018; Lima et al., 2021; Neves et al., 2022).

Handroanthus spongiosus (Rizzini) S. Grose (Bignoniaceae) is a tree species endemic to the semiarid Caatinga Domain that preferentially develops in sandy soils in seasonally dry forests. It is considered “Endangered” (EN), and has been negatively impacted by deforestation for agriculture, livestock raising and logging (MMA, 2022). The plant is locally known as “cascudo”, “ipê-amarelo”, “ipê-cascudo”, and “sete-cascas”. Its main commercial use is by the timber industry, given the high quality of its wood (Silva et al., 2023). It occurs preferentially in sandy soils of the Caatinga, in forests with intermediate stages of succession (Lohmann et al., 2020), generally with low density of individuals and low recruitment of seedlings (Silva et al., 2023).

We sought then to understand how abiotic factors and plant traits are linked to the phenological patterns of four natural populations of *H. spongiosus*. The scarcity of studies covering more than two years focusing on the phenological behavior of this species limits our ability to manage its populations and to collect seeds for Caatinga reforestation efforts. There is a great need for native seeds to execute Brazilian ecological restoration policies (Brasil, 2017) and to fulfill international agreements or goals (such as the decade of restoration proposed by the UN [United Nations, 2019]) that could help mitigate the effects of global climate change. The main goal of this study was therefore to better understand the phenological behavior of *H. spongiosus*, examine how environmental aspects affect the phenology of this species over space and time in SDTF sites, and to provide support for seed harvesting. Those objectives were approached by studying the vegetative and reproductive phenologies of *H. spongiosus* in different SDTF sites and then examining their relationships with temporal changes in abiotic factors and plant traits. To that end, we addressed the following questions: (i) are there spatial-temporal variations in the phenophases among populations? (ii) Which abiotic variables trigger the vegetative and reproductive phenophases in those populations? (iii) When should *H. spongiosus* seeds be harvested? We expected to find the seasonal patterns among *H. spongiosus* populations in the SDTF to be concentrated in times of greatest water availability, but with divergences among the phenological behaviors of their populations related to distinct functional traits

selected for by differences in certain environmental variables (rainfall volumes and soil properties).

2. Material and methods

2.1. Species and study sites

The phenological monitoring of *H. spongiosus* trees was focused on individuals approximately 10 m tall growing in four fragmented SDTF remnants in Pernambuco State, Brazil (Fig. 1). The study sites were located near the villages of Pau Ferro (8°55'57.4" S, 40°43'19.8" W, 431 m) (HUEFS 243,297), Caiçara (9°07'24.5" S, 40°23'16.1" W, 393 m) (HUEFS 252,490), Cristália (8°5'56.3" S, 40°19'27.1" W, 403 m) (HUEFS 259,093), and Jutaí (8°33'35.7" S, 40°12'1.9" W, 418 m) (HUEFS 259,094). The above listed vouchers deposited in the HUEFS herbarium. All of the sites dominated by anthropized vegetation composed of secondary forests and pasture; the sites were each separated by more than 10 km.

The Pau Ferro and Caiçara populations are found in relatively conserved arboreal Caatinga vegetation without recent disturbances (more than 20 years), with the presence of the families Euphorbiaceae (*Croton blanchetianus*), Malvaceae (*Gaya aurea*), Asteraceae (*Centratherum punctatum*), Bignoniaceae (*Tabebuia aurea* and *Handroanthus impetiginosus*), Anarcadiaceae (*Schinopsis brasiliensis* and *Spondias tuberosa*). The Jutaí and Cristália populations, on the other hand, are found in shrubby-arboreal Caatinga vegetation that has been highly disturbed by goat grazing and the felling of trees for fence construction. The main families found in Jutaí and Cristália were Bromeliaceae (*Neoglaziovia variegata* and *Bromelia laciniosa*), Fabaceae (*Libidibia ferrea*, *Cenostigma microphyllum*, *Mimosa tenuiflora* and *Senna macranthera*), Apocynaceae (*Aspidosperma pyriforme*), Burseraceae (*Commiphora leptophloeos*), Boraginaceae (*Varronia globosa*) and Cactaceae (*Cereus jamacaru*, *Xiquexiqué gounellei* and *Melocactus bahiensis*).

The study region has a low mean annual precipitation rate (between 300 mm and 1000 mm) and a high annual potential evapotranspiration rate (between 1.500 mm and 2.000 mm) (Prado, 2003). The climate is semiarid (classified as BSh), with mean annual temperatures between 25 and 30 °C; both the rainy season (usually from November to April – the austral summer) and the dry season (usually from May to September) are extremely variable in their lengths and intensities in different years (Sampaio, 2010; Alvares et al., 2013).

The predominant soil types in the Pau Ferro and Caiçara sites are eutrophic yellow latosols developed from sedimentary materials, with sandy and clayey textures in their A horizon (Embrapa, 2018); the soils in the Cristália and Jutaí sites are orthic chromic luvisols typical of semiarid regions, with high concentrations of gravel and stones in the surface horizon, which are generally susceptible to erosion (Santos et al., 2018; Embrapa, 2018).

2.2. Study area

2.2.1. Environmental variables

Meteorological data (Fig. 2) were obtained from Embrapa Semiárido meteorological stations, located in Cristália (8°48'39.5" S, 40°22'2.6" W) (Cristália site), Bebedouro (9°08'12.3" S, 40°18'31.6" W) (Caiçara site), Cruz de Salinas (8°50'26.1" S, 40°36'5.2" W) (Pau Ferro site), and Vini Brasil (08°48'55.6" S, 40°41'37.2" W) (Jutaí site) (Fig. 1). The photoperiods of the study sites were obtained using ModelE AR5 Simulations (NASA, 2020) during the 36-month duration of the study (June/2019 - May/2022). The meteorological data are separated by periods: Period 1 = June/2019 - May/2020, Period 2 = June/2020 - May/2021, and Period 3 = June/2021 - May/2022.

The accumulated rainfall varied between periods and study sites (Table 1). The sites having rainfall rates >500 mm were Pau Ferro in the first (841.47±28.49 mm) and third periods (962.64±24.44 mm); Caiçara in the third period (596.65±11.91 mm); Cristália in the first

