

Vegetative and reproductive phenology of *Copaifera langsdorffii* Desf. in different phytophysionomies

Fenologia vegetativa e reprodutiva de *Copaifera langsdorffii* Desf. em diferentes fitofisionomias

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Abstract

The phenology has been discussed according to climatic variations and the environmental characteristics of each physiognomy, trying to identify if there is variation in the vegetative and reproductive phenophases, for *Copaifera langsdorffii* Desf. in areas of the Cerradão, Carrasco and Humid Forest, Chapada do Araripe in Northeast Brazil and if they are correlated with seasonality. Monthly observation censuses were conducted on 10 individuals from each area from January 2019 to December 2020. The continuous, sub-annual, annual, and supra-annual classes were taken into account. The intensity and synchrony of individuals were evaluated, and seasonality was tested using Spearman's correlation with local weather variables. The species presented a semi-deciduous vegetative phenological strategy, with peaks occurring mainly at the end of the rainy season and the beginning of the dry season. The flowering pattern of *C. langsdorffii* was considered annual and seasonal, because flowering occurred at similar periods in the three areas, with peaks in December and January. Fructification occurred annually, with seasonality only in the phytophysionomy of the Cerradão. *C. langsdorffii* bore fruit during the rainy season in the Cerradão, Carrasco and Humid Forest, with the exception only of 2020 in the Carrasco and Humid Forest, where individuals bore fruit during both

the rainy and dry seasons. According to the correlation results, precipitation, temperature, and humidity shape the reproductive patterns of *C. langsdorffii*, which may also occur in populations of this species in other environments.

Keywords: Chapada do Araripe; Fabaceae; Flowering and fruiting pattern; Seasonality.

Resumo

A fenologia tem sido discutida de acordo com as variações climáticas e as características ambientais de cada fisionomia, procurando identificar se há variação nas fenofases vegetativa e reprodutiva, para *Copaifera langsdorffii* Desf. em áreas do Cerradão, Carrasco e Mata Úmida, Chapada do Araripe no Nordeste do Brasil e se estão correlacionadas com a sazonalidade. Foram realizados censos mensais de observação em 10 indivíduos de cada área de janeiro de 2019 a dezembro de 2020. Foram consideradas as classes contínua, subanual, anual e supraanual. A intensidade e sincronia dos indivíduos foram avaliadas e a sazonalidade foi testada por meio da correlação de Spearman com variáveis climáticas locais. A espécie apresentou estratégia fenológica vegetativa semidecídua, com picos ocorrendo principalmente no final da estação chuvosa e início da estação seca. O padrão de floração de *C. langsdorffii* foi considerado anual e sazonal, pois a floração ocorreu em períodos semelhantes nas três áreas, com picos em dezembro e janeiro. A frutificação ocorreu anualmente, com sazonalidade apenas na fitofisionomia do Cerradão. *C. langsdorffii* frutificou durante a estação chuvosa no Cerradão, Carrasco e Mata Úmida, com exceção apenas de 2020 no Carrasco e Mata Úmida, onde os indivíduos frutificaram durante as estações chuvosa e seca. De acordo com os resultados de correlação, precipitação, temperatura e umidade moldam os padrões reprodutivos de *C. langsdorffii*, o que também pode ocorrer em populações desta espécie em outros ambientes.

Palavras-chave: Chapada do Araripe; Fabaceae; Padrão de floração e frutificação; Sazonalidade.

Resumen

Se ha discutido la fenología según las variaciones climáticas y las características ambientales de cada fisionomía, tratando de identificar si existe variación en las fenofases vegetativa y reproductiva, para *Copaifera langsdorffii* Desf. en áreas del Cerradão, Carrasco y Selva Húmeda, Chapada do Araripe en el Nordeste de Brasil y si se correlacionan con la estacionalidad. Se realizaron censos de observación mensuales a 10 individuos de cada zona desde enero de 2019 hasta diciembre de 2020. Se tomaron en cuenta las clases continua, subanual, anual y supraanual. Se evaluó la intensidad y sincronía de los individuos y se probó la estacionalidad mediante la correlación de Spearman con las variables climáticas locales. La especie presentó una estrategia fenológica vegetativa semidecidual, con picos ocurriendo principalmente al final de la estación lluviosa e inicio de la estación seca. El patrón de floración de *C. langsdorffii* se consideró anual y estacional, debido a que la floración ocurrió en períodos similares en las tres áreas, con picos en diciembre y enero. La fructificación ocurrió anualmente, con estacionalidad solo en la fitofisionomía del Cerradão. *C. langsdorffii* fructificó durante la estación lluviosa en el Cerradão, Carrasco y Selva Húmeda, con excepción solo de 2020 en Carrasco y Selva Húmeda, donde los individuos fructificaron tanto en la estación lluviosa como en la seca. De acuerdo con los resultados de la correlación, la precipitación, la temperatura y la humedad dan forma a los patrones reproductivos de *C. langsdorffii*, que también pueden ocurrir en poblaciones de esta especie en otros ambientes.

Palabras clave: Chapada do Araripe; Fabáceas; Patrón de floración y fructificación; Estacionalidad.

1. Introduction

Phenology is the major component of plant fitness (O'Neil, 1997) and knowledge of plant phenology is critical to understanding community and population dynamics, since season, duration, and degree of synchronism of the various phenological phases have strong implications for plant structure, functioning, and regeneration, as well as the quality and quantity of resources available to consuming organisms (Williams et al., 1999). Phenology represents the process of active selection in which different resource allocation strategies at the various stages of the life cycle provide different rates of reproductive success and not a random adjustment of plants to environmental changes (Sarmiento & Monasterio, 1983).

Phenology is a science that has assumed high importance in recent decades as a measure to study the impacts of climate change on plant species (Silva et al., 2020). As such, phenology is a good indicator of environmental changes such as variations in temperature, precipitation, and relative humidity, as it is strongly influenced by these changes (Cleland et al., 2007; Mendoza et al., 2017; Pau et al., 2011; Wolkovich & Cleland, 2014), as well as by the genetic character of the species (Kozlov et al., 2019).

As the climate warms and weather patterns change, modern biology seeks to quantify the effects of these changes on plants (Pau et al., 2011) as they induce changes in the development (Burrows et al., 2011; Parmesan, 2007) and reproduction of

many plant species. The effects of such changes on plants occur in events such as bud production, flowering, and onset of senescence, advancing or delaying them according to the conditions to which they are exposed (Ellwood et al., 2019).

In addition to the relationship with climate change, the knowledge and understanding coming from phenological studies of tree species in natural ecosystems are of basic interest in ecological research on biodiversity, productivity and community organization and on the interactions of plants with fauna, as well as also being of great importance in programs for conservation of genetic resources, forest management and planning of wilderness areas (Camacho & Orozco, 1998; Mendoza et al., 2017; Morellato et al., 2013; Talora & Morellato, 2000).

Phenology naturally varies across years and locations, leading to interannual variation in the relative timing of species interactions (Høye & Forchhammer, 2008; Rudolf, 2018; Thackeray et al., 2016) and this variation tends to increase with climate change (Pearse et al., 2017). Recent studies indicate that even small changes in the timing of species interactions can result in substantial changes in the outcome of species interactions (Alexander & Levine, 2019; Cleland et al., 2015; Godoy & Levine, 2014; Murillo-Rincón et al., 2017; Rasmussen et al., 2014; Rudolf, 2018; Stier et al., 2013; Young et al., 2015).

Plants have a broad plasticity in their ecological behavior due to architectural characteristics (Sposito and Santos, 2001) and allometric patterns particular to the environmental situation, which promotes a large morphological spectrum to achieve adaptive success and colonize different ecosystems (Costa et al., 2012).

