Floresta e Ambiente 2022; 29(3): e20220002
https://doi.org/10.1590/2179-8087-FLORAM-2022-0002
ISSN 2179-8087 (online)

ORIGINAL ARTICLE – Silviculture

Environmental and Plant Variables Influence *Dalbergia nigra* (Fabaceae) Phenology - Implications for Seed Production

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Abstract

Studies of plant phenology in the Atlantic Forest can be enhanced by a greater understanding of the factors regulating vegetative and reproductive cycles. *Dalbergia nigra* (Vell.) Allemão ex Benth. is endemic and vulnerable in the Atlantic Forest. We analyzed abiotic aspects and plant traits that modulate the phenologies of *D. nigra* by monitoring 135 individuals in four subpopulations from different remnant forests for 24 months. The growth and shapes of the plants, as well as environmental variables, were determined. Circular analysis evidenced phenological variations among subpopulations and evaluation periods. Multiple factor analysis evidenced that phenological variations are mainly correlated with precipitation, temperature, and tree height. The combination of environmental conditions and plant characteristics affect synchronicity and phenological intensity. Low fruiting intensity (less than 50%) limits seed production and recruitment. We emphasize the importance of forest remnants and the need to increase *D. nigra* populations in future reforestation projects.

Keywords: Atlantic Forest, jacaranda, intrapopulation variation, reforestation.

1. INTRODUCTION AND OBJECTIVES

Phenological patterns are far more complex in tropical forests than in temperate forest ecosystems, and much less understood (Babweteera et al., 2018). The analysis of phenological data of historically and continually devastated plant populations in Atlantic Forest ecosystems can be significantly enhanced by a better understanding of the regulatory and controlling triggers of their vegetative and reproductive cycles – information essential for their management and conservation (Morellato et al., 2016; Menezes et al., 2018). In addition to rainfall variability in tropical rainforests, local environmental factors such as photoperiod, temperature, altitude, soil types (Souza & Funch, 2017; Santos et al., 2020), as well as plant traits such as height and canopy diameter (Babweteera et al., 2018; Ouédraogo et al., 2018) represent important intrapopulational or subpopulational variations that can influence the timing and synchrony of leafing and reproductive events (Santos et al., 2020; 2021).

The analysis of phenological variability within populations can provide information about how they are able to persist and reproduce under the influence of different environmental filters. Such studies, however, have been operationally restricted by time limitations and sampling difficulties (Santos et al., 2020; 2021). Atlantic Forest remnants, however, favor testing hypotheses of populational phenological dynamics (Milani et al., 2021) as those small, isolated fragment of disturbed secondary vegetation (generally less than 50 ha and under intense anthropogenic pressure) grow on highly diverse soil types, in varying landscapes, at different elevations (Liebsch et al., 2016; Godoy-Veiga et al., 2018).

Dalbergia nigra (Vell.) Allemão ex Benth. is a hardwood tree endemic to the Atlantic Forest in Brazil. The species is considered vulnerable to extinction (Filardi et al., 2020) due to the high commercial value of its wood and the high fragmentation of its natural habitat (Martinelli & Moraes, 2013; Regnier, 2019). *D. nigra* generally displays an aggregated distribution in the southern region of Bahia State where it has its highest occurrence, but with a low population density (~0.8 individuals per hectare) (Rêgo & Possamai, 2003). This survey of the species was part of a forest tree monitoring project in the Atlantic Forest (initiated in November 2013) that presented the opportunity of examining variations in the rhythms of leaf fall, flushing, flowering, and fruiting associated with environmental variables and plant traits, and was mainly designed to subsidize fruit and seed production. Phenological studies are important tools for understanding the factors that influence *D. nigra* reproduction and seed production in areas where selective logging has strongly impacted their habitat (Guariguata & Ostertag, 2001; Orellana et al., 2020).

In view of the importance of determining the vulnerability status is of *D. nigra* populations growing in the Atlantic Forest in northeastern Brazil, we examined how local abiotic factors there and plant traits drive its phenological cycles. We sought to understand how those environmental factors and plant characteristics can influence supplies of quality seeds in light of the commitment made by Brazil in 2015 at the 21st Conference of the Parties to the United Nations Framework Convention on Climate Change (UNFCCC) to restore forests by 2030. Allied to this, the UN established 2021-2030 as the Decade of Restoration (WRI Brasil, 2021), with the goal of planting 12 million hectares of forests (Brazil, 2017). Specifically, the present study addressed the following questions: (i) Are there phenological variations between subpopulations of *D. nigra*? (ii) What environmental variables and/or plant traits affect its reproductive phenology, and therefore seed production? We hypothesized that there would be phenological variation between sites, in terms of both phenophase synchrony and intensity. We also expected that some environmental variables (such as precipitation and temperature) and plant traits (such as tree height and diameter) would more strongly affect the reproductive phenology of the species.

2. MATERIALS AND METHODS

2.1. Species and study sites

Phenological monitoring of *D. nigra* trees approximately 10 meters tall was carried out in four fragmented Atlantic Forest remnants (Figure 1) in Bahia State, Brazil. All of the sites had anthropized vegetation composed of secondary forests and pasture and are more than 10 km apart. The soil types in each forest fragment were classified according to Brasil (1983). The study area region has a warm and humid climate type Aw according to Köppen system (1948) with dry winters and mean annual temperatures of 26° C in summer and 24° C in winter; mean annual precipitation ranges from 1000 to 1500 mm, with heavy rains generally from November to April (Alvares et al., 2013).