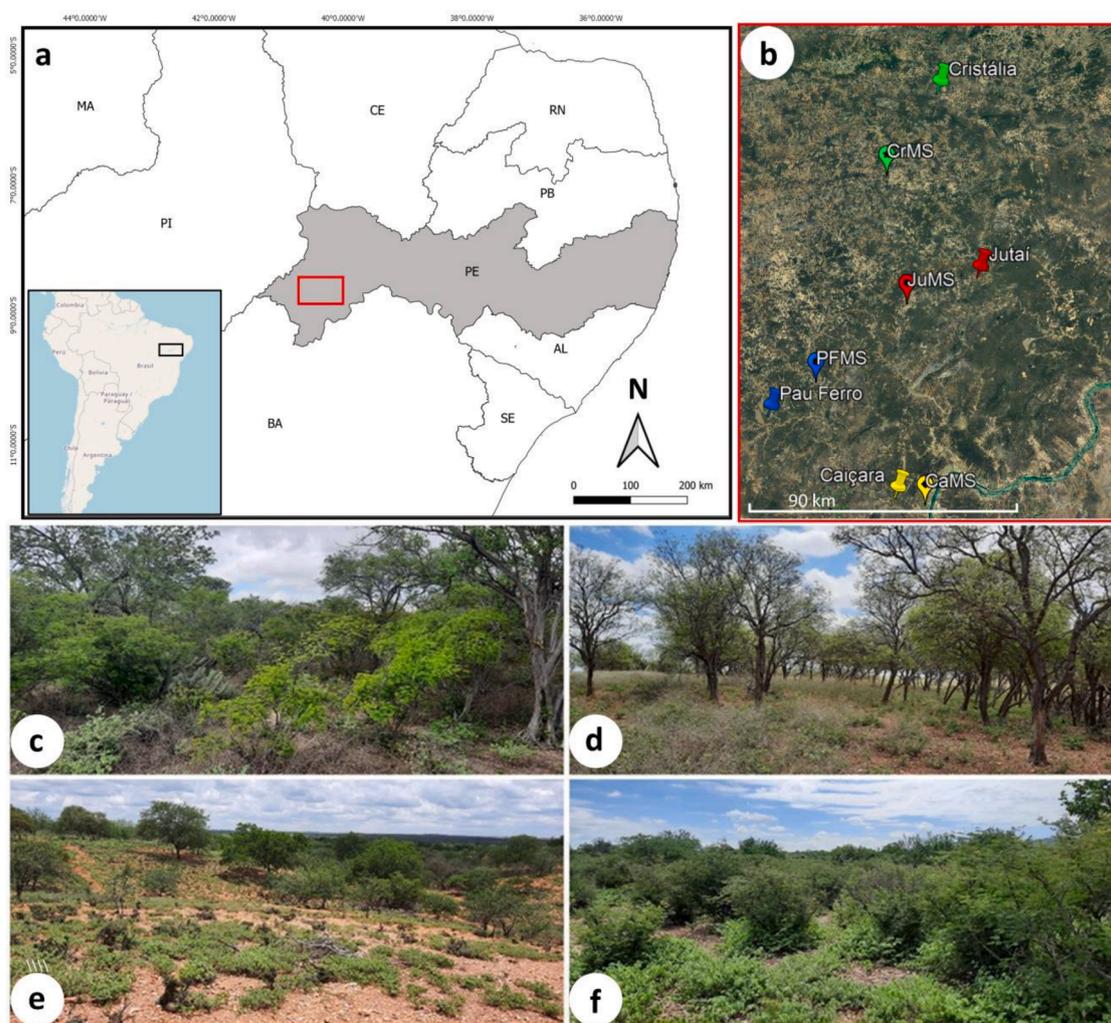


Fig. 1. Study sites and physiological traits of *Handroanthus spongiosus* (Rizzini) S. Grose in four sites in northeastern Brazil. (a). Location map of the study area. (b). Location of populations and meteorological stations: PFMS - Pau Ferro Meteorological Station; CaMS - Caiçara Meteorological Station; CrMS – Cristália Meteorological Station; JuMS - Jutai Meteorological Station. (c). Pau ferro. (d). Jutai. (e). Cristália. (f). Caiçara. Photographs taken during the rainy season.

(849.16±29.93 mm) and third periods (590.19±14.80 mm); and Jutai in the third period (556.97±14.28 mm). The highest and lowest monthly mean temperatures were observed in Pau Ferro in the first period (28.40 ±0.58 °C) and Caiçara in the second (26.36±0.48 °C) (Table 1).

Four composite soil samples (0–20 cm) were collected in each study site. Each composite sample was taken by mixing soils from four random points, totaling 16 composite samples. These random collection points were distributed so that all of the trees evaluated in the population were within the area sampled. The physical and chemical properties of these samples were analyzed in the Laboratory of Soil, Water and Plant Analysis (Embrapa Semiárido - PE), according Donagema et al. (2011). Total Porosity and Soil Density were determined by the tension table (tension of 6 kPa) and the volumetric ring methods respectively; soil granulometry was determined by the pipette and Textural Triangle method (Embrapa, 2009). The chemical analyses consisted of determinations of E.C. in saturation paste, pH in water (1:2.5 soil:water ratio); Al, Ca, Mg (exchangeable extracted with 1 mol L⁻¹ KCl, analyzed by titration); P, K and Na (extracted by Mehlich extractor 1); Cu, Fe, Mn and Zn (Mehlich 1 Extraction and determination by Flame Atomic Absorption Spectrophotometry), SB and CTC (Calcium Acetate Extraction), according to Embrapa (2009).

2.2.2. Phenological data and plant traits

A total of 87 healthy adult individuals of *H. spongiosus* (growing at

least 20 m apart) were geo-referenced and marked with aluminum tags. The numbers of individuals accompanied in each of the four sites varied according to their population sizes: Cristália ($n = 20$ individuals), Caiçara ($n = 17$ individuals), Pau Ferro ($n = 30$ individuals), and Jutai ($n = 20$ individuals). The plant traits examined were: total plant height (PlantH), trunk height (TrunkH), and diameter at breast height (DBH) (Silva et al., 2022). Phenological observations were made visually (using binoculars) during monthly visits to each tree, for 36 months (June/2019 - May/2022) during three different periods: Period 1 = June/2019 - May/2020, Period 2 = June/2020 - May/2021, and Period 3 = June/2021 - May/2022. The vegetative phenophases evaluated were: (i) leaf flushing (shoots in formation, having light green tones); (ii) young leaves (developed leaves, but light green in color); (iii) mature leaves (developed and expanded leaves, with dark green tones); (iv) leaf fall (absence of leaves on the branches). The reproductive phenophases were: (v) flower buds; (vi) flowering (anthesis); (vii) immature fruits (newly formed fruits, greenish); (viii) Mature fruits (brown colored fruits); (ix) seed dispersal (fruits starting to open and dispersing seeds). Phenophase intensities were estimated during field observations using a semi-quantitative scale consisting of five categories (0–4) at 25% intervals (Fournier, 1974). The intensities of the phenophases were measured as the ratio of the sum of each category multiplied by 100, and the maximum Fournier number (4) multiplied by the number of individuals (Martin-Gajardo and Morellato, 2003). We determined the

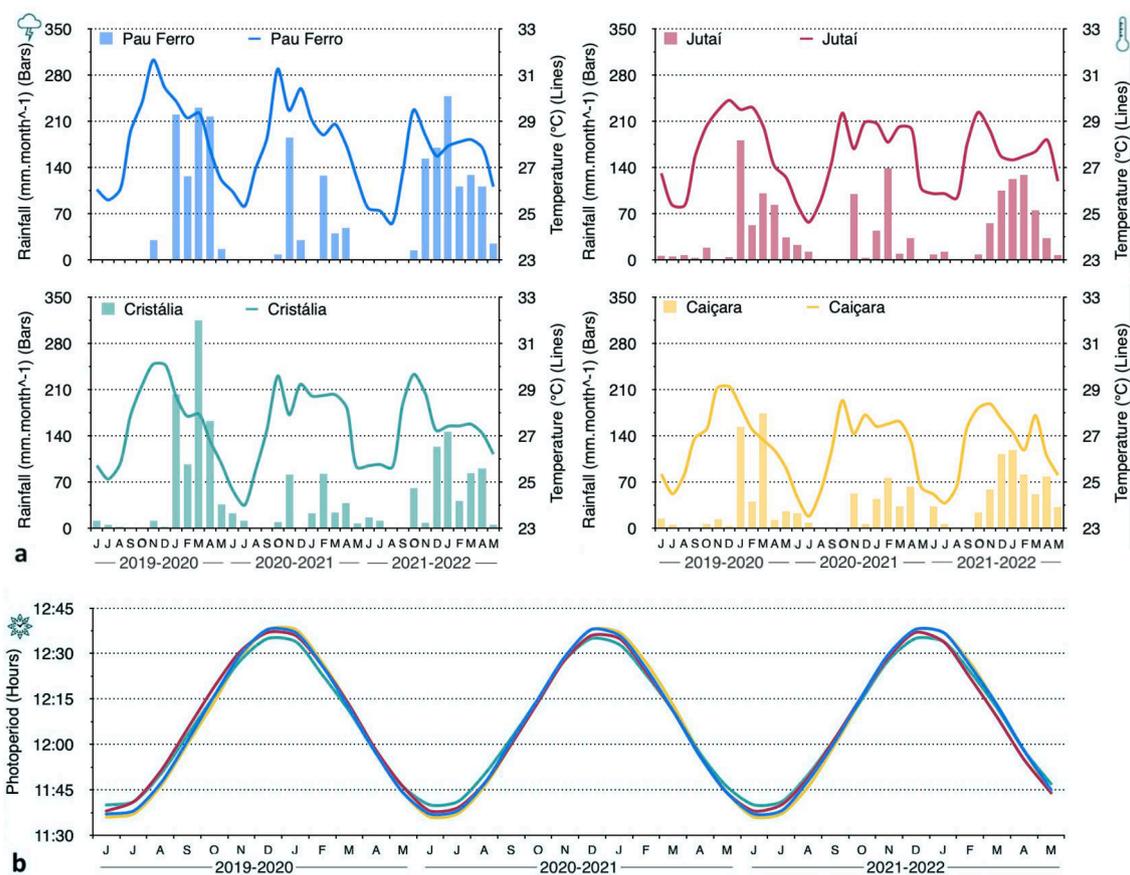


Fig. 2. Meteorological data for the *H. spongiosus* study sites were evaluated for 36 months (June/2019 to May/2022) in northeastern Brazil. (a). Monthly average air temperature (lines), and accumulated monthly rainfall (bars). (b). Photoperiod.