The evolutionary explanations for the adaptive success of plant species in different environments, according to Niklas (1994), are: efficiency in light interception and resource utilization, mechanical stabilization, and the ability to reproduce in the site. Several biological characteristics define the competitive ability of plants to perpetuate in different physiognomies (Costa et al., 2012). A minimal morphological nuance in certain species can provide sufficient fitness for them to develop environmental plasticity (Costa et al., 2012).

Copaifera langsdorffii (Fabaceae) is a tropical tree species widely distributed in South America (Carvalho, 2003). In Brazil, it occurs in the Caatinga, Cerrado, Carrasco, Atlantic Forest and Amazon biomes (Fagundes, 2014), when adults reach a height of 2-35 m, depending on environmental conditions (Costa et al., 2012, 2016) This species has great medicinal potential, being of great importance for communities, and is indicated for the treatment of various diseases (Macêdo et al., 2018; Pasa et al., 2005; Ribeiro et al., 2014; Saraiva et al., 2015; Veiga and Pinto, 2002).

Copaifera langsdorffii is generalist (Oliveira-Filho and Fontes, 2000) because it has a wide distribution and occupation in different environments (Laboriau, 1966). The plasticity maybe reflected in changes in the patterns of the species' population forms, according to the environmental conditions existing during its colonization in the phyto-physiognomies (Costa et al., 2012).

Phenological studies lead to a better understanding of plant behavior, with a correlation with changes in the biotic and abiotic environment, covering the seasonal patterns of flowering, fruiting and leaf change (Vilela et al., 2008). Studies focusing on the characterization of plant phenophases are indispensable for understanding the dynamics of plant populations, functioning as indicators of plant responses to local climatic and edaphic conditions (Medeiros et al., 2016; Vieira and Carvalho, 2009).

Phenology has been discussed as a function of climatic variations and environmental characteristics of each physiognomy, seeking to answer the following questions: (i) does *C. langsdorffii* flower and fruit seasonally in the Cerradão, Carrasco and Humid Forest? (ii) does the species present variation in the vegetative and reproductive phases when analyzed in different phyto-physiognomies? (iii) does the vegetative and reproductive phenology of the species, according to physiognomy, correlate with climate seasonality? In order to understand the phenological variations of plant species in different types of environments, this study aims to analyze the vegetative and reproductive phenology (flowering and fruiting)

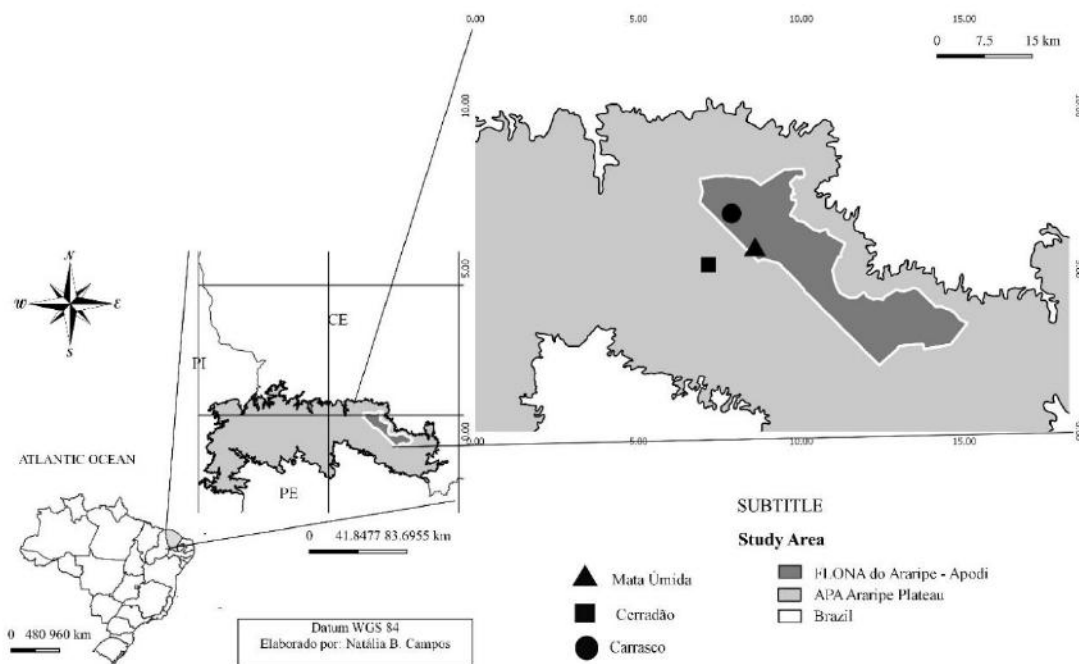
of *C. langsdorffii* in the Cerradão, Carrasco and Humid Forest physiognomic forms in the Chapada do Araripe region in northeastern Brazil.

2. Material and Methods

2.1 Area of Study

The research was carried out in the Araripe National Forest, in areas of Cerradão (39°W 35' 08" 7S 20' 36"), Carrasco (39°W 33' 47" 7S 15' 35") and Humid Forest (39°W 31' 46" 7S 18' 42") (Fig. 1), situated in the municipality of Crato, Ceará, Brazil. Located within the Caatinga domain in northeastern Brazil, the Chapada do Araripe encompasses the states of Ceará, Pernambuco and Piauí and has a tabular surface, with altitude ranging from 700 m to 1000 m.

Figure 1. Geographic location of the study areas in Chapada do Araripe, Ceará, Brazil.



Source: Authors.

The predominant soils are red-yellow ferralsols, litholic neosols, and red-yellow acrisols. Due to this mosaic, there are various phyto-physiognomies and different environmental gradients throughout the area of the plateau (IPECE, 2016; Oliveira & Barbosa, 2019; Souza & Oliveira, 2006). The ferralsols are present at the top of the plateau, being deep and of low fertility, with Cerrado, Cerradão, and Carrasco vegetation cover. The neosols cover the sides and slope areas, being very shallow and stony soils of low fertility, presenting a transition belt from the Subperenifolia Forest (Ombrophilous Forest) to the Hypoxerophilous Caatinga. Finally, the acrisols are located in the middle to lower parts, being shallow soils that have high fertility and vegetation consisting of the Subperenifolia Forest and Hypoxerophilous Caatinga (Souza & Oliveira, 2006).

In the Chapada do Araripe there is a significant source of raw material for the extraction of plant resources by local traditional communities; their economic activities include the harvesting of timber and non-timber products, mainly for trade, as well as agriculture and livestock (MMA, 2004). Notable among the natural products extracted are *Caryocar coryaceum* Wittm., *Dimorphandra gardneriana* Tul., *Himatanthus drasticus* (Mart.) Plumel, *Stryphnodendron rotundifolium* Mart. and *C. langsdorffii*, which are used for their fruits, latex, bark and resin oil mainly for medicinal purposes and informal trade (MMA, 2004).

2.2 Data Collection

2.2.1 Phenological observations

Thirty adult individuals of *C. langsdorffii* were randomly selected and marked, 10 in the Cerradão area, 10 in the Carrasco and 10 in the Humid Forest in the Chapada do Araripe. Individuals were marked during walks in the three phyto-physiognomies with good visibility of the crown and a minimum height of 5 m as inclusion criteria, and which presented Diameter at Breast Height (DBH) ≥ 21 and ≤ 150 and Diameter at Base ≥ 26 and ≤ 140 centimeters. Monthly phenological observations were conducted from January/2019 to December/2020, totaling 24 observations. The sampled individuals were numbered and marked with identification plates to facilitate their location in the field.