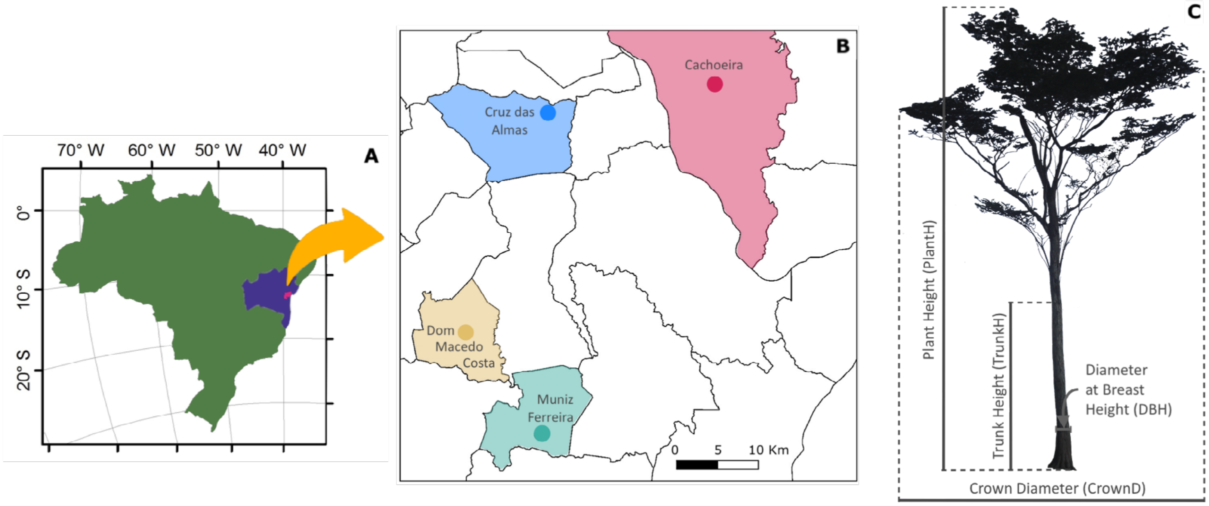

Figure 1. Location of the study area. (A, B) Location of the four subpopulations of *Dalbergia nigra* (Vell.) Allemão ex Benth Fabaceae in Cachoeira, Cruz das Almas, Dom Macedo Costa, and Muniz Ferreira, in Bahia State, Brazil. (C) Plant traits examined.

2.2. Phenological data and plant traits

A total of 135 healthy adult individuals of *D. nigra* were mapped and marked with aluminum tags. The numbers of individuals accompanied in each of the four sites varied according to the sizes of their subpopulations: Cachoeira (n=34 individuals) (12°37'42.5"S; 38°53'30.1"W, 177.64m), Cruz das Almas (n=54 individuals) (12°39'35.3"S; 39°5'15.1"W, 218.66m), Dom Macedo Costa (n=30 individuals) (12°54'43"S; 39°10'14.1"W, 180.83m) and Muniz Ferreira (n=17 individuals) (13°1'26.1"S; 39°5'5.8"W, 90.05m). Phenological observations were performed on a monthly basis during a 24-month period (July/2014 - June/2016). The vegetative phenophases observed were leaf flushing and leaf fall; the reproductive phenophases observed were the presence of buds, flowers, immature fruits, mature fruits and fruit dispersal. Phenophase intensities were estimated during field observations using a semi-quantitative scale composed 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 & Morellato, 2003). We determined the Bencke & Morellato (2002) index based on the percentage of individuals in the population manifesting a certain phenological event, assessed as asynchrony, or low, or high synchrony. The plant traits examined were total plant height (PlantH), trunk height (TrunkH), crown diameter (CrownD), diameter at breast height (DBH), crown shape (CrownS), and trunk shape (TrunkS) (Nogueira & Medeiros, 2007).

2.3. Environmental variables

Monthly average temperature data (°C) for each population were obtained using Multiple Linear Regression (MRL) to generate 12 temperature matrices representing the months of July/2014 through June/2016 for each subpopulation based on climatic data from 56 meteorological stations distributed throughout Bahia State maintained by the National Institute of Meteorology (INMET) and Embrapa Mandioca e Fruticultura. We used latitude, longitude, and altitude data from each meteorological station to obtain the coefficients β_0, β_1, β_2 and β_3, and thus assemble the 12 equations used to generate the monthly temperature maps for Bahia State.

The calculation was performed by Equation 1:

$$[\mathrm{T} = \boldsymbol{\beta}_0 + \boldsymbol{\beta}_1 \mathrm{Y} + \boldsymbol{\beta}_2 \mathrm{X} + \boldsymbol{\beta}_3 \mathrm{Alt}] \quad (1)$$

T: air temperature (°C);

β_0: regression constant;

Y: geographic coordinate Y (latitude);

X: geographic coordinate X (longitude);

Alt: altitude (m);

β_1, β_2 and β_3: regression coefficients for the variables.

We used a pixel resolution of 90 m, spatialized for the entire state, which was sufficient for ensuring good coverage of the individuals in the populations. We employed the geostatistics method through ordinary spherical kriging for data interpolation to determine the total rainfall data (mm) for each month. The rainfall stations were the same as used for temperature determinations. The photoperiod of each subpopulation was obtained using ModelE AR5 Simulations (NASA, 2021) during the 24-month duration of the study (July/2014 - June/2016).

2.4. Statistical analysis

QGIS version 3.10.12 programs (QGIS Development Team, 2020) were used to develop the spatial analysis of the climate data. The analyzes were performed using R Core Team software (2020) (the statistical packages used are specified below). The data of the variables evaluated in the four subpopulations were deposited in the figshare public repository (Duarte & Silva, 2021).

The seasonality of the reproductive phenological events of *D. nigra* in each site in each year were evaluated using circular statistical analyses (Morellato et al., 2010), employing R environment software (R Core Team, 2020) with the addition of the "circular" package (Agostinelli & 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 January, 30° representing February, and so forth, until 330° representing December). 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 that the Rayleigh test indicated as significant, were considered seasonal (Morellato et al., 2010). The nonparametric Mardia-Watson-Wheeler test (W) (Batschelet, 1981; Mardia & Jup, 2000) was used to assess whether there are differences in the phenophases among the subpopulations, and whether there are differences in the phenophases of the subpopulations among the evaluation periods. This test consists of evaluating whether two or more circular samples (angles) differ among the mean dates or mean months ($p < 0.05$).