Table 1

Study sites of *H. spongiosus* in the SDTF in northeastern Brazil. Mean environmental variables, including elevation, soil type, temperature, rainfall, photoperiod, and plant traits are indicated.

Variable/Site	Pau Ferro	Jutai	Cristália	Caiçara
Period (12 months)	Accumulated monthly rainfall (mm y ⁻¹)			
Period 1	841.47 ±28.49	497.29 ±16.05	849.16 ±29.93	452.12 ±17.38
Period 2	440.32 ±17.28	366.26 ±12.93	301.96 ±8.38	308.42 ±7.92
Period 3	962.64 ±24.44	556.97 ±14.28	590.19 ±14.80	596.65 ±11.91
	Mean air temperature (°C)			
Period 1	28.40±0.58	27.89±0.48	27.58±0.50	26.83±0.43
Period 2	28.19±0.52	27.45±0.48	27.36±0.56	26.36±0.48
Period 3	27.11±0.44	27.34±0.34	27.24±0.37	26.49±0.44
	Photoperiod (hours)			
Period 1	11.90±0.12	11.92±0.12	11.90±0.11	11.90±0.12
Period 2	11.90±0.12	11.89±0.12	11.90±0.11	11.90±0.12
Period 3	11.91±0.12	11.90±0.12	11.91±0.11	11.90±0.12
Altitude (m)	431±2.51	418±1.13	403±0.65	393±0.22
Soil	EYL	OCL	OCL	EYL
	Plants			
PlantH (m)	5.72±0.15	6.68±0.18	7.76±0.17	5.16±0.23
TrunkH (m)	1.87±0.08	2.25±0.10	1.98±0.08	2.14±0.10
DBH (cm)	14±0.1	18±0.1	26±0.1	16±0.1

OCL = Orthic Chromic Luvisols; EYL = Eutrophic Yellow Latosols; PlantH = Total plant height; TrunkH = Trunk height; DBH = Diameter at breast height; Period 1 = June/2019 to May/2020; Period 2 = June/2020 to May/2021; Period 3: June/2021 to May/2022. Means are followed by the standard error.

activity index based on the percentage of individuals in each population manifesting a certain phenological event (Bencke and Morellato, 2002). Leaf longevity was estimated through evaluations of the peaks of leaf flushing and leaf fall of individuals (scores 3 or 4 on the Fournier scale). We calculated average leaf longevity in months between the respective phenophases in the observed phenological cycles (Oliveira et al., 2014; Santos et al., 2020). We evaluated flowering patterns (flower phenophase) for the species based on data from the four populations, considering the frequency and duration of the episodes (Newstrom et al., 1994); flowering strategies were classified according to Gentry (1974).

2.3. Data analysis

The seasonality of the phenological events of *H. spongiosus* at each site in each period were evaluated using circular statistical analyses (Morellato et al., 2010), employing R environment software (R Core Team, 2022) with the addition of the “circular” package (Agostinelli and Lund, 2017). The frequency of each phenophase was calculated based on the total number of individuals accompanied every month. Months were converted into angles at intervals of 30° (0° representing June, 30° representing July, and so forth, until 330° representing May). The mean angles and (r) vector lengths were calculated. Angle significance was tested using the Rayleigh test (z) for circular distributions (Zar, 2010). The phenological events with significant mean angles ($p < 0.05$) were transformed into mean dates. Phenophases whose vector lengths (r) were > 0.5 (and whose Rayleigh tests indicated as significant) were considered seasonal (Morellato et al., 2010). The nonparametric Mardia-Watson-Wheeler test (W) (Batschelet, 1981; Mardia and Jupp, 2000) was used to assess whether there were differences in the phenophases among the populations, and whether there were differences in phenophases between the evaluated periods. This test consists of

evaluating whether two or more circular samples (angles) differed among the mean dates or mean months ($p < 0.05$). The multiple factor analysis (MFA) used the R package determine the relationships between environmental variables, plant traits, and phenophases, considering the directions and lengths of vectors (Novaes et al., 2020). Vectors close to each other have positive relationships, while vectors positioned opposite each other (at 180°) show negative relationships.

The influences of temporal meteorological conditions on plant phenophases were evaluated using generalized additive models (GAMs) of the “mgcv” package (Wood, 2011), using a Gaussian error structure to model the relationships between dependent variables (phenophase activity index) and predictors (mean air temperature, monthly accumulated rainfall, and photoperiod) as a smoothing function. This relationship was tested and evaluated through the significance (p -value) for each smoothing term (s), Deviance (explained) and R2 (adjusted). The choice of models was also made using these parameters. From these analyses, partial dependence (PD) graphs were constructed using the “ggplot2” package (Villanueva and Chen, 2019) to show how each environmental variable interacts with the phenophases. A complete model was used for each phenophase, inserting all meteorological variables. The formula for GAM is:

$$g(\mu) = \sum f(x) \quad (1)$$

where g is a specific binding function, (μ) the average expected response and $\sum f(x)$ are smooth functions of the covariates (Ma et al., 2022). The Gaussian distribution and the identity link function were used to model the data. GAMs are valuable tools as they maximize predictive qualities by estimating nonparametric functions of predictor variables through connections with the dependent variable that are established by a linkage function (Wood, 2011; Murphy et al., 2019). All analyzes were performed using R Software (R Core Team, 2022).

3. Results

3.1. Environmental variables and plant traits

The tallest plants (PlantH) and greatest diameters at breast height (DBH) were found in Cristália, while the tallest trunks (TrunkH) were found in Jutai (Table 1). Regarding the physical-chemical parameters of the soil, there were higher densities and greater amounts of sand in the Pau Ferro site, while the Cristália and Jutai sites had the highest levels of clay and the highest sums of bases (SB), CEC, Fe and Zn (Table 2).

3.2. Vegetative phenology and leaf longevity

All of the vegetative phenophases of *H. spongiosus* were seasonal in the four monitored populations during the three observation periods, with small variations of their intensity and activity indices (Fig. 3; Table 3). The peaks of activity of leaf flushing (late October - early November), young leaves (October - November), and mature leaves (February - March) occurred during the rainy season (Fig. 3a-b). Leaf flushing and young leaf events were concentrated in just a few months (Table 3), with activity values above 80% and intensities generally below 60% (Fig. 3a-b). The mature leaves exhibited activity values above 80% and intensities above 60%, distributed from December to June (Fig. 3c; Table 3). The markedly seasonal leaf fall occurred between April and October, during the dry season, with activity and intensity peaks in July and August (100%) (Fig. 3d; Table 3). The entire crown was renewed during each study period, with clear and separate episodes of leaf flushing and total leaf fall (up to 100%), with leaf longevity of 7.2–7.7 months (deciduous habit), with no variations among sites and periods (Supplementary Table 1). The populations differed during at least one of the evaluation periods for each vegetative phenophase (Supplementary Table 2).

Table 2

Physical and chemical soil characteristics of *H. spongiosus* sites in the SDTF in northeastern Brazil.