2.2.2 Collection of material and botanical identification

Copaifera langsdorffii was collected in the three study areas (Cerradão, Carrasco and Humid Forest) and taken to the Laboratory of Plant Ecology of the Regional University of Cariri. The collected material was placed in plastic bags and treated according to the usual herborization techniques (Mori et al., 1989). The testimonial material was incorporated into the collection of the Caririense Dárdano de Andrade-Lima Herbarium of the Universidade Regional do Cariri (HCDAL/URCA) registered as N° 14.312 (Cerradão), N° 14.313 (Carrasco) and N° 14.314 (Humid Forest).

2.2.3 Obtaining meteorological data

Precipitation data for the years 2019 and 2020 were acquired by the Ceará Meteorology and Water Resources Foundation (FUNCEME) referring to the Lameiro post in the city of Crato, Ceará, which is located 12.4 km from the Humid Forest area, 20.4 km from the Cerradão and 24.4 km from the Carrasco (FUNCEME, 2021). The temperature and relative humidity data for the years 2019 and 2020 were obtained from the National Institute of Meteorology (INMET) referring to the weather station of the City of Barbalha, Ceará (INMET, 2021).

2.3 Data Analysis

2.3.1 Analysis of phenological data

The occurrence of vegetative and reproductive phenophases was qualitatively evaluated from direct observation of the marked plants, where the presence or absence of a phenophase was recorded (Bencke & Morellato, 2002). In this study, the presence of floral buds and open flowers was considered as flowering period and the presence of green and ripe fruits as fruiting period.

In relation to vegetative phenological events, the classes Deciduous (if losing leaves completely for periods longer than one month) and Semi-deciduous (if producing new leaves before or together with the loss of the old leaves, so that when the old leaves fall, the tree already has new or mature leaves) were considered (Araújo & Haridasan, 2007; Franco et al., 2005; Lenza & Klink, 2006).

To verify the frequency patterns of flowering and fruiting, the classification proposed by Newstrom *et al.* (1994) was used where four classes are considered: 1) continuous (throughout the year, with little or no interruption); 2) subannual (more than one event per year); 3) annual (one event per year); 4) supra-annual (events at intervals of two or more years).

The methodology of Newstrom *et al.* (1994) was also used to analyze how much each phenophase was expressed in a period of time, that is, the time span, in months, of each vegetative or reproductive event, recognizing three distinct classes: 1) short - phenophases lasting up to one month; 2) intermediate - phenophases lasting 2 to 5 months; and 3) long - phenophases lasting 6 months or more.

In relation to synchrony, which corresponds to the proportion of individuals sampled that are manifesting a particular phenological event, the methodology adopted was that of Bencke and Morellato (2002), with < 20% considered asynchronous, from 20% to 60% slightly synchronous and > 60% with high synchrony.

Two evaluation methods were applied to the collected data. The first method, Fournier's Percent Intensity, proposed by Fournier (1974), values obtained in the field using a semi-quantitative interval scale of five categories (0 to 4) and a 25% interval between each category (0 = 0%; 1 = 1 to 25%; 2 = 26 to 50%; 3 = 51 to 75% and 4 = 76 to 100%) enabled an estimate of the percentage intensity of the phenophase in each individual. In each month, the intensity values obtained for all individuals of each species are totaled and divided by the maximum possible value (number of individuals multiplied by four).

The value obtained, which corresponds to a proportion, is then multiplied by 100 to transform it into a percentage value. The second method, Activity Index (or percentage of individuals), is considered simpler, in which only the presence or absence of the phenophase in the individual is verified, without estimating intensity or quantity Fournier (1974). This method of analysis has a quantitative character at the population level, indicating the percentage of individuals of the population that are manifesting a certain phenological event. This method also estimates the synchrony between individuals of a population (Morellato et al., 1990), taking into account that the greater the number of individuals manifesting the phenophase at the same time, the greater the synchrony of this population.

2.3.2 Statistical Analysis

Circular histograms were drawn with the frequency distributions to check for seasonality in the expression of the vegetative and reproductive phenophases. Based on the circular statistics, the months were transformed into angles at 30° intervals and then the following were calculated: the average angle or mean date (μ), the concentration of the event around this date (r) and the circular standard deviation (dp). The average angle (μ) is the period around which a particular phenophase was recorded in the majority of individuals (Silveira et al., 2013).

Rayleigh's test (z) was used to determine the significance of the average angle; when it shows significance, it indicates seasonality in the phenophase. The intensity of concentration around the average angle, indicated by r , varies from 0 (phenological activity evenly distributed throughout the year) to 1 (phenological activity concentrated in a period of the year). Was used the program ORIANA 4.02 (Kovach, 2013).

To identify which abiotic factors: precipitation (mm), temperature (°C) and relative humidity (%) were correlated with the onset of vegetative and reproductive phenophases, the relationship of these variables was tested with the activity and intensity of each of the phenophases using Spearman's Correlation test (r_s) in BIOESTAT 5.0 software (Ayres et al., 2007).

3. Results

3.1 Presence of Leaves

The species studied presented a semi-deciduous vegetative phenological strategy, that is, all the individuals sampled remained with leaves throughout the study, varying only in the intensity of this phenophase. Thus, the only analysis of the circular statistics available was the Mean Vector (μ), equal to 248.199° for the Cerradão, Carrasco and Humid Forest areas for both years analyzed (Table 1). There was no correlation with the Activity Index (Table 2).

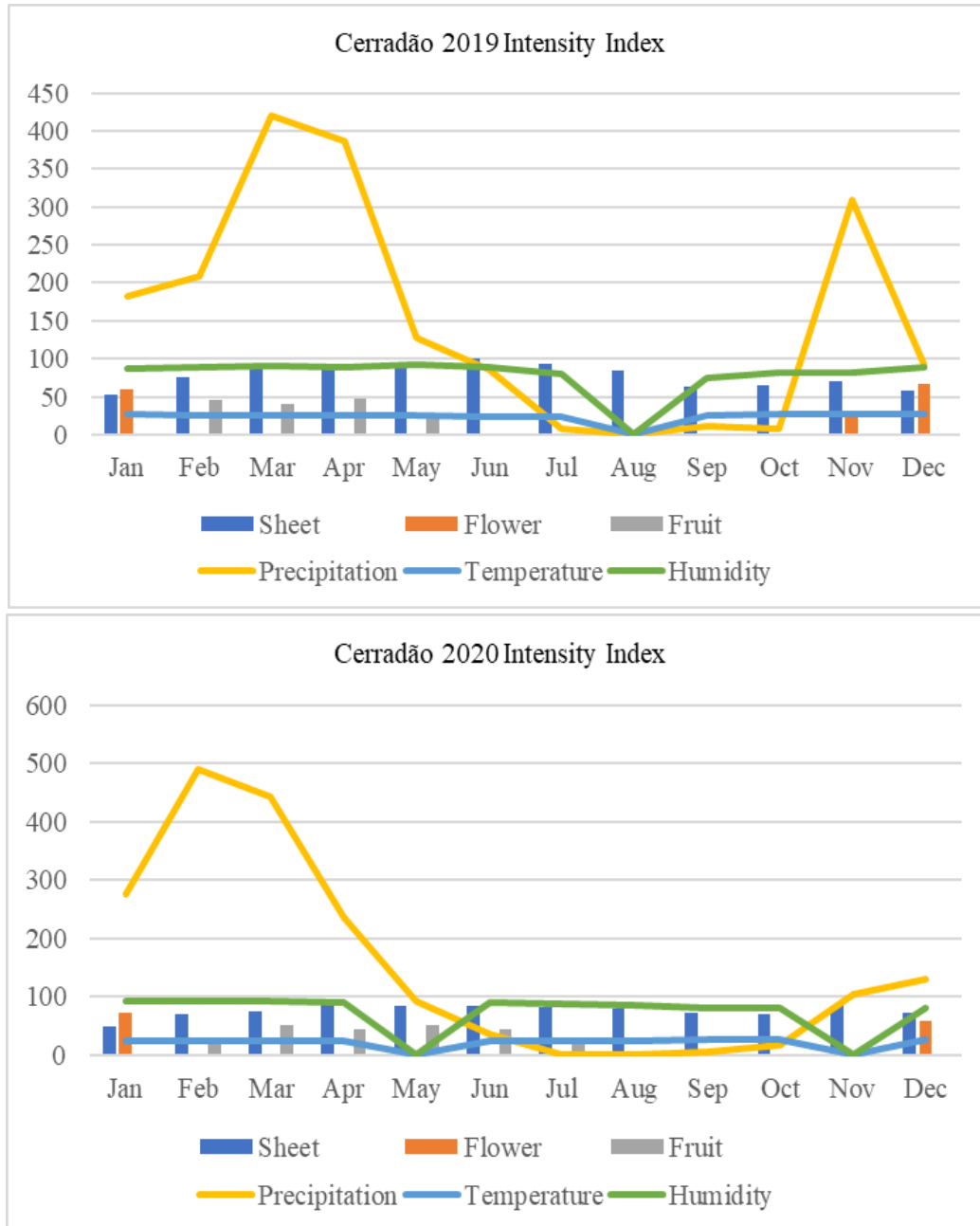
For the Intensity Index, the Cerradão showed significant negative correlation with temperature for 2019 ($r_s = -0.69$; $p = 0.0117$) and 2020 ($r_s = -0.74$; $p = 0.0052$) (Table 3). The intensity peaks in this area occurred in June/2019 (100%) and April/2020 (87.5%) which corresponds to the beginning of the dry period and end of the rainy period in the region (Figure 2).