The multiple factor analysis (MFA) used the R package "FactoMiner" program (Lê et al., 2008) with the monthly mean data of each subpopulation being used to understand variations among the subpopulations and evaluation periods (July/2014 - June/2016), and the relationships between environmental variables, plant traits, and vegetative and reproductive phenophases. Qualitative variables were converted into quantitative variables, adopting increasing numbers (1, 2, 3…) to characterize common/primitive types (smaller values), applying larger values to rarer forms or more derived/modified anthropogenic variables. The environmental and plant variables in MFA were considered supplementary and were not used for calculating the explained variance.

3. RESULTS

3.1. Environmental and plant variables

The soil types found in the subpopulation sites were: Lithic Entisol (Muniz Ferreira), Ultisols (Dom Macedo Costa), Yellow and Red oxysols (Cruz das Almas) and Yellow ultisol (Cachoeira), at elevations between 90 and 218 masl (Table 1). Minimum and maximum temperatures varied between 22° C and 28° C (Figure 2), with a trend towards higher temperatures in the subpopulation at Muniz Ferreira, which occurred at a lower elevation. Rainfall also varied among the subpopulations, with a maximum of 1258 mm in Dom Macedo Costa and a minimum of 841 mm in Cachoeira (Table 1); the first year of the study was notably rainier in all subpopulation sites (Figure 2A). There were only small variations in photoperiod among subpopulations (up to 6 minutes among the shortest days and 3 minutes among the longest days) (Figure 2B), which were therefore barely noticeable due to the low amplitude between the shortest and the longest day (up to 1 hour and 31 minutes). *D. nigra* subpopulations were found in secondary forest environments, mainly in anthropized areas where pastures had been established (Table 1). The individuals of the Dom Macedo Costa subpopulation evidenced greater heights, crown diameters, and diameters at breast height, while the greatest trunk heights were observed among individuals of the Muniz Ferreira and Dom Macedo Costa subpopulations. The shapes of the crowns were generally irregular and the trunks generally straight (Table 1).

Table 1. Study sites of *Dalbergia nigra* (Vell.) Allemão ex Benth, Fabaceae in the Atlantic Forest, Bahia State, Brazil. Mean environmental variables, including elevation, soil type, temperature, rainfall, photoperiod, vegetation characteristics, and plant traits are indicated.

Variables/Subpopulation		Cachoeira		Cruz das Almas		Dom Macedo		Muniz Ferreira	
Period (12 months)		jul. 2014 – jun. 2015	jul. 2015 - jun. 2016	jul. 2014 - jun. 2015	jul. 2015 - jun. 2016	jul. 2014 - jun. 2015	jul. 2015 - jun. 2016	jul. 2014 – jun. 2015	jul. 2015 - jun. 2016
Environment	Altitude (m)	177.64±2.15		218.66±0.53		180.83±0.96		90.05±2.94	
	Soil	Yellow Ultisol		Yelllou oxi/Red oxi.		Ultisol		Lithic Entisol	
	Temp (°C)	24.7±0.46	25.3±0.47	24.7±0.46	25.3±0.47	24.9±0.43	25.5±0.46	25. 4±0.43	25.9±0.45
	Rain. (mm.ano^{-1})	1148.8±21.26	841.4±16.70	1258.2±21.47	859.1±15.33	1152.2±17.98	937.9±17.07	1229.3±20.10	1041.64±19.05
	Photop (hours)	12:06±0h 5m	12:06±0h 5m	12:06±0h 5m	12:06±0h 5m	12:06±0h 5m	12:06±0h 5m	12:06±0h 5m	12:06±0h 5m
	Vegetation	Anthropized		Anthropized		Forest/Anthropized		Forest/Anthropized	
Plants	Numbers of individuals	34		54		30		17	
	CrownD (m)	10.9±0.48		8.12±0.55		12.11±0.45		9.6±0.98	
	PlantH(m)	13.58±0.49		11.15±0.48		16.46±0.73		13.05±0.93	
	TrunkH (m)	1.48±0.25		2.32±0.36		3.05±0.52		3.51±0.46	
	DBH (m)	0.37±0.02		0.34±0.03		0.45±0.03		0.35±0.04	
	CrownS	Umbeliform/Irregular		Irregular		Umbeliform/Irregular		Umbeliform/Irregular	
	TrunkS	Straight /Crooked		Straight /Crooked		Straight		Straight /Crooked	

Acronyms/Abbreviations: Rain.: Rainfall. Photop.: Photoperiod. Oxi.: Oxisols. CrownD: Crown diameter. PlantH: Total plant height. TrunkH: Trunk height. DBH: Diameter at breast height. CrownS: Crown shape. TrunkS: Trunk shape. The means are followed by the standard error.