Variable	Pau Ferro	Jutai	Cristália	Caiçara
Soil Density (mg m^{-3})	1.52±0.02 a	1.34±0.02 b	1.20±0.03 c	1.35±0.05 b
Particle Density (mg m^{-3})	2.58±0.02 a	2.56±0.02 a	2.46±0.02 b	2.56±0.02 a
Total Porosity (%)	41.80±0.54 c	46.60±0.72 b	52.00±1.35 a	46.00±1.83 b
Total Sand (g kg)	699.09 ±26.67 a	539.00 ±36.74 b	427.77 ±46.64 c	464.00 ±22.35 c
Silt (g kg)	235.00 ±33.68 c	355.00 ±33.08 b	391.00 ±9.12 b	427.00 ±23.31 a
Clay (g kg)	67.00 ±22.81 c	104.08 ±5.96 b	180.70 ±8.97 a	66.80 ±22.60 c
EC (mS cm)	1.01±0.39 c	1.06±0.24 b	1.96±0.96 a	1.96±0.41 a
pH	4.92±1.23 b	5.93±0.15 a	5.00±0.21 b	5.38±0.15 a
P (mg dm^{-3})	6.72±0.67 b	4.66±0.40 c	4.90±1.44 c	12.45±1.20 a
K (mg dm^{-3})	0.22±0.03 c	0.67±0.10 a	0.55±0.06 a	0.36±0.10 b
Na (mg dm^{-3})	0.08±0.00 b	0.21±0.03 a	0.25±0.04 a	0.18±0.03 a
Ca (mg dm^{-3})	1.50±1.20 c	3.90±0.26 a	2.24±0.26 b	2.23±1.00 b
Mg (mg dm^{-3})	0.71±0.53 c	1.68±0.09 a	1.26±0.03 b	0.93±0.32 c
AL (cmolc dm^{-3})	0.28±0.01 a	0.00±0.00 c	0.14±0.03 b	0.19±0.09 b
SB (cmolc dm^{-3})	2.48±1.19 c	6.64±1.27 a	4.20±0.22 b	3.83±1.01 b
CEC (cmolc dm^{-3})	2.48±1.23 c	6.68±0.26 a	4.24±0.22 b	3.83±1.29 c
Cu (mg dm^{-3})	0.74±0.06 c	0.82±0.16 c	1.09±0.06 b	1.65±0.16 a
I (mg dm^{-3})	18.60±1.12 a	22.80±3.15 a	21.60±4.00 a	15.70±0.58 b
Mn (mg dm^{-3})	25.20 ±13.50 b	63.20±2.33 a	23.20±1.58 b	23.50±3.56 b
Zn (mg dm^{-3})	1.50±0.26 c	4.40±0.47 a	2.87±0.83 b	1.84±0.24 c

EC = electrical conductivity; pH = potential of hydrogen determined in water; P = phosphorus, Mg²⁺ = magnesium; Ca²⁺ = calcium; Na = sodium; K⁺ = exchangeable potassium; H + Al = potential acidity; SB = sum of bases (Ca+2 + Mg+2 + Na+1 + K + 1); CEC = cation exchange capacity (H + Al + SB); V% = base saturation (SB/CTC)*100; Cu = Copper; I = Iron; Mn = manganese; Zn = zinc. Means followed by different lowercase letters on the same line differ statistically by the Tukey test at a 0.05° of probability. Means (± standard error).

3.3. Reproductive phenophases

All of the reproductive phenophases of *H. spongiosus* were strongly seasonal, occurring between October and December, during the rainy season, in all of the four monitored populations and during the three observation periods, with only small variations in their intensity and activity indices (Fig. 4; Table 4). Flower bud production initiated at the end of October and beginning of November (Fig. 4a), 48 h after rains with >10 mm of accumulated volume, temperatures >26 °C, and photoperiods >12 h of sunlight (Fig. 2). The populations showed low variations of peak activity and flower bud intensity among periods and among study sites (Fig. 4a). The flowering phenophase is annual, of intermediate duration, concentrated in the months of October and November, and with peak intensity in the last month (Fig. 4b; Table 4). Flowering is of the big-bang type, massive, with the flowers remaining in anthesis for up to two days, followed by senescence events, wilting, and corolla abscission. Regarding fruit set, there was a peak of production of immature fruits and mature fruits with greater intensity in the month of November for all populations and for all periods evaluated (Fig. 5a-b; Table 4). The first immature fruits began to appear between the sixth and eighth day after flower opening. The phenophases mature fruit and seed dispersing occurred between the eighth and twelfth day after the appearance of the first immature fruits, usually in November (occasionally in early December). Seed dispersal occurred concomitantly with mature fruit between November and December, with peak intensity and activity in November (Fig. 5c; Table 4). The populations differed in at least one of the periods evaluated for each reproductive phenophase (Supplementary Table 2).

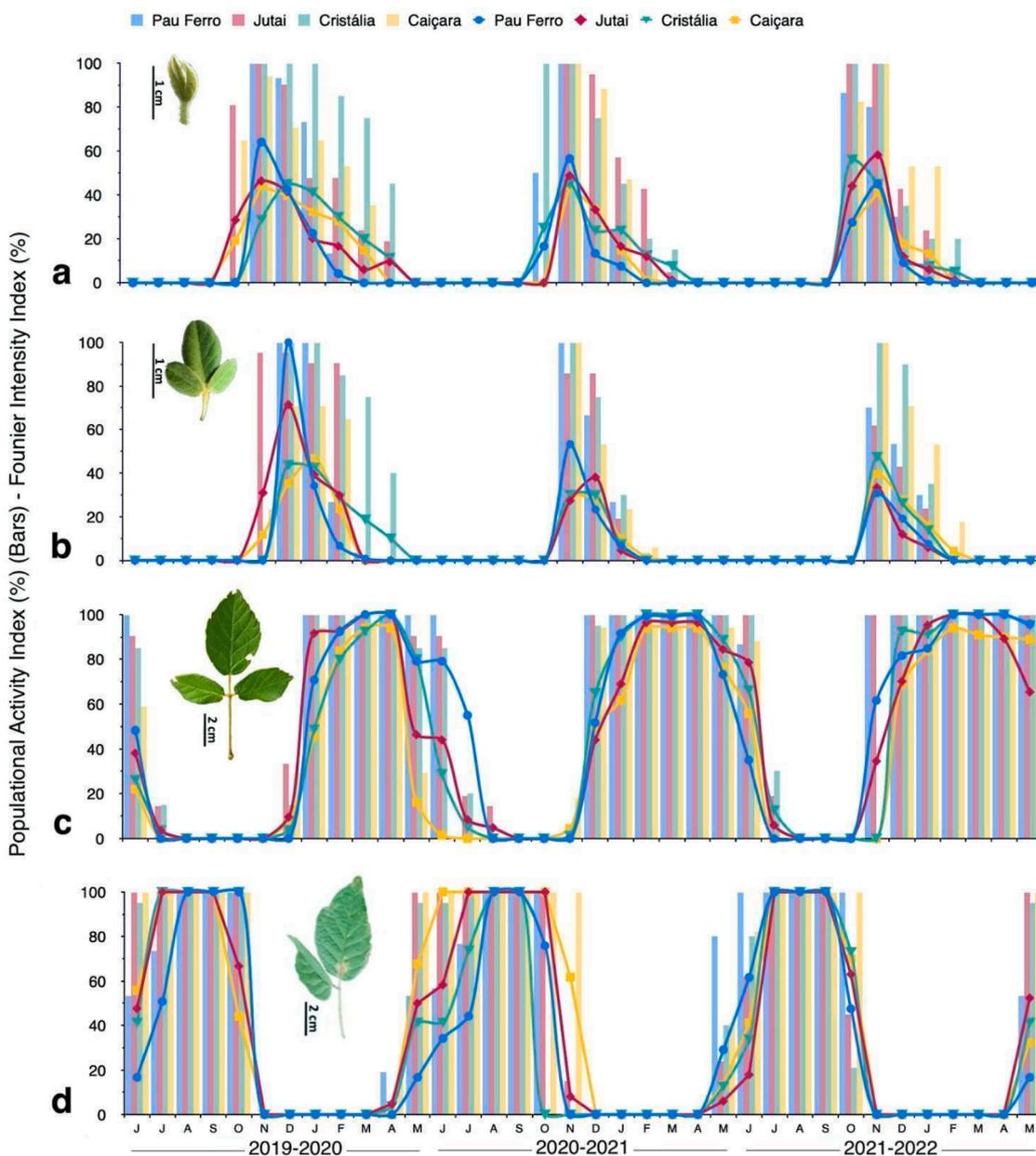


Fig. 3. Vegetative phenophases of *H. spongiosus* during 36 months (June/2019 to May/2022) in populations (different colors) located in SDTF, in northeastern Brazil. (a). Leaf flushing. (b). Young leaf. (c). Mature leaf. (d). Leaf fall. Activity Index (Bars) and Fournier Intensity Index (%) (lines).