In the Carrasco the Intensity Index showed significant positive correlation in 2019 with humidity ($r_s = 0.68$; $p = 0.0134$) and in 2020, significant negative correlation with temperature ($r_s = -0.67$; $p = 0.0155$) (Table 3). The highest intensity

peaks in the Carrasco corresponded to the months of May/2019 (97.5%) and April/2020 (82.5%) during which the rains are already ceasing, indicating the end of the rainy season (Figure 3).

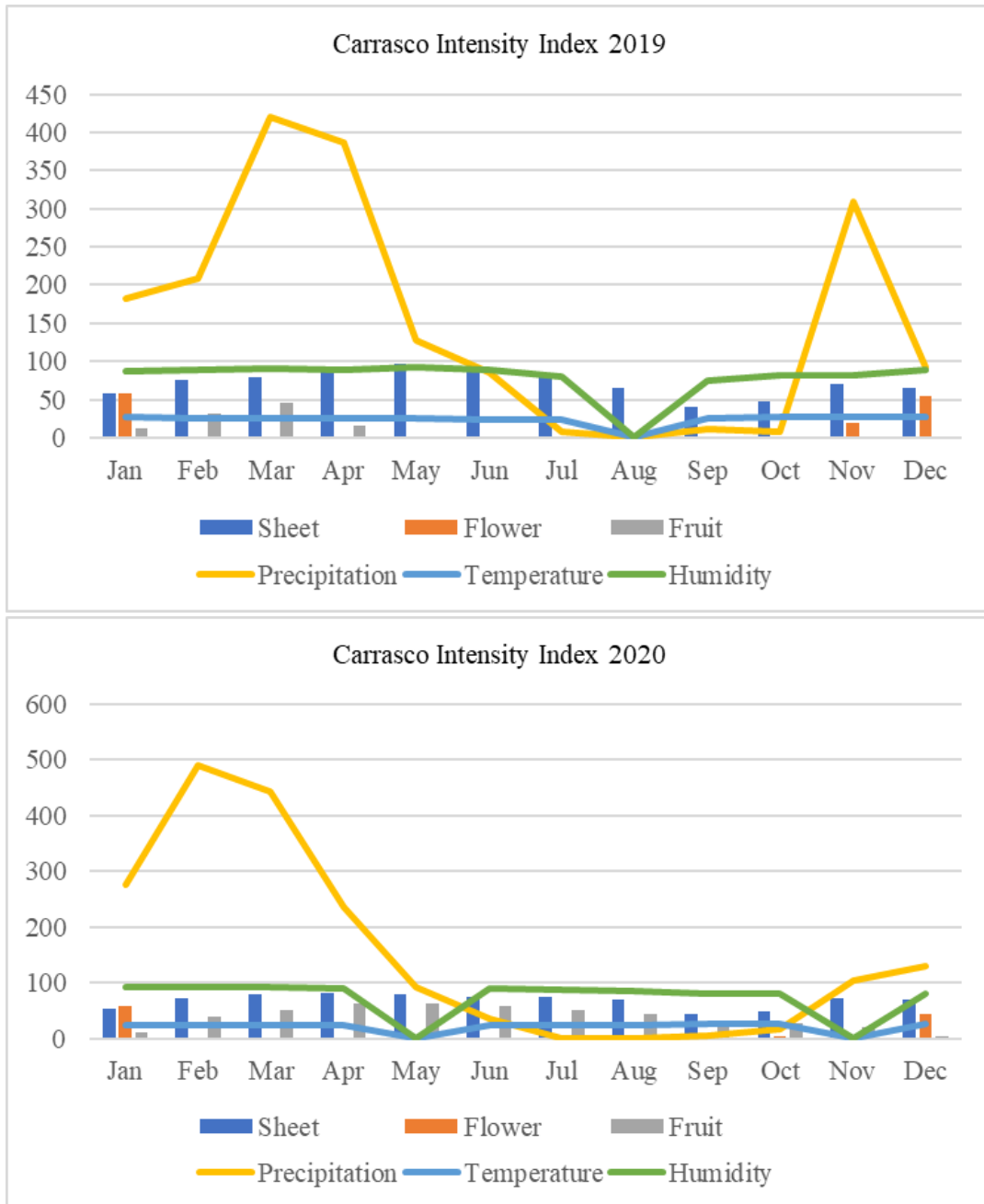
In the Humid Forest, a significant negative correlation occurred for the Intensity Index in 2019 with temperature ($r_s = -0.63$; $p = 0.0277$) (Table 3) (Figure 4). In the Humid Forest, the highest intensity peaks occurred in July/2019 (97.5%) and August/2020 (90%), which corresponds to the beginning of the dry period in the region (Figure 4).

Figure 2. Cerradão Phytophysiology: Intensity Index for Precipitation, Temperature and Humidity in the years 2019 and 2020, Northeastern Brazil