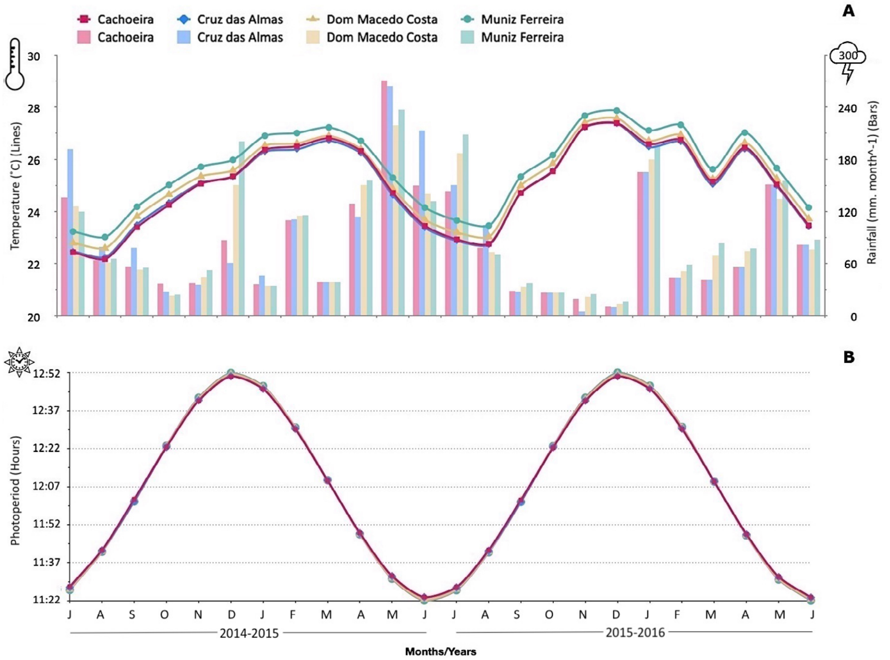

Figure 2. Environmental variables at the *Dalbergia nigra* (Vell.) Allemão ex Benth, study sites, evaluated for 24 months (July/2014 through June/2016), in Bahia State, Brazil. A. Mean temperature (lines) and monthly rainfall (bars). B. Photoperiod.

3.2. Vegetative and reproductive phenology

The vegetative phenophases of *D. nigra* evidenced very similar intensities and synchronies in the different subpopulation sites and years (Figure 3). Leaf flushing, however, tended to be higher in September during the first period. There was low variation in leaf flushing intensity (Fournier) among subpopulations, although with higher intensities from July to December/2014, especially in Cachoeira (Figure 3A). The leaf fall rhythm was continuous, but more intense from July through November during the two study periods (Figure 3B).

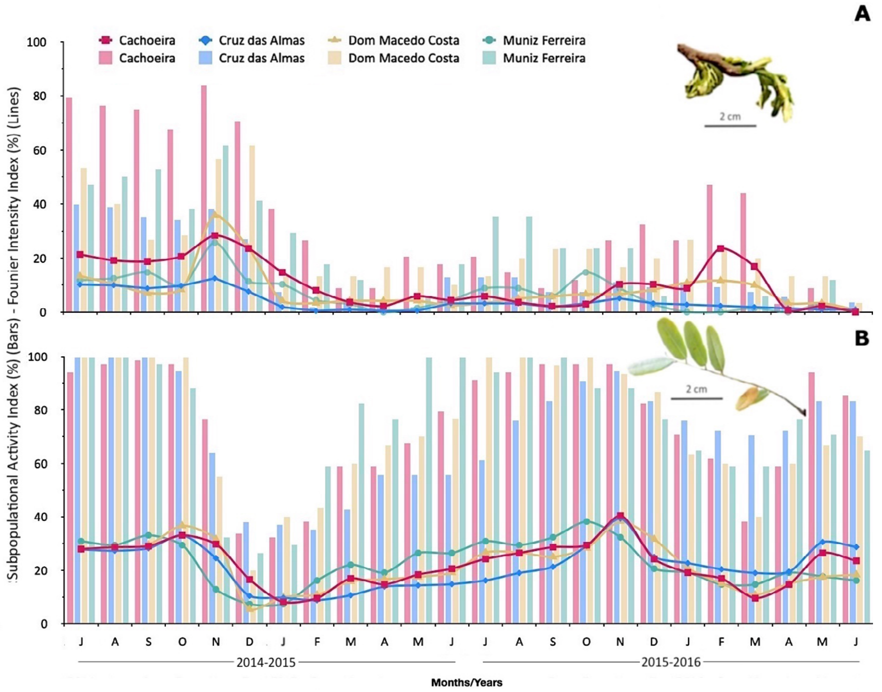

Figure 3. Vegetative phenophases and evaluation criteria (insets) of the four subpopulations (Cachoeira, Cruz das Almas, Dom Macedo Costa and Muniz Ferreira) of *Dalbergia nigra* (Vell.) Allemão ex Benth, Fabaceae, during 24 months (July/2014 through June/2016), Bahia State, Brazil. A. Leaf flushing. B. Leaf fall. Activity Index (Bars) and Fournier Intensity Index (%) (Lines).

D. nigra exhibited variations of flowering and fruiting intensities and synchronies in the different sites (Figure 4). Additionally, *D. nigra* evidenced seasonal flower buds and flowers events during the two evaluation periods (Figure 4A and 4B; Table 2). There were variations in the mean dates of flower buds and flowers among the subpopulations (Table 2). The peak of flowering activity was observed between October and November, during periods of increased photoperiod length (Figure 4). The lengthy process of fruit development resulted in the almost constant presence of immature fruits in the subpopulations (Figure 5A). The presence of mature fruits and fruit dispersal demonstrated seasonality in most of the subpopulations (except in the Cruz das Almas site during the second evaluation period), with peaks of activity between August and December (Figure 5B and C; Table 2). The reproductive phenophases showed annual variations ($p < 0.05$) among the subpopulations (Table 3), except for the subpopulations of Dom Macedo Costa and Muniz Ferreira, as they did not differ in terms of their timings of emissions of flower buds and flowers in the first evaluation period, and the subpopulations of Muniz Ferreira and Cruz das Almas, which also did not differ in terms of their timings of issuance of flower buds, flowers, and immature fruits.