3.4. Effects of environmental variables and plant traits on phenology

Multiple Factor Analysis (MFA) evidenced that the vegetative phenophases (LeafFlush and MatureLeaf) have positive relationships with each other, and that they increase when the presence of YoungLeaf is reduced. The reproductive phenophases have stronger relationships (vector directions and lengths) among floral buds (Buds) and flowers and the formation of immature and mature fruits (ImmatureF and MatureF) (Fig. 6). The effects of environmental variables and plant traits on the phenology of *H. spongiosus* evidenced that leaf formation (LeafFlush and MatureLeaf) is related to plant height (PlantH and TrunkH), especially among trees that grow in more pedogenically developed soils (Orthic Chromic Luvisols in Jutai and Cristália) that contain more clay and higher cation exchange capacities (CEC) (Table 1-2). Moreover, the populations with smaller diameters at breast height (DBH) (Pau Ferro and Caiçara) had greater numbers of plants producing buds and flowers (Table 1; Fig. 4).

The generalized additive models (GAMs) evidenced meteorological variables as smoothing aspects and produced models with explanatory powers varying between 0.47 and 0.93 for R², and Deviance values oscillating between 0.52 and 0.95 (Supplementary Table 3). The GAMs indicate how the dependent variables (phenophases) were influenced along the distribution interval by each predictor (meteorological variables) (Fig. 7) – which had not been detected in the MFA (Fig. 6). Precipitation and photoperiod were the meteorological variables that most explained the vegetative phenophases (Supplementary Table 3; Fig. 7b-c). It can be noted that the vegetative phenophases were sensitive to low precipitation volumes (slightly more than 30 mm) and day lengths (with an average of 12 h), as they promote significant increases in leaf emission. Temperature reduced uncertainty in shoot emission between 26 and 28 °C (Fig. 7a). There were low positive linear relationships between temperature, young leaves, and leaf fall, although those relationships were not significant (Supplementary Table 3). High temperatures and high rainfall volumes caused high uncertainty in the vegetative

Table 3

Circular statistical analyses of the occurrences of vegetative phenophases in populations of *H. spongiosus*, monitored from June/2019 - May/2022 in SDTF in northeastern Brazil.

Variable	Pau Ferro			Jutai			Cristália			Caiçara		
	Period1	Period2	Period3	Period1	Period2	Period3	Period1	Period2	Period3	Period1	Period2	Period3
Leaf flushing												
Mean angle	179.41°	152.56°	142.05°	176.70°	184.28°	148.76°	212.61°	162.57°	151.22°	182.08°	174.19°	157.07°
Mean date	Nov	Nov	Oct	Nov	Dec	Oct	Jan	Nov	Nov	Dec	Nov	Nov
VL (r)	0.89	0.89	0.92	0.67	0.85	0.87	0.69	0.77	0.83	0.70	0.91	0.85
RT (z)	0.894	0.892	0.923	0.669	0.848	0.872	0.689	0.769	0.825	0.699	0.912	0.853
RT (p)	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Young leaves												
Mean angle	200°	168.07°	171.85°	194.11°	169.33°	170.60°	228.13°	169.43°	171.07°	203.38°	168.02°	177.47°
Mean date	dec	nov	nov	dec	nov	nov	jan	nov	nov	dec	nov	nov
VL (r)	0.93	0.93	0.92	0.84	0.94	0.92	0.78	0.93	0.93	0.88	0.91	0.88
RT (z)	0.933	0.932	0.922	0.837	0.943	0.923	0.783	0.931	0.931	0.876	0.915	0.88
RT (p)	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Mature leaves												
Mean angle	285°	270°	252.71°	279.50°	272.19°	257.40°	281.06°	270.47°	274.15°	265.09°	252.38°	267.93°
Mean date	Mar	Mar	Feb	Mar	Mar	Feb	Mar	Mar	Mar	Feb	Feb	Feb
VL (r)	0.64	0.53	0.43	0.58	0.49	0.39	0.61	0.51	0.49	0.65	0.62	0.53
RT (z)	0.644	0.533	0.431	0.584	0.487	0.393	0.608	0.511	0.492	0.649	0.622	0.535
RT (p)	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Leaf fall												
Mean angle	57.24°	54.83°	51.92°	45°	58.77°	40.76°	46.26°	39.13°	35.71°	42.83°	68.98°	46.95°
Mean date	Jul	Jul	Jul	Jul	Jul	Jul	Jul	Jul	Jul	Jul	Aug	Jul
VL (r)	0.64	0.65	0.68	0.64	0.69	0.68	0.65	0.79	0.72	0.62	0.59	0.64
RT (z)	0.637	0.648	0.682	0.644	0.694	0.683	0.647	0.789	0.716	0.622	0.589	0.642
RT (p)	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001

VL (r) = Vector length; RT (z) = Rayleigh Test (z); RT (p) = Rayleigh Test (p); Period 1 = June/2019 to May/2020; Period 2 = June/2020 to May/2021; Period 3; June/2021 to May/2022.

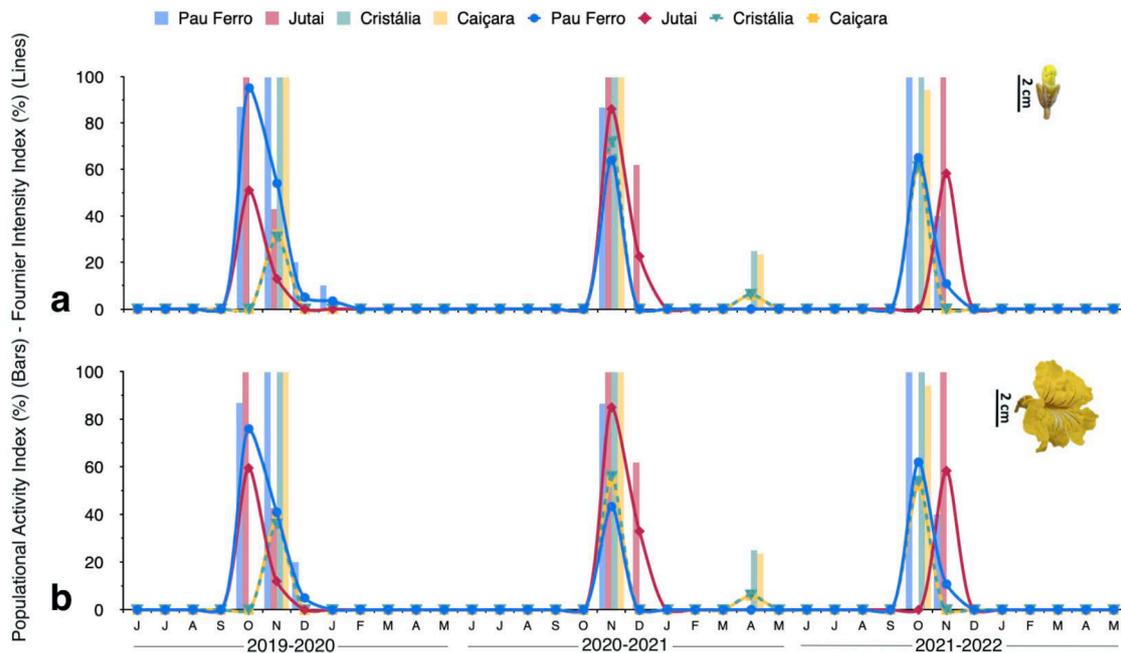


Fig. 4. Reproductive phenophases of *H. spongiosus* along 36 months (June/2019 to May/2022) in populations (different colors) located in SDTF in northeastern Brazil. (a). Flower bud. (b). Flower. Activity Index (Bars) and Fournier Intensity Index (%) (lines).

phenophase data (increased confidence intervals). Temperature and photoperiod were the environmental variables that most influenced the reproductive phenophases over time (Fig. 7d-e). Low rainfall has been shown to be the sensitive threshold for initiating flower bud formation and flowering, even if that effect is not significant (Supplementary Table 3; Fig. 7e).