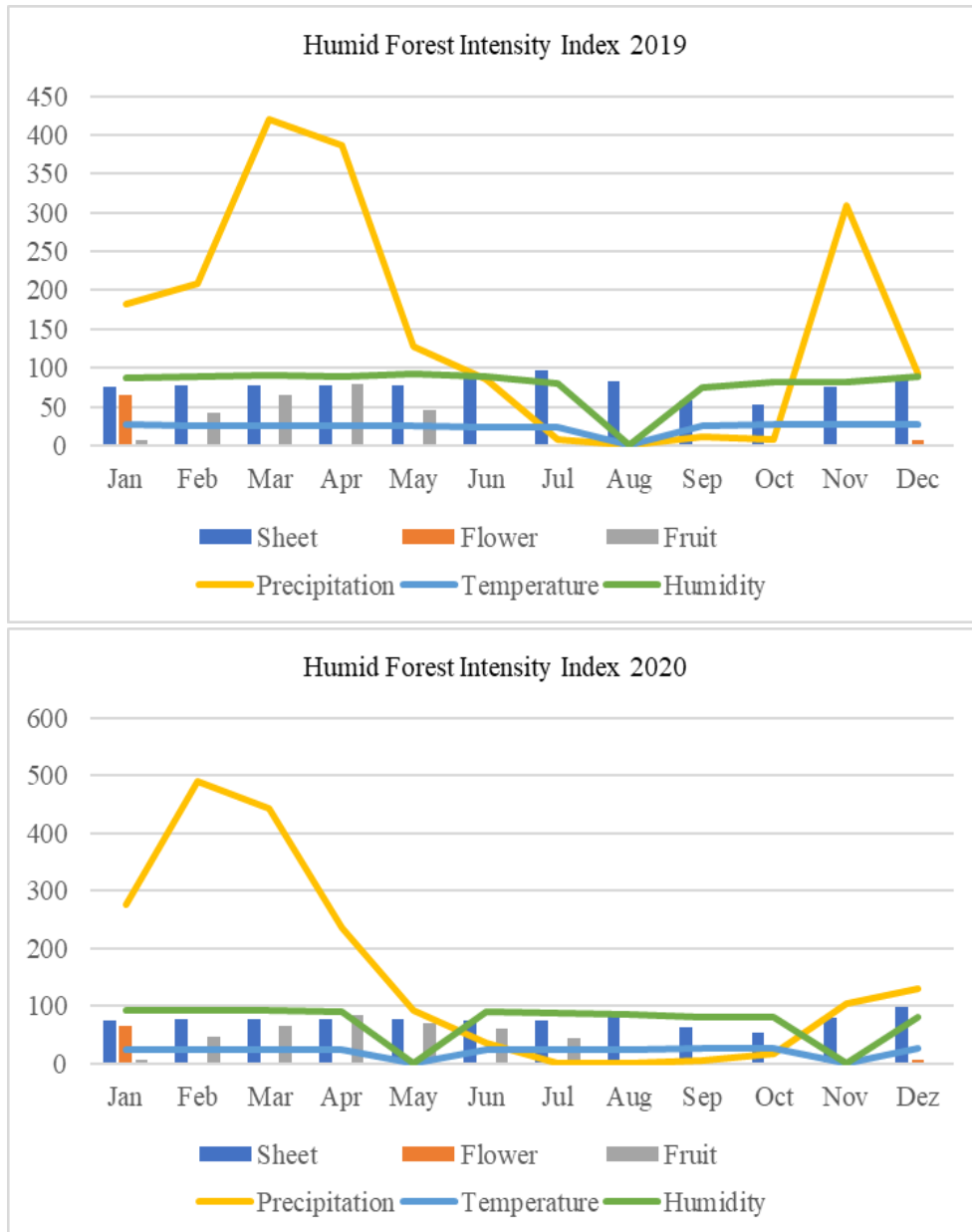
Source: Authors.

Figure 3. Carrasco Phytophysiology: Intensity Index for Precipitation, Temperature and Humidity in the years 2019 and 2020, Northeastern Brazil.



Source: Authors.

Figure 4. Phytophysiology Humid Forest: Intensity Index for Precipitation, Temperature and Humidity in the years 2019 and 2020, Northeastern Brazil.



Source: Authors.

Table 1: Circular statistical analyzes for the occurrence of seasonal patterns of vegetative and reproductive phenophases for *Copaifera langsdorffii* Desf. in phytophysionomies of Cerradão, Carrasco and Mata Úmida, Northeastern Brazil.

	Sheet Presence						Flower Presence						Presence of Fruits					
	Cerradão		Carrasco		Humid Forest		Cerradão		Carrasco		Humid Forest		Cerradão		Carrasco		Humid Forest	
	2019	2020	2019	2020	2019	2020	2019	2020	2019	2020	2019	2020	2019	2020	2019	2020	2019	2020
Number of Observations	120	120	120	120	120	120	25	21	21	20	10	10	25	40	25	76	37	46
Mean Vector (μ)	248,1	248,1	248,1	248,1	248,1	248,1	336,2	347,0	335,8	342,8	357,0	357,0	65,10	109,9	31,9	162,8	73,17	88,29
	99°	99°	99°	99°	99°	99°	06°	22°	88°	24°	99°	99°	4°	09°	18°	08°	9°	5°
Length of Mean Vector (r)	0	0	0	0	0	0	0,925	0,954	0,928	0,931	0,988	0,988	0,823	0,585	0,87	0,178	0,821	0,731
Median							330°	0°	330°	330°	0°	0°	60°	120°	30°	150°	60°	90°
Rayleigh Test (p)							0,005	1,37E-08	0,000	0,000	< 1E-12	< 1E-12	0,000	0,000	8,51E-09	9,00E-02	4,63E-11	3,58E-11

(p)<0,001. Source: Authors.

Table 2: Spearman correlation (r_s) considering the Activity Index between abiotic factors and the vegetative and reproductive phenophase of *Copaifera langsdorffii* Desf.

Phenophase	Phytophysiognomy	2019						2020						
		Precipitation		Temperature		Humidity		Precipitation		Temperature		Humidity		
		r_s	p	r_s	p	r_s	p	r_s	p	r_s	p	r_s	p	
Sheet	<i>Cerradão</i>	-	-	-	-	-	-	-	-	-	-	-	-	
	<i>Carrasco</i>	-	-	-	-	-	-	-	-	-	-	-	-	
	Humid Forest	-	-	-	-	-	-	-	-	-	-	-	-	
Activity Index	Flower	r_s	p	r_s	p	r_s	p	r_s	p	r_s	p	r_s	p	
		<i>Cerradão</i>	0,221	0,4901	0,6122*	0,0343	-0,0691	0,8311	0,5534*	0,0619	0,4888	0,1067	0,2675	0,4006
		<i>Carrasco</i>	0,2111	0,5101	0,615*	0,0333	-0,0643	0,8427	0,1931	0,5476	0,662*	0,019	-	0,8203
Fruit	Humid Forest													
		<i>Cerradão</i>	0,0753	0,8162	0,3817	0,2208	-0,0054	0,9868	0,3339	0,2888	0,4416	0,1506	0,0969	0,7644
		r_s	p	r_s	p	r_s	p	r_s	p	r_s	p	r_s	p	
Fruit	<i>Carrasco</i>													
			0,6429*	0,0241	-0,0672	0,8355	0,7522*	0,0048	0,351	0,2632	-0,533	0,0743	0,458	0,1343
			0,6632*	0,0187	0,2002	0,5327	0,4254	0,1679	-0,3739	0,2311	-0,4121	0,1831	0,2595	0,4154
Fruit	Humid Forest													
			0,7216*	0,008	-0,0239	0,9412	0,7614*	0,004	0,3605	0,2496	-0,4735	0,1199	0,5632	0,0565

* Significant results ($p \leq 0.05$). Number of pairs 12. Source: Authors.

Table 3: Spearman correlation (rs) considering the Intensity Index between abiotic factors and the vegetative and reproductive phenophase of *Copaifera langsdorffii* Desf.