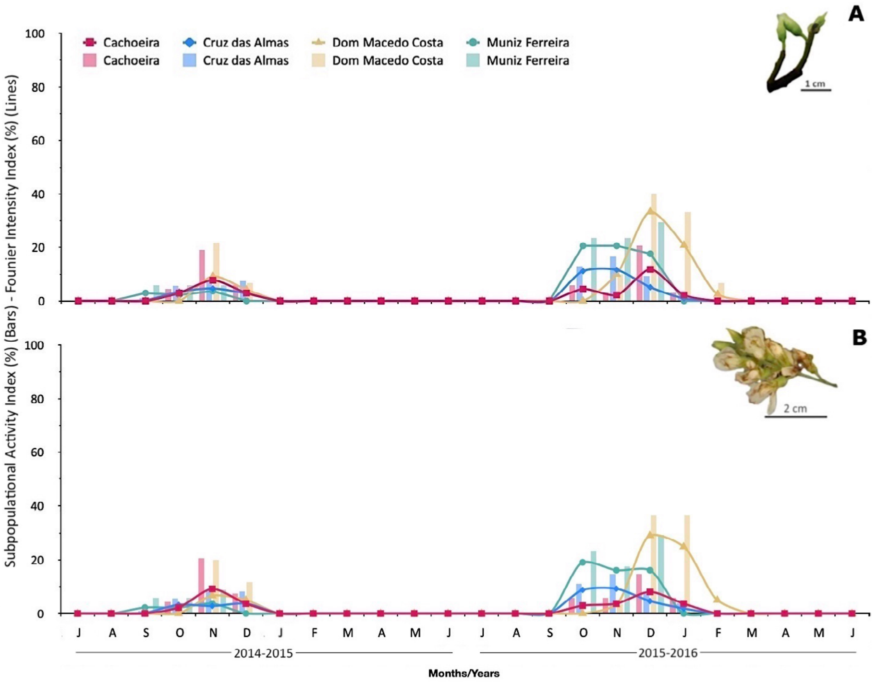

Figure 4. Reproductive phenophases and evaluation criteria (insets) of the four subpopulations (Cachoeira, Cruz das Almas, Dom Macedo Costa and Muniz Ferreira) of *Dalbergia nigra* (Vell.) Allemão ex Benth, for 24 months (July/2014 through June/2016), Bahia State, Brazil. A. Flower buds. B. Flowers. Activity Index (Bars) and Fournier Intensity Index (%) (Lines).

Table 2. Circular Statistical Analyses of the occurrence of seasonal flowering and fruiting, and the results of the Mardia-Watson-Wheeler (W) test for the reproductive phenophases of *Dalbergia nigra* (Vell.) Allemão ex Benth, Fabaceae monitored from July/2014 to June/2016 in subpopulations in Bahia State, Brazil.

	Frequency of individuals							
Statistical parameters	Cachoeira		Cruz das Almas		Dom Macedo Costa		Muniz Ferreira	
	Flower buds							
	July of 2014 – June of 2015	July of 2015 – June of 2016	July of 2014 – June of 2015	July of 2015 – June of 2016	July of 2014 – June of 2015	July of 2015 – June of 2016	July of 2014 – June of 2015	July of 2015 – June of 2016
Mean angle	122.07°	139.63°	118.94°	119.59°	127.11°	162.27°	90.00°	122.05°
Mean date	November	November	October	October	November	December	October	November
Mean length of vector (*r*)	0.95	0.87	0.90	0.90	0.98	0.92	0.91	0.91
Rayleigh Test (z)	0.97	0.90	0.89	0.91	0.97	0.93	0.93	0.94
Rayleigh Test (*p*)	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
W (*p*)	9.45 (0.003)		0.0086 (0.926)		60.62 (<0.001)		23.729 (<0.001)	
	Flowers							
Mean angle	122.81°	139.63°	120.97°	122.57°	131.17°	163.35°	90.52°	122.24°
Mean date	November	November	November	November	November	December	October	November
Mean length of vector (*r*)	0.96	0.87	0.89	0.88	0.97	0.96	0.91	0.90
Rayleigh Test (z)	0.97	0.88	0.90	0.89	0.98	0.95	0.92	0.93
Rayleigh Test (*p*)	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
W (*p*)	7.70 (0.0072)		0.0863 (0.769)		87.269 (<0.001)		18.409 (<0.001)	

Table 2. Continued...

Statistical parameters	Frequency of individuals							
	Cachoeira		Cruz das Almas		Dom Macedo Costa		Muniz Ferreira	
	Flower buds							
	July of 2014 – June of 2015	July of 2015 – June of 2016	July of 2014 – June of 2015	July of 2015 – June of 2016	July of 2014 – June of 2015	July of 2015 – June of 2016	July of 2014 – June of 2015	July of 2015 – June of 2016
	Immature fruits							
Mean angle	296.86°	296.04°	280.29°	257.57°	278.55°	279.97°	345.80°	245.60°
Mean date	April	April	April	March	April	April	June	March
Mean length of vector (*r*)	0.19	0.23	0.22	0.15	0.29	0.39	0.18	0.28
Rayleigh Test (z)	0.19	0.23	0.21	0.16	0.30	0.40	0.22	0.34
Rayleigh Test (*p*)	< 0.001	< 0.001	< 0.001	0.005	< 0.001	< 0.001	< 0.001	< 0.001
W (*p*)	0.0089 (0.924)		3.8724 (0.0497)		1.8267 (0.1902)		149.06 (<0.001)	
	Mature fruits							
Mean angle	60.07°	358.28°	61.41°	110.82°	31.12°	64.17°	50.77°	13.25°
Mean date	September	September	August	October	August	September	August	July
Mean length of vector (*r*)	0.67	0.61	0.76	0.11	0.64	0.60	0.62	0.72
Rayleigh Test (z)	0.68	0.62	0.79	0.16	0.67	0.66	0.66	0.76
Rayleigh Test (*p*)	< 0.001	< 0.001	< 0.001	0.1171	< 0.001	< 0.001	< 0.001	< 0.001
W (*p*)	0.0603 (0.806)		29.462 (<0.001)		35.134 (<0.001)		50.201 (<0.001)	
	Fruit dispersal							
Mean angle	94.23°	86.53°	54.97°	154.96°	62.25°	88.93°	76.76°	42.09°
Mean date	October	September	August	December	September	September	September	August
Mean length of vector (*r*)	0.78	0.67	0.89	0.24	0.83	0.71	0.72	0.68
Rayleigh Test (z)	0.78	0.68	0.89	0.24	0.84	0.74	0.76	0.74
Rayleigh Test (*p*)	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
W (*p*)	1.796 (0.1814)		91.709 (<0.001)		26.179 (<0.001)		33.323 (<0.001)	