4. Discussion

Based on a temporal set (36 months) of vegetative and reproductive data of four populations of *H. spongiosus*, our initial hypotheses were confirmed, and showed that the seasonal phenological patterns in the SDTF were concentrated during times of greatest water availability and evidenced only slight spatial-temporal variations. Such divergences among the phenological behaviors of their populations were related to distinct functional traits selected for by differences in certain

Table 4

Circular statistical analyses of the occurrence of reproductive phenophases in populations of *H. spongiosus*, monitored from June/2019 – May/2022 in SDTF populations in northeastern Brazil.

Variable	Pau Ferro			Jutaí			Cristália			Caíçara		
	Period1	Period2	Period3	Period1	Period2	Period3	Period1	Period2	Period3	Period1	Period2	Period3
Flower buds												
Mean angle	142.84°	150°	128.45°	128.75°	161.29°	150°	150°	159.06°	120°	150°	158.17°	120°
Mean date	Oct	Nov	Oct	Oct	Nov	Nov	Nov	Nov	Oct	Nov	Nov	Oct
VL (r)	0.92	1	0.97	0.97	0.97	1	1	0.63	1	1	0.66	1
RT (z)	0.918	0.998	0.972	0.972	0.968	0.997	0.997	0.635	0.992	0.998	0.658	0.997
RT (p)	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Flowers												
Mean angle	140.14°	150°	128.45°	128.75°	161.29°	150°	150°	159.06°	120°	150°	158.17°	120°
Mean date	Oct	Nov	Oct	Oct	Nov	Nov	Nov	Nov	Oct	Nov	Nov	Oct
VL (r)	0.94	1	0.97	0.972	0.97	1	1	0.63	1	1	0.66	1
RT (z)	0.945	0.998	0.972	0.971	0.968	0.997	0.997	0.635	0.997	0.998	0.658	0.997
RT (p)	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Immature fruits												
Mean angle	154.61°	150°	156.79°	150°	161.29°	150°	150°	154.93°	150°	150°	158.13°	150°
Mean date	Nov	Nov	Nov	Nov	Nov	Nov	Nov	Nov	Nov	Nov	Nov	Nov
VL (r)	0.98	1	0.98	1	0.97	1	1	0.76	1	1	0.54	1
RT (z)	0.975	0.998	0.976	0.989	0.968	0.997	0.997	0.759	0.997	0.998	0.536	0.997
RT (p)	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Mature fruits												
Mean angle	156.62°	154.87°	159.34°	155.48°	161.29°	158.75°	155.87°	153.13°	155.87°	150°	164.74°	158.99°
Mean date	Nov	Nov	Nov	Nov	Nov	Nov	Nov	Nov	Nov	Nov	Nov	Nov
VL (r)	0.97	0.98	0.97	0.98	0.97	0.97	0.98	0.83	0.98	1	0.53	0.97
RT (z)	0.970	0.981	0.971	0.979	0.968	0.972	0.978	0.832	0.978	0.998	0.535	0.971
RT (p)	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Seed dispersal												
Mean angle	162.06°	151.63°	153.34°	155.48°	154.66°	153.57°	155.87°	153.13°	153.80°	150°	169.30°	159.35°
Mean date	Nov	Nov	Nov	Nov	Nov	Nov	Nov	Nov	Nov	Nov	Nov	Nov
VL (r)	0.88	0.99	0.99	0.98	0.98	0.99	0.98	0.83	0.98	1	0.55	0.9
RT (z)	0.878	0.993	0.986	0.979	0.982	0.986	0.978	0.832	0.985	0.998	0.547	0.901
RT (p)	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001

VL (r) = Vector length; RT (z) = Rayleigh Test (z); RT (p) = Rayleigh Test (p); Period 1 = June/2019 to May/2020; Period 2 = June/2020 to May/2021; Period 3; June/2021 to May/2022.

environmental variables (rainfall volumes and soil properties). The regional austral summer climate in the study area, with high rainfall and long day lengths, favored flushing and flower bud production in all of the populations. Precipitation and photoperiod exhibited key roles as drivers of the vegetative phenophases; temperature and photoperiod were the environmental variables that most influenced the reproductive phenophases.

4.1. Vegetative phenology

The vegetative phenophases showed immediate responses to water availability and the increase in the photoperiod at the onset of the rainy season, with all individuals responding simultaneously (Pezzini et al., 2014; Alberton et al., 2019; Borchert, 1994a, 1994b; Neves et al., 2022; Souza et al., 2020). Those responses highlight the synergic regulation of tropical plant phenology by rainfall and photoperiod variations (increasing rainfall and photoperiod during the austral summer) as observed in their triggering of leaf flushing in *H. spongiosus* (Borchert, 1994a, 1994b). In general, leaf flushing in deciduous Bignoniaceae is known to be regulated by the combined effects of photoperiod and rainfall (Lobo-Segura, 2019). The initiations, durations, and intensities of the phenophases varied among the populations, and were associated with spatial-temporal variations in the quantities and distributions of rainfall (Venter and Witkowski, 2019). *H. spongiosus* is characterized by having high density wood (Grose and Olmstead, 2007), which limits its water storage capacity (Borchert, 1994b). The phenology of species having high density wood has been found to be directly related to the availability of soil water, especially among species living in seasonally dry tropical ecosystems (Lima and Rodal, 2010; Lima et al., 2021; Neves et al., 2022).

H. spongiosus evidenced a decrease in the formation of both young and mature leaves as well as increased leaf fall with increasing

temperatures under dry conditions – which is considered a strategy for efficient water use and water loss avoidance due to evapotranspiration in SDTF habitats (Reich, 1995; Goldstein et al., 2008; Toledo et al., 2012; Araújo and Lobo, 2020; Silva et al., 2022). Leaf fall in plants growing in seasonal ecosystems can be influenced by increases in temperature, or soil water availability, factors then can act independently or together (Borchert et al., 2002; Asgarzadeh et al., 2010; Luna-Nieves et al., 2022). The present work evidenced that clayey soils with high porosity favored greater leaf formation. Luizão et al. (2004) noted that well-drained clayey soils favor the growth of tall trees with large biomasses (high leaf formation, for example). Soils with high percentages of sand and reduced porosity, however, resulted in reduced growth, although with greater formation of buds and flowers (which may reflect abscisic acid production by their roots under water stress conditions) (Tuteja, 2007; Taiz et al., 2017).

Leaf fall was strongly influenced by a photoperiod <12 h, corroborating what is known concerning photoperiod triggering of leaf senescence in tropical trees by changing hormone levels (Taiz et al., 2017). Additionally, the period of reduced rainfall between April and October (the dry austral winter with monthly rainfall rates <10 mm) overlaps diminished relative humidity of the air and soil water availability, negative plant water balances due to high evapotranspiration rates, and reduced stomata control by older leaves (Borchert, 2000).