Phenophase	Phytophysiognomy	2019						2020						
		Precipitation		Temperature		Humidity		Precipitation		Temperature		Humidity		
		r _s	p	r _s	p	r _s	p	r _s	p	r _s	p	r _s	p	
Intensity Index	Sheet	<i>Cerradão</i>	0	ns	-	0,0117	0,331	0,2932	-0,2195	0,4931	-	0,0052	-	0,4307
					0,6972*				0,7469*		0,2513			
		<i>Carrasco</i>	0,3895	0,2107	-0,4561	0,136	0,6877*	0,0134	0,2963	0,3497	-	0,0155	0,2399	0,4527
	Humid Forest	<i>Cerradão</i>	-0,2246	0,4827	-	0,0277	0,1426	0,6583	0,2622	0,4103	-0,264	0,407	-	0,7012
					0,6311*								0,1239	
		<i>Carrasco</i>	0,2295	0,4731	0,6058*	0,0368	-0,0734	0,8206	0,2292	0,4736	0,3772	0,2267	-	0,3831
	Flower	<i>Cerradão</i>	0,2111	0,5101	0,4222	0,1714	-0,0643	0,8427	0,5609*	0,0577	0,4781	0,1158	0,2942	0,3532
														0,2772
		<i>Carrasco</i>	0,0753	0,8162	0,3817	0,2208	-0,0054	0,9868	0,3339	0,2888	0,4416	0,1506	0,0969	0,7644
	Fruit	<i>Cerradão</i>	r _s	p	r _s	p	r _s	p	r _s	p	r _s	p	r _s	p
			0,6865*	0,0136	-0,0832	0,7971	0,6948*	0,0121	0,1641	0,6104	-	0,0377	0,3591	0,2516
		<i>Carrasco</i>	0,7406*	0,0059	0,1373	0,6705	0,5201*	0,083	-0,1107	0,7319	-	0,0523	0,1916	0,5509
	<i>Cerradão</i>	0,7486*	0,0051	-0,0468	0,8852	0,7174*	0,0086	0,4286	0,1644	-0,4504	0,1417	0,4504	0,1417	

Source: Authors.

3.2 Flowering

The flowering of *C. langsdorffii* was recorded for the Cerradão, Carrasco, and Humid Forest annually. Variation in the permanence of this phenophase was observed in each phyto-physiognomy, where the Cerradão showed an intermediate form (two to four months), the Mata Úmida a short one (one month), and the Carrasco a short and intermediate form among individuals (one to three months).

The Cerradão manifested this phenophase in November 2019 with 50% of individuals and in January and December/2019 with 100% (Figure 5A). In 2020 this phenophase occurred in January and December in all sampled individuals, manifesting high synchrony and in February at 10% (Figure 5B). The circular statistics show us that in 2019 and 2020 the Mean Vector (μ) is equal to 336.206° and 347.022° respectively, which indicates high activity between December and January. The length of Mean Vector (r) is equal to 0.925 and 0.954 respectively, representing high activity of the phenophase (Table 1).

The Median was 330° and 0° respectively, and the Rayleigh Test (p) equal to 0.005 and $1.37E-08$ respectively, showing seasonality for this phenological event only in the year 2019 (Table 1). Flowers showed significant positive correlation of the Activity Index in 2019 with temperature ($r_s = 0.61$; $p = 0.0343$) and in 2020 with precipitation ($r_s = 0.58$; $p = 0.045$) (Table 2) (Figure 6). So did the Intensity Index, with a significant positive correlation in 2020 with precipitation ($r_s = 0.5534$; $p = 0.0619$) (Table 3) (Figure 2). There was no significant negative correlation for this phyto-physiognomy in this phenophase (Table 1).

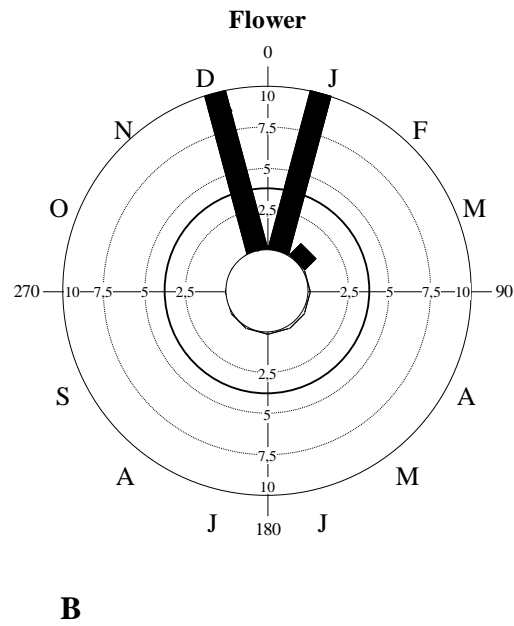
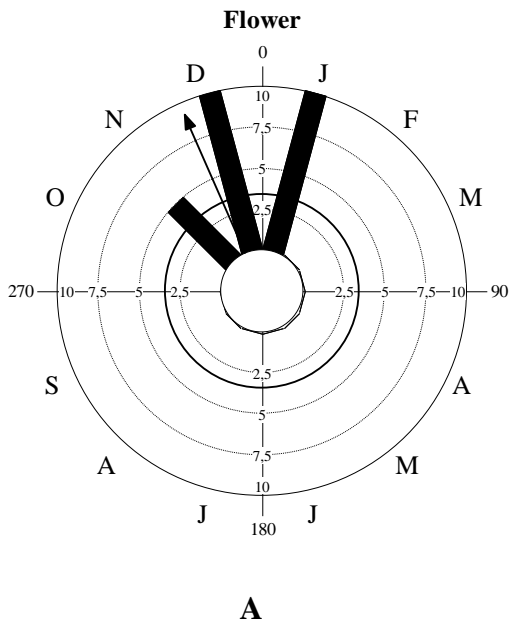
In the Carrasco the presence of flowering was recorded in January, November and December/2019 in 80%, 40% and 90% of individuals respectively (Figure 5C) and 2020 in January, October and December with 100%, 10% and 90% respectively (Figure 5D). The circular statistics show us that in 2019 and 2020 the Mean Vector (μ) was 335.888° and 342.824° respectively, which indicate activity between December and January (Table 1).

The Length of Mean Vector (r) was equal to 0.928 and 0.931 respectively, representing high phenophase activity (Table 1). The Median was 330° in both years studied and the Rayleigh Test (p) was equal to 0.0003 and 0.000003 respectively, showing seasonality for this phenological event in the two years of research (Table 1). Flowers showed significant positive correlation of Activity Index in 2019 and 2020 with temperature ($r_s = 0.61$; $p = 0.0333$ and $r_s = 0.66$; $p = 0.019$) (Table 2) (Figure 7). So did the Intensity Index, with a significant positive correlation in 2019 with temperature ($r_s = 0.60$; $p = 0.0368$) (Table 3) (Figure 3). There was no significant negative correlation for this phyto-physiognomy in this phenophase (Table 3).

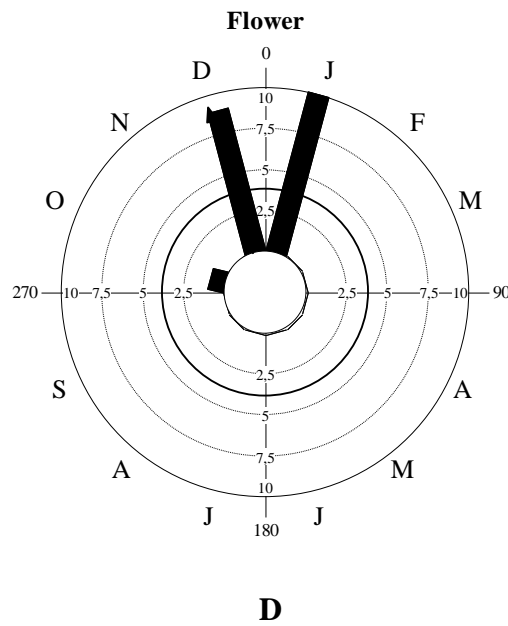
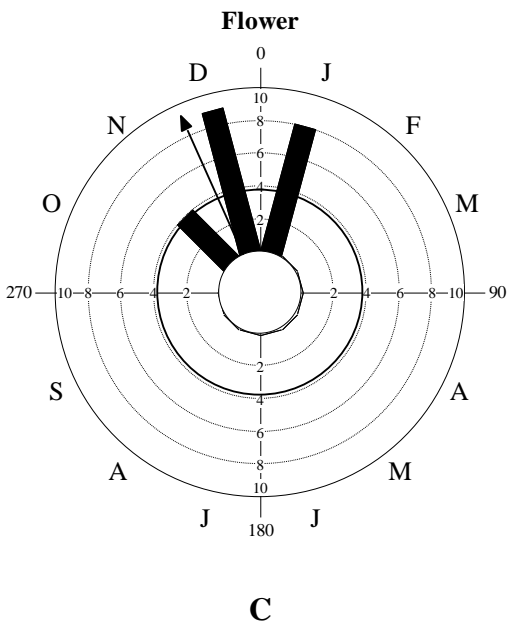
In the Humid Forest, flowering occurred for 2019 and 2020 in January (90%) and December (10%), with high synchrony in January for both survey years (Figure 5E and F). Circular data for 2019 and 2020 were equal, with Mean Vector (μ) equal to 357.099° , with high peak activity in January (Table 1). The Length of Mean Vector (r) was equal to 0.988, representing high phenophase activity (Table 1). The Median was 0° and the Rayleigh Test (p) was $< 1E-12$, showing that there was no seasonality for this phenological event in the two research years (Table 1). There were no significant values in Spearman's correlation either positive or negative for the Activity (Figure 8) and Intensity (Figure 4) Indices in 2019 and 2020 (Table 2 and 3).