$r > 0.5$ indicates synchrony; $P < 0.05$ indicates statistical differences, using the Mardia-Watson-Wheeler (W) test. Uniform distribution – $p > 0.05$, using the Rayleigh test (z)

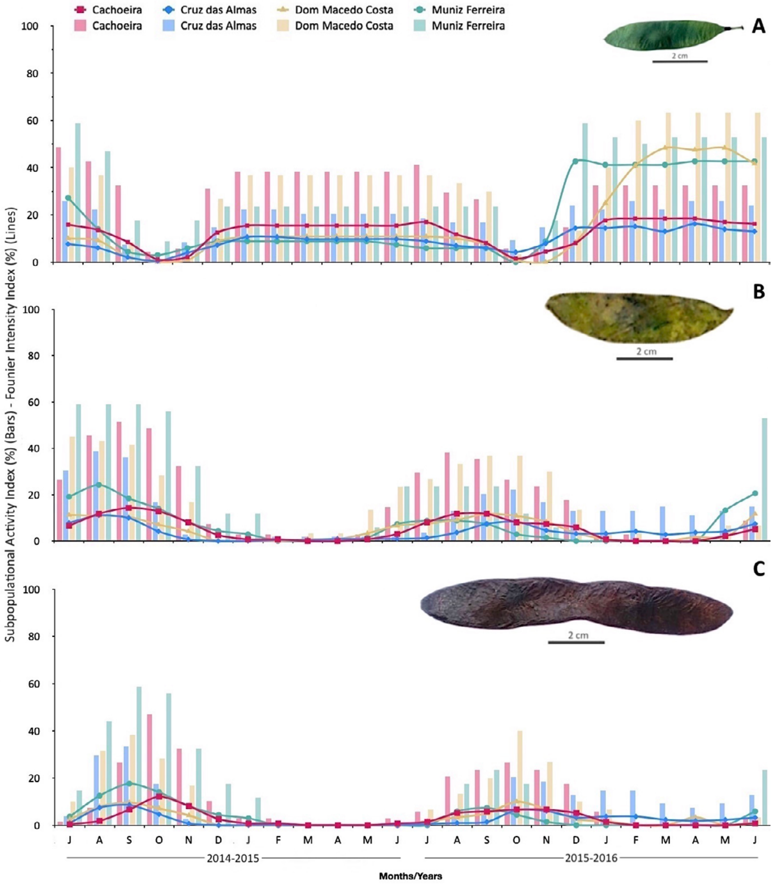

Figure 5. Reproductive phenophases and evaluation criteria (insets) of the four subpopulations (Cachoeira, Cruz das Almas, Dom Macedo Costa and Muniz Ferreira) of *Dalbergia nigra* (Vell.) Allemão ex Benth, Fabaceae for 24 months (July/2014 through June/2016), Bahia State, Brazil. A. Immature fruits. B. Mature fruits. C. Fruit dispersal. Activity Index (Bars) and Fournier Intensity Index (%) (Lines).

Table 3. Results of the Mardia-Watson-Wheeler (W) test used to analyze variations among the reproductive phenophases of *Dalbergia nigra* (Vell.) Allemão ex Benth, Fabaceae as monitored in four subpopulations in Bahia State, Brazil, from July 2014 to June 2016.

		Mardia-Watson-Wheeler (W)									
		Flower buds		Flowers		Immature fruits		Mature fruits		Fruit dispersal	
Subpopulations		W	*p*	W	*p*	W	*p*	W	*p*	W	*p*
Dom Macedo Costa x Muniz Ferreira	July of 2014 – June of 2015	0.49	0.4878	5.45	0.0235	11.42	< 0.001	164.85	< 0.001	9.83	< 0.001
	July of 2015 – June of 2016	115.94	< 0.001	133.04	< 0.001	31.75	< 0.001	76.39	< 0.001	48.38	< 0.001
Dom Macedo Costa x Cruz das Almas	July of 2014 – June of 2015	39.17	< 0.001	49.16	< 0.001	0.62	0.4329	145.19	< 0.001	2.69	0.1027
	July of 2015 – June of 2016	87.23	< 0.001	88.18	< 0.001	5.25	0.0223	0.21	0.6459	39.81	< 0.001
Dom Macedo Costa x Cachoeira	July of 2014 – June of 2015	125.72	< 0.001	157.08	< 0.001	0.52	0.4707	149.06	< 0.001	46.30	< 0.001
	July of 2015 – June of 2016	20.00	< 0.001	26.96	< 0.001	4.60	0.0322	12.41	< 0.001	0.15	0.7000
Muniz Ferreira x Cruz das Almas	July of 2014 – June of 2015	9.99	0.003	15.25	< 0.001	34.54	< 0.001	173.80	< 0.001	19.09	< 0.001
	July of 2015 – June of 2016	0.25	0.6169	0.00	0.9522	1.43	0.2321	67.47	< 0.001	105.61	< 0.001
Muniz Ferreira x Cachoeira	July of 2014 – June of 2015	26.41	< 0.001	37.87	< 0.001	71.63	< 0.001	133.56	< 0.001	13.44	< 0.001
	July of 2015 – June of 2016	11.24	< 0.001	9.01	0.0034	41.51	< 0.001	49.68	< 0.001	39.61	< 0.001
Cruz das Almas x Cachoeira	July of 2014 – June of 2015	68.02	< 0.001	79.04	< 0.001	0.56	0.4529	154.63	< 0.001	66.74	< 0.001
	July of 2015 – June of 2016	11.01	< 0.001	5.90	0.0178	13.26	< 0.001	13.77	< 0.001	41.30	< 0.001

$p < 0.05$ indicates statistical differences, using the Mardia-Watson-Wheeler (W) test.