Leaf fall is a functional characteristic of SDTF tree species that allows them to tolerate long periods of drought (Borchert, 1994b; Hoffman et al., 2011; Chaturvedi et al., 2021). Those trees can survive under severe semiarid conditions by compensating for low soil water availability and water pressure deficits through strong stomata control that limits evapotranspiration and restricts photosynthesis. During the short rainy season, on the other hand, those same trees maximize their growth rates (as seen in the present study) by concentrating the formation of leaf buds and young leaves during the rainy months (October and

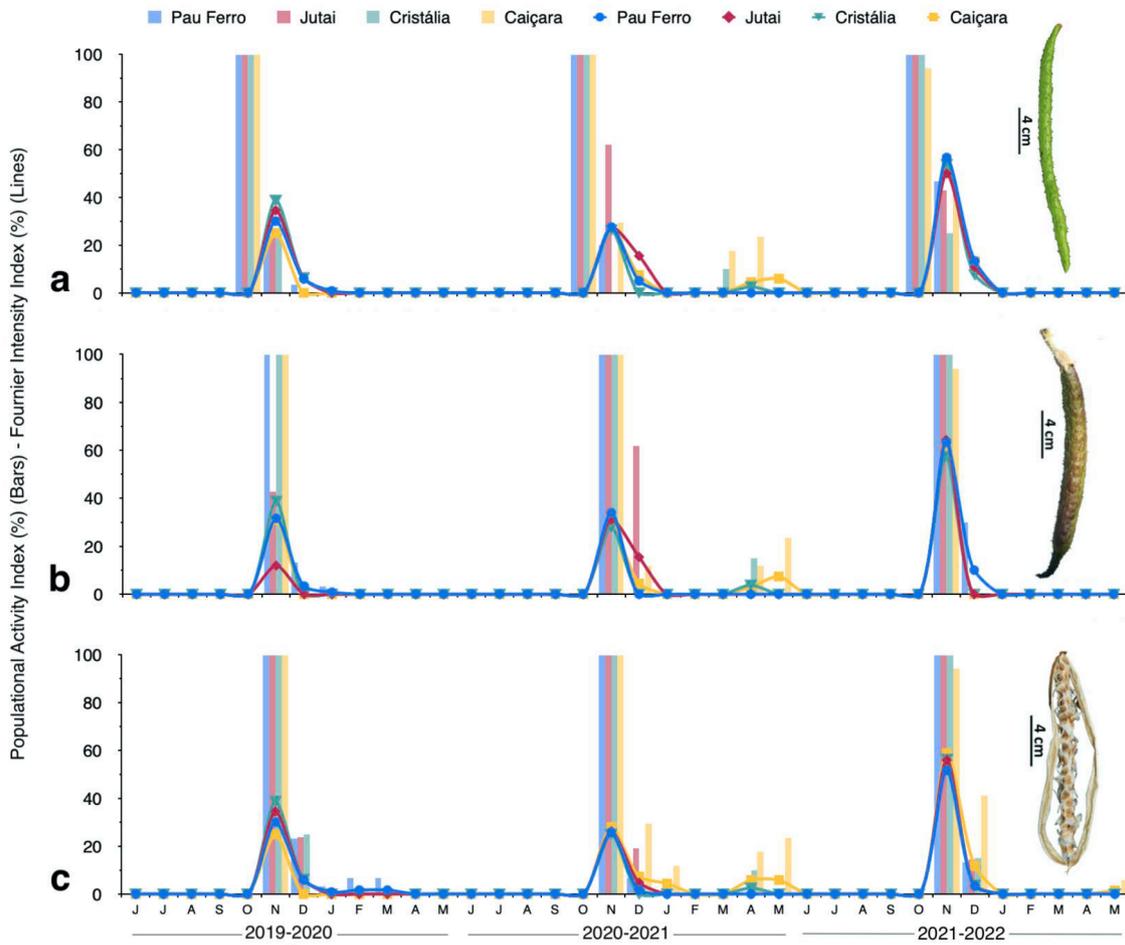


Fig. 5. Reproductive phenophases of *H. spongiosus* during 36 months (June/2019 to May/2022) in populations (different colors) located in SDTF, in northeastern Brazil. (a). Immature fruit. (b). Mature fruit. (c). Seeds dispersing. Activity Index (Bars) and Fournier Intensity Index (%) (lines).

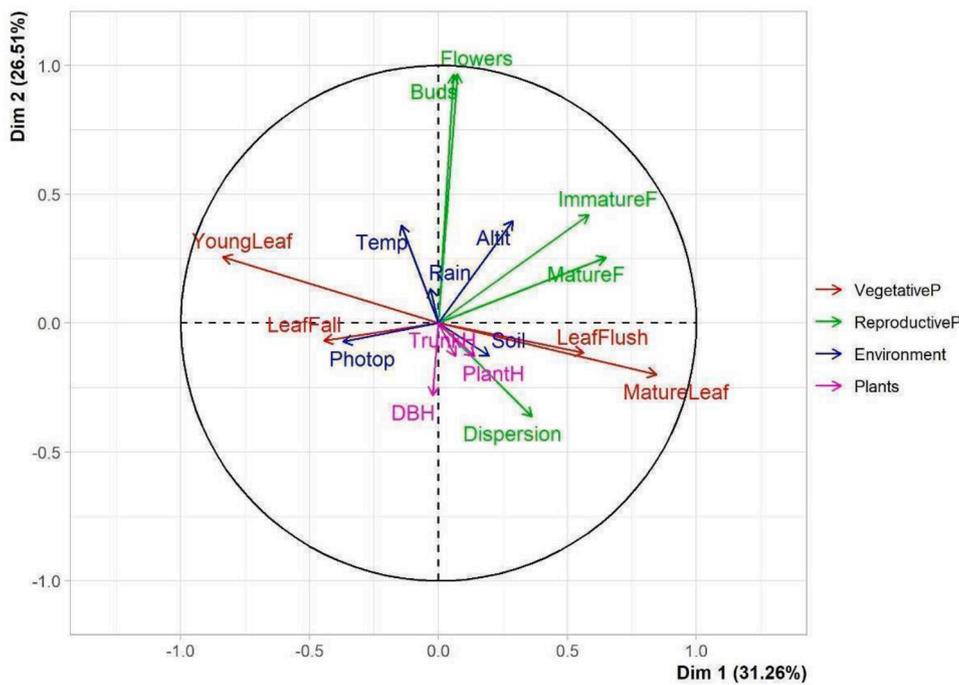


Fig. 6. Multiple Factor Analysis (MFA) of the phenology (VegetativeP and ReproductiveP), plant traits of *H. spongiosus*, and the abiotic variables of the study sites in SDTF, in northeastern Brazil. Rain = Rainfall; Photop = Photoperiod; Temp = Mean temperature; Soil = Soil type; Altit = Altitude; PlantH = Total plant height; TrunkH = Trunk height; DBH = Diameter at breast height; LeafFlush = Leaf flushing; YoungLeaf = Young leaf; LeafFall = Leaf fall; MatureF = Mature fruits; ImmatureF = Immature fruits; Dispersion = Dispersed seeds; VegetativeP = Vegetative phenophases; ReproductiveP = Reproductive phenophases.