Figure 5. Circular histograms of individual frequencies of peak flowering dates of *Copaifera langsdorffii* Desf. in areas of *Cerradão*, *Carrasco* and Humid Forest in Chapada do Araripe, Northeastern Brazil. The bars represent the frequencies of individuals with phenophase for the two years of observation (January 2019 to December 2020). The arrow points to the average date (mean angle) and the arrow length corresponds to the r value (degree of seasonality), ranging from 0 to 1. For details of the analysis, see Table 1.

A - Flower *Cerradão* 2019
 B - Flower *Cerradão* 2020

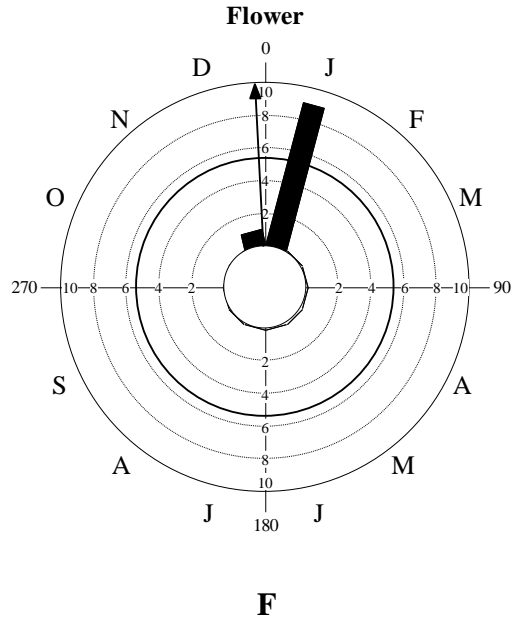
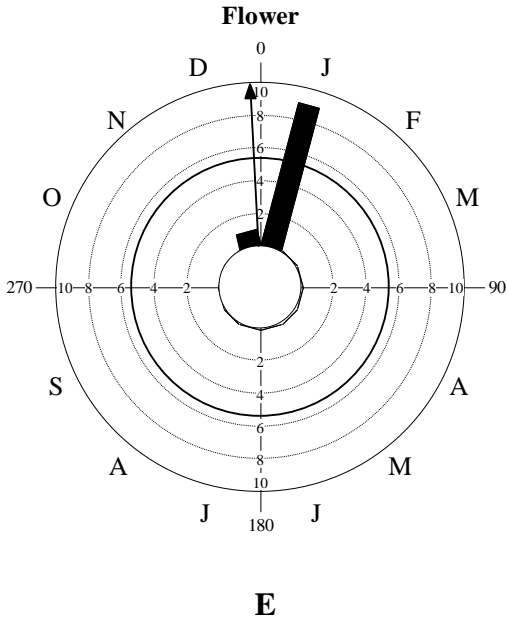


C - Flower *Carrasco* 2019
 D - Flower *Carrasco* 2020



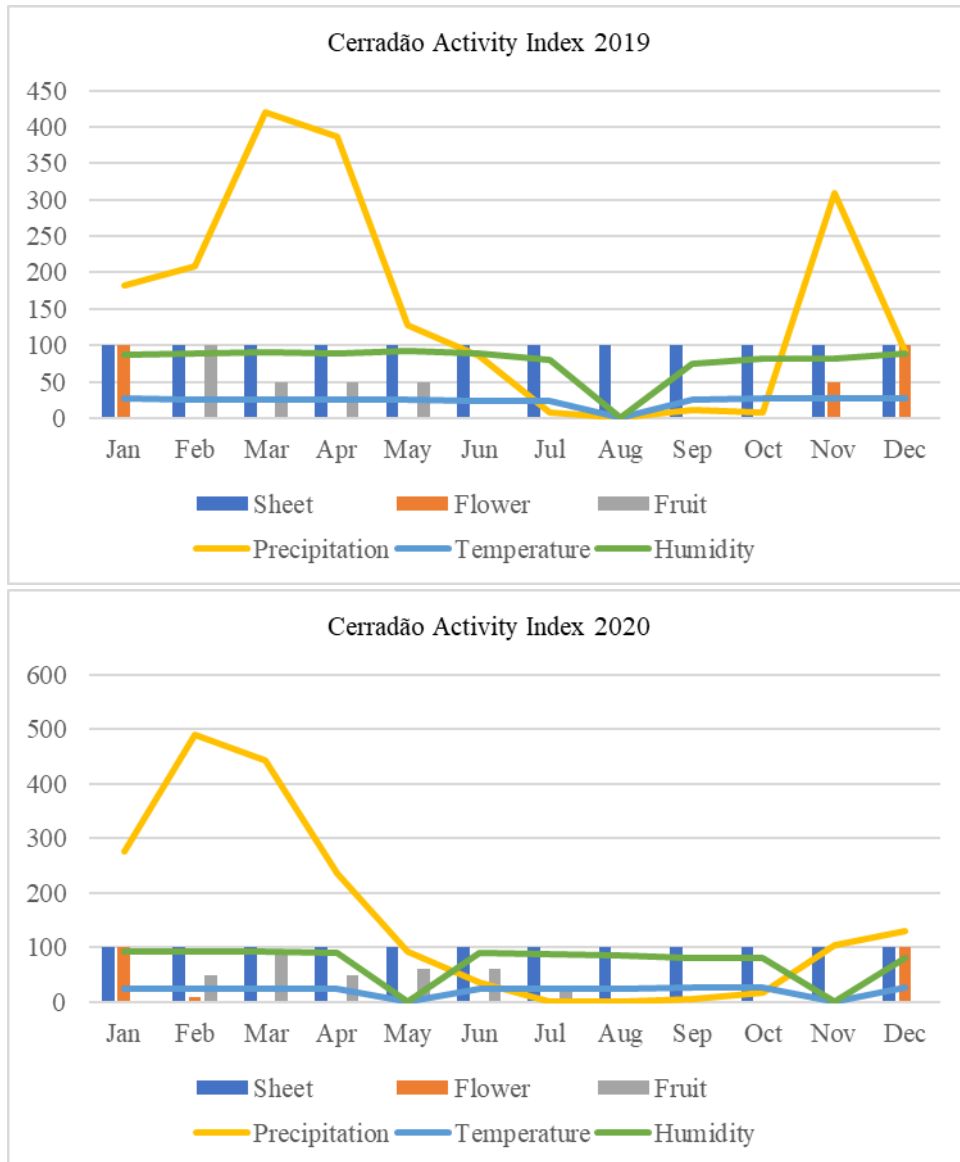
E - Flower Humid Forest 2019

F - Flower Humid Forest 2020



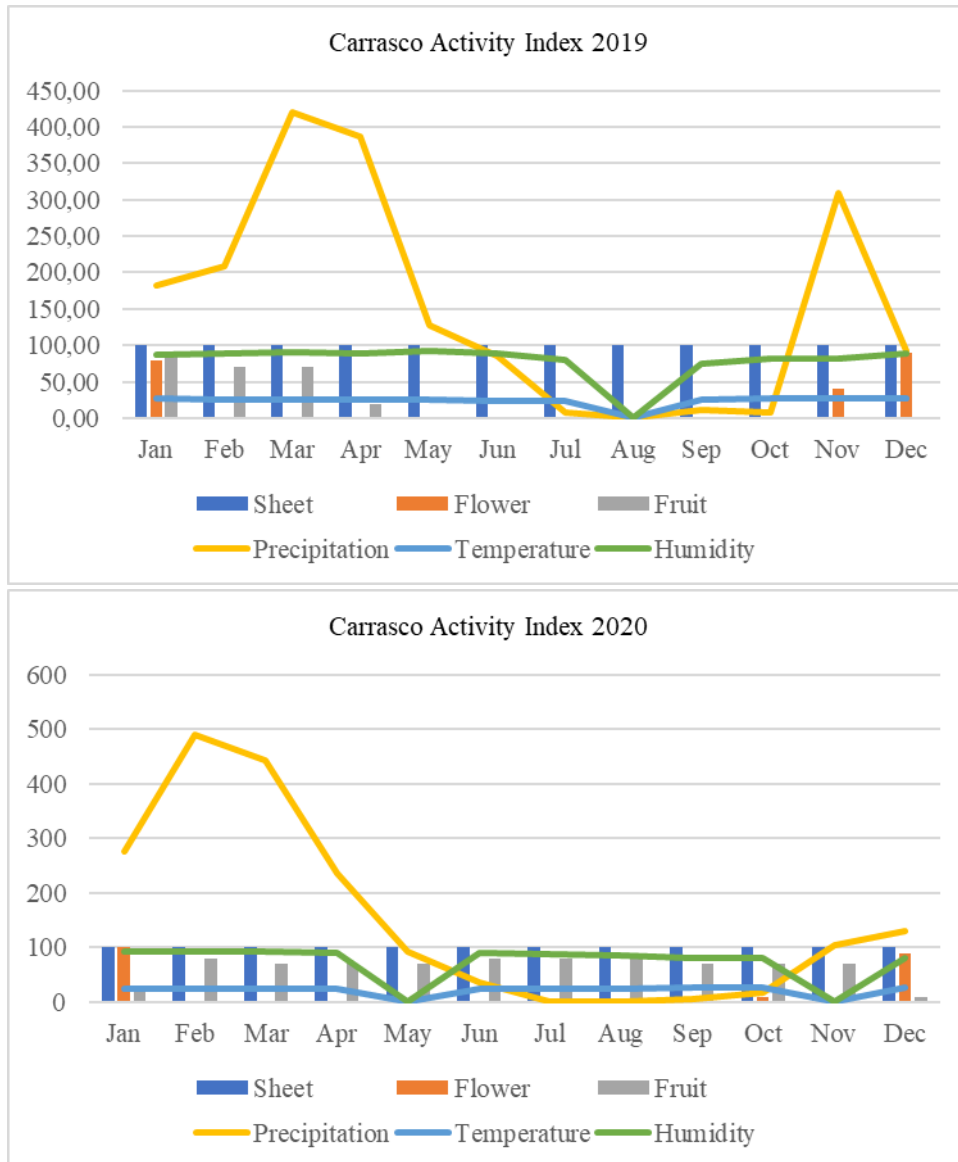
Source: Authors.

Figure 6. Cerradão Phytophysiology: Activity Index for Precipitation, Temperature and Humidity in 2019 and 2020, Northeast Brazil



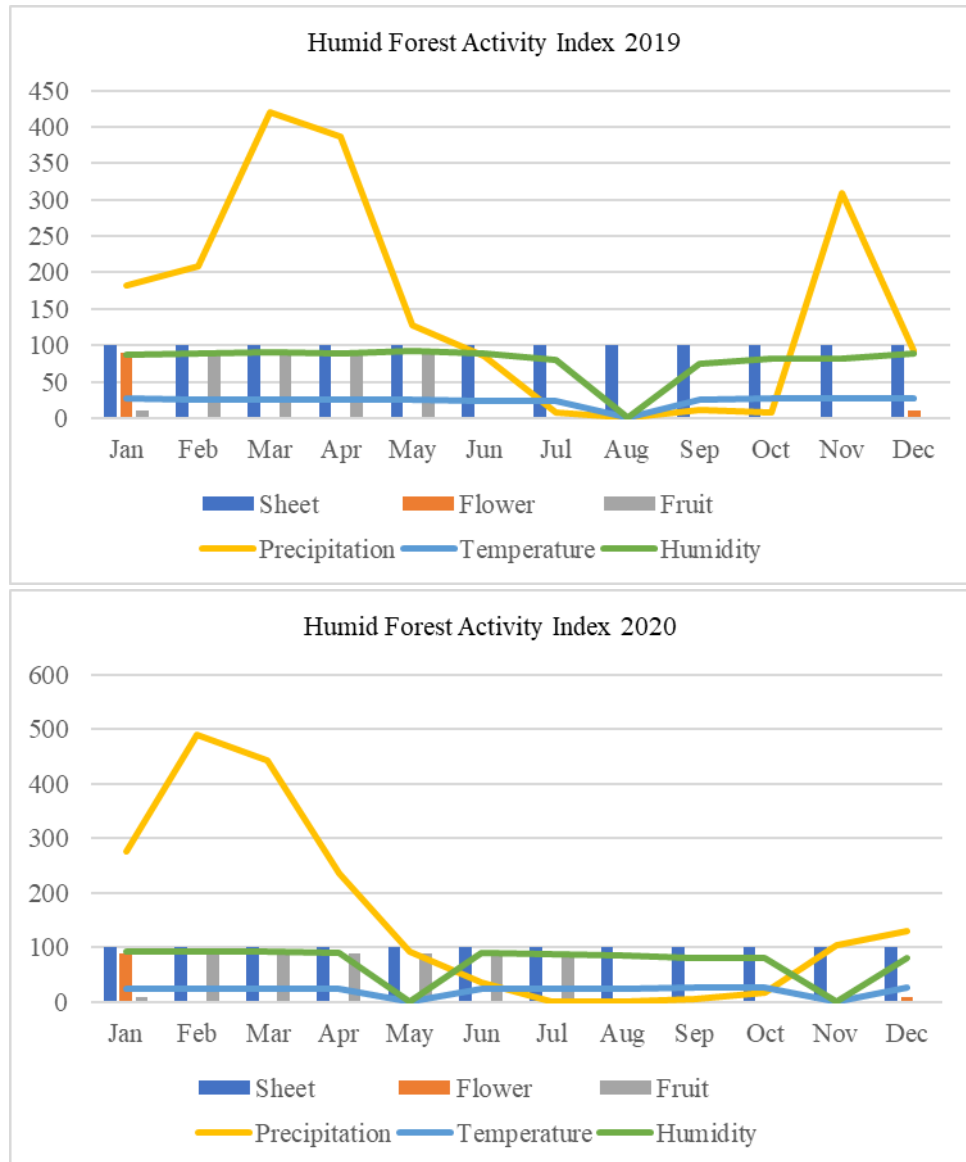