3.3. *Effects of environmental variables and plant traits on phenology*

The MFA showed that the phenological responses of *D. nigra* were robust, with 75.37% of the variance explained [Dimension 1 (50.14%) + Dimension 2 (25.23%)] (Figure 6).

In terms of the vegetative phenophases of leaf flushing (LeafFlush) and leaf fall (LeafFall), was greater in places, and at times, with less precipitation (Rain), and in places with higher temperatures (Temp). The reproductive phenophases of *D. nigra* [the production of flower buds (Buds) and flowers (Flowers)] were observed to be more frequent in subpopulations growing in localities with less rainfall. Additionally, the productions of immature fruits (ImmatureF) were more frequent in subpopulations in which the plants showed greater growth (PlantH and TrunkH). Other environmental variables (photoperiod, soil type, vegetation type and elevation) and plant traits (crown diameters, DBH, trunk and crown shapes), did not evidence direct relationships with the vegetative and reproductive phenophases (Figure 6). It was notable that larger plants (plant and trunk heights, crown diameters, DBH) occurred at lower elevation sites, with higher temperatures (variable in the same quadrant) in less pedologically developed soils (Entisols and Ultisols), in Forest type vegetation (variables in opposite quadrants) (Figure 6).

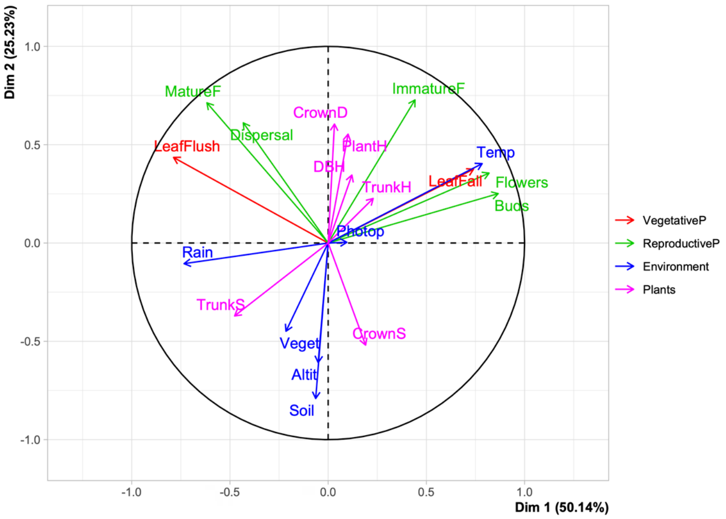

Figure 6. Multiple factorial analysis (MFA) of the environmental and plant variables (supplementary) as well as the phenophases of the four subpopulations (Cachoeira, Cruz das Almas, Dom Macedo Costa and Muniz Ferreira) of *Dalbergia nigra* (Vell.) Allemão ex Benth, Fabaceae for 24 months (July/2014 through June/2016), Bahia State, Brazil. Where: Rain = Rainfall, Photop = Photoperiod, Temp = Mean temperature, Soil = Soil type, Altit = Altitude, Veget = Vegetation type, CrownD = Crown diameter, PlantH = Total plant height, TrunkH = Trunk height, DBH = Diameter at breast height, CrownS = Crown shape, TrunkS = Trunk shape, LeafFlush = Leaf flushing, LeafFall = Leaf fall, MatureF = Mature fruits, ImmatureF = Immature fruits. VegetativeP = Vegetative phenophases, ReproductiveP = Reproductive phenophases.

4. DISCUSSION

Our results confirm the hypothesis that there would be phenological variations among the different study sites. Additionally, environmental (precipitation and temperature) and plant variables (PlantH and TrunkH) were found to affect the reproductive phenology of the species, and consequently its seed production potential. Studies concerning variations in phenological behavior within and among woody plant populations and their habitats can help to better understand their spatio-temporal variations as survival strategies in different environments (Goulart et al., 2005; Santos et al., 2020; Costa et al., 2021) and aid in elucidating how local abiotic factors and plant traits influence phenological patterns (Moraes et al., 2017; Neves et al., 2017; Santos et al., 2021).

Previous analyses of those same *D. nigra* subpopulations (growing in remnant areas of Atlantic Forest in the Recôncavo basin of Bahia State that had experienced intense fragmentation) evidenced aggregated spatial distribution patterns (Duarte et al., 2016a; Poelking et al., 2016); those anthropogenic disturbances were likewise recognized as causes of local microclimatic variations and edge effects that could modify plant growth and development and affect seed dispersal (Guariguata & Ostertag, 2001; Melo et al., 2006; Broadbent et al., 2008; Nève et al., 2008; Laurance et al., 2018).

The spatio-temporal variations in the phenologies of subpopulations growing in relatively nearby areas of fragmented forest habitats have only begun to be explored (Freire et al., 2013; Athayde & Morellato, 2014; Menezes et al., 2018). Marked leaf renewal activity was observed in our work, as both the fall and emission of new leaves occurred during the study period, with greater emission intensity in the months following rainy periods – a type of behavior observed in humid forests where abundant water availability allows greater leaf longevity (Seino, 2001). In the present research, environments with low climatic seasonality with no well-defined dry season evidenced continuous leaf formation, which allowed the maintenance of high photosynthetic rates throughout the year (Jackson, 1978; Wagner et al., 2016; Milani et al., 2021).