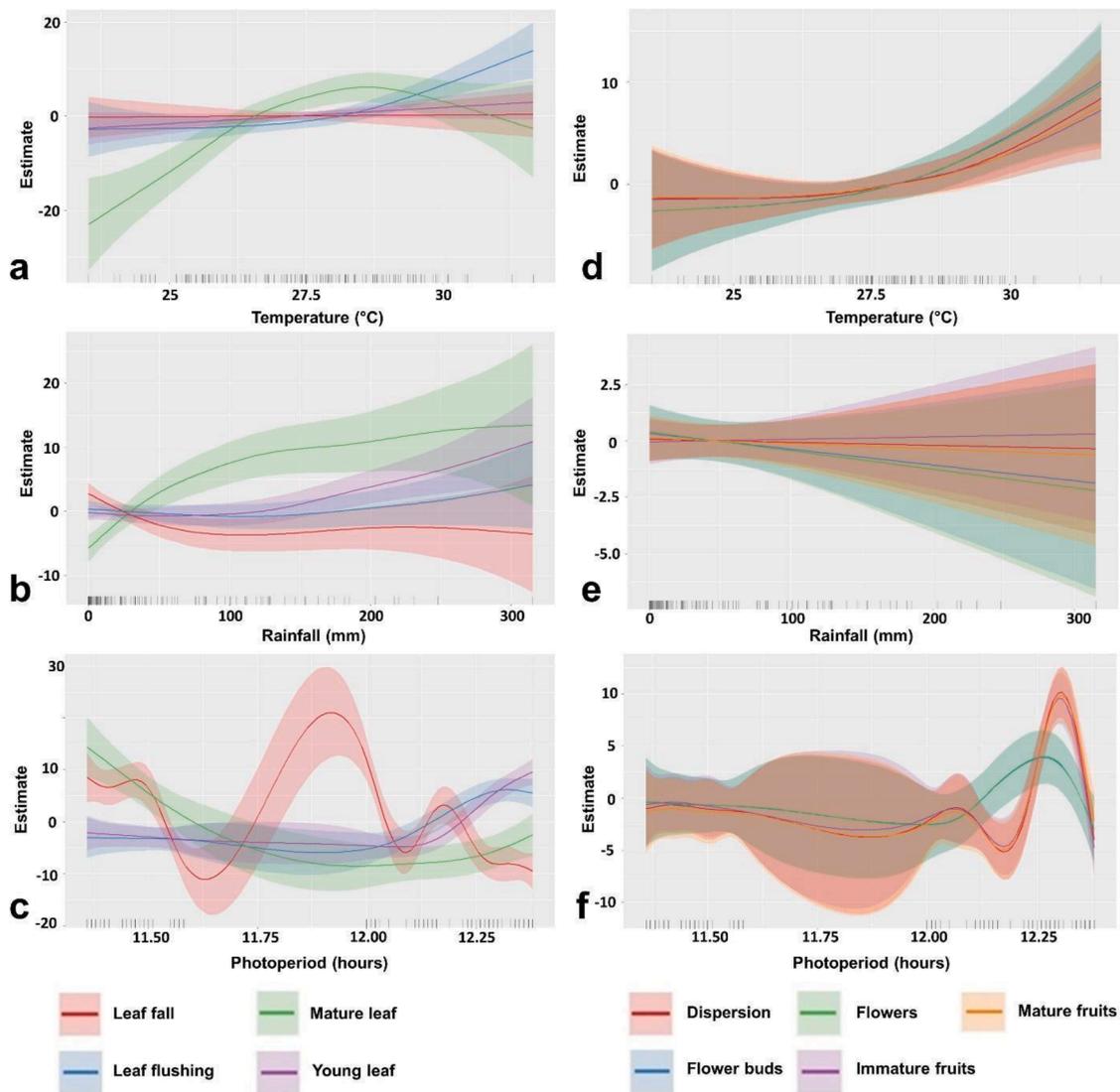


Fig. 7. Partial dependence of the generalized additive model (GAM) for the vegetative and reproductive phenophases of *H. spongiosus* and the abiotic variables of study sites in SDTF, in northeastern Brazil. Partial dependence of the (a) vegetative phenophases on the average monthly temperature, (b) vegetative phenophases on accumulated monthly rainfall, (c) vegetative phenophases on photoperiod, (d) reproductive phenophases on the mean monthly temperature, (e) reproductive phenophases on accumulated monthly rainfall, and (f) reproductive phenophases on photoperiod. The shaded areas represent the 95% confidence intervals. The Estimate Value indicates the intensity with which a meteorological variable influences a given phenophase.

November). There are, however, other tree species in the same ecoregion that are not deciduous during the dry season, as they make rigorous physiological adjustments that reduce water losses and allow for the continuation of photosynthetic activities (Santos et al., 2015; Chaturvedi et al., 2021). The increase in leaf fall under drier conditions among plants in the Caiçara population, with probable growth reductions, may be intensified by the forecasts of increased duration and intensity of droughts predicted by the International Panel of Climate Change (IPCC) (United Nations, 2023).

4.2. Reproductive phenology

The reproductive phenophases of *H. spongiosus* evidenced annual patterns (Newstrom et al., 1994) that were limited to the rainy season. It is likely that those reproductive phenological events are triggered by combinations of increased photoperiods, temperatures, and precipitation (Reich and Borchert, 1982; Rivera et al., 2002; Nunes et al., 2012; Pezzini et al., 2014; Lima et al., 2012; Neves et al., 2017, 2021), as it is well-known that plants can use more than one environmental trigger to regulate flowering (Silva et al., 2021). The emergence of flower buds

and flowers in the Caatinga domain has mainly been attributed to the decreased water stress after the first rains in the dry period, and to increasing temperatures (Andrade et al., 2020), as seen, for example, with the reproductive phenology of *Z. joazeiro* Mart. (Nadia et al., 2007). But changes in onset dates, frequencies, and intensities of reproductive phenophases in seasonally dry tropical areas can nonetheless be observed in response to interannual variations in rainfall (Luna-Nieves et al., 2017).

It is known that plant growth also affects the intensity of the reproductive phenophases of trees, as has been reported for *Dalbergia nigra* (Vell.) Allemão ex Benth. (Silva et al., 2022). In that study, photoperiod was shown to be the environmental factor that most strongly affected reproductive phenological variables (flowering and seed dispersal) when receiving >12 h of sunlight, indicating that it can be used by individuals of *H. spongiosus* to synchronize flowering among plants in different localities; that same effect was observed in *Croton heliotropifolius* Kunt. (Costa et al., 2021). The reproductive initiation of *H. spongiosus* occurring after days with more than 12 h of sunlight suggest that this is a long-day plant (LDP) (Bennie et al., 2016).

The explosive flowering (Gentry, 1982) and fruiting of *H. spongiosus*

was concentrated at the beginning of the rainy season, with heavy flowering after the first 10 mm of rainfall (in October), followed by the dispersal of anemochoric seeds 12 days later (in November). This can be considered a strategy that takes advantage of the increased visibility of flowers as well as the efficient dispersal of anemochoric seeds among naked branches – thus facilitating both pollinator attraction and seed dispersal (Elzinga et al., 2007; Mendoza et al., 2017), as well as subsequent seedling establishment during the rainy season (which extends until April). The global climate changes predicted by the IPCC (United Nations, 2023) can therefore be expected to affect reproductive aspects of *H. spongiosus*, as temperature increases above 28 °C can increase water restrictions, with consequent reductions of flowering intensity – leading to decreased availability of the floral resource required by pollinators (native bees).

5. Conclusion

Populations of *H. spongiosus* showed distinct initiations, peaks, and durations of their vegetative phenophases, mainly in terms of budding and mature leaves; their reproductive phenophases, on the other hand, showed little spatial-temporal variation. The vegetative and reproductive phenophases of the populations studied, with the overlapping formation of new leaves, floral buds, and fruits occurred at the beginning of the rainy season. Photoperiods >12 h and rainfall >10 mm were found to be drivers for breaking bud dormancy. The effects of secondary plant traits (such as tree height on leaf flushing and mature leaves) were most pronounced among plants growing on more pedogenically developed soils with higher clay contents. Tree populations growing on sandy soils and having smaller diameter at breast height (DBH), on the other hand, evidenced greater numbers of plants producing buds and flowers. Seeds should be harvested as soon as the fruits are mature in November, before seed dispersal occurs, as collection delays will reduce their availability, especially in plants with smaller DBH values that more actively produce buds, flowers, and fruits. In light of the global climate changes predicted by the IPCC (United Nations, 2023), increases in leaf fall and reductions of flowering intensity are likely, as verified in the studied populations, with cascade effects on floral resource availability for pollinators (native bees). Our results, in addition to being important for understanding the phenological rhythms of this endemic and threatened species, are robust, as they were undertaken for over two years and evaluated four populations and more than 80 individuals, and therefore lay the groundwork for seed collection programs of native Caatinga species and the implementation of reforestation programs.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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