D. nigra also showed continuous leaf fall in individuals, with almost no variations between subpopulations, but with low intensity from November to April, months in which the lowest rainfall, a mechanism for water saving in plants where low moisture levels encourage leaf abscission to minimize the area of transpiration (Vilela et al., 2008; Toledo et al., 2012; Araújo et al., 2020). Pontara et al. (2016), studying *D. nigra* in a topographical gradient in the Atlantic Forest, observed new leaf buds at the beginning of the rainy season and leaf fall at the beginning of the dry season. That was partially in agreement with our results, as we observed continuous leaf flushing and leaf fall events, with an increase under the same conditions.

Light hydric stress can stimulate abscisic acid production by the roots and increase intracellular concentrations of soluble carbohydrates, amino acids, and proline to prevent deleterious drought effects (Tuteja, 2007; O'Brien & Benková, 2013; Rademacher, 2015; Ferchichi et al., 2018; Chong et al., 2019). In some species, those changes are responsible for initiating flowering and reproduction (Sandip et al., 2015). There was strong seasonality in flowering (floral buds and flowers), which was distributed from August to January in the first year and September to March in the second, periods of low rainfall and increased temperature. The seasonal flowering pattern (Newstrom et al., 1994) observed during the two periods studied occurred with variations in mean dates among the subpopulations.

The alternation of flowering among plants in the same subpopulation in different years can produce seeds with genetically distinct constitutions, with different parental contributions to gene flow that could avoid endogamic depression. *D. nigra* individuals in small remnant populations show high genetic variation (Ribeiro et al., 2005; Silva-Júnior et al., 2020), so that the intra- and inter-subpopulation variations of flowering and fructification may be considered strategies to avoid endogamic depression, which will be important for seed production by native Brazilian forests species, especially within a scenario of global climate change. The strategy of alternating flowering in different individuals within a subpopulation must be considered in seed production programs, as harvesting from different plants during different periods could improve access to the genetic diversity of those subpopulations (Huenneke, 1991; Gaudinier & Blackman, 2020).

Immature fruits occurred throughout the year in the subpopulations, and fruit dispersal was seasonal in the period before the rains – with moisture conditions favorable to subsequent seed germination (Poschlod et al., 2010; Morellato et al., 2016; Mendoza et al., 2017; Mendoza et al., 2018; Novaes et al., 2020) varying among subpopulations depending on the location of each parent tree. We observed that the trees on the forest fragment edges (or close to those edges) produced more fruits than those growing in the forest interior, which may be due to trees along the forest edges receiving greater incidences of light and higher temperatures than those in the forest interior (where there is greater shading and competition) (Laurance et al., 2018). The characteristics that improve stomatal conductance and photosynthetic performance in *D. nigra* (high stomatal densities and high percentages of leaf area occupied by stomatal pores that improve CO_2 uptake) were usually found in plants growing under full sunlight (Boardman, 1977; Mendes et al., 2001; Moreira et al., 2014).

We also observed that the ripening period of *D. nigra* fruits was relatively long (between 6 and 7 months), with greater mature fruit intensities in the months of May and January (coinciding with the period of lower temperatures), and that dispersal coincided with the beginning of the dry season with temperature increases – providing ideal conditions for fruit drying (Poschlod et al., 2010; Novaes et al., 2020). In light of the superpositioning of the phenophases of immature and mature fruits in the subpopulations, the harvesting of *D. nigra* seeds must be undertaken at more than one moment in the same subpopulation.

During the phenophase of fruit ripening, between July and January, it is possible to find dispersed fruits, which represent potential losses of fruits/seeds before active harvesting takes place. Fruit production intensity was generally close to 15%, which reveals limitations of the fruit production potential of the subpopulations (Duarte et al., 2016b), with variations in fruit production between consecutive years representing a limiting factor for commercial seedling production (Carvalho, 2003). Additionally, the fruits have low numbers of seeds (from 1 to 3 each) (Braz et al., 2009; Silva & Costa, 2014). As such, the data evidence limitations for Planaveg Reforestation Programs, given its projection for planting 12 million hectares (Brasil, 2017) and the UN proposal for the Decade of Restoration (2021-2030) (WRI Brasil, 2021).

5. CONCLUSIONS

Variations were observed among the subpopulations of *D. nigra* in terms of phenological trait intensities and the average dates of their reproductive events, with indirect effects of environmental conditions on plant growth that can affect the initial reproductive potentials of the floral buds, flowers, and fruits. Spatio-temporal phenological variations in *D. nigra* populations have not been previously recorded, with our results demonstrating the importance of undertaking phenological studies in different locations.

As immature fruits remain on the plants for many months (7-8), it was not possible to establish a clear relationship between the formation of mature fruits and dispersal, with those phenomena occurring during periods of reduced precipitation and at the beginning of the rainy season. As fruit (and seed) production are concentrated in just a few individuals of *D. nigra* at any given time, attention must be paid to guaranteeing genetic variability when producing seedlings for reforestation purposes, as those seeds may originate from half-sibling plants. There will always be limitations on seed production, however, as the production of mature fruits in *D. nigra* did not exceed 50% in the various subpopulations. In addition to the restricted gene flow caused by population fragmentation, the low intensity production of fruits and seeds by *D. nigra* problematizes the potential harvesting of its seeds. Considering the limitations facing the production of native seeds, it is possible that we will not have sufficient supplies to meet target demands in the immediate future, especially if reforestation actions are not properly and immediately executed. That reality reveals the importance of actively conserving the remaining subpopulations of the species and the need for proactive measures that would allow the expansion of *D. nigra* to other areas and thus reduce its vulnerability.

ACKNOWLEDGEMENTS

We thank FAPESB-SECTI-BA for the financial support (Termo de Outorga RED0012/2013) and to Biologist Samuel Pereira da Silva for his assistance in data collection.

SUBMISSION STATUS

Received: 6 Jan. 2022
Accepted: 7 Jun. 2022
Associate editor: Geângelo Calvi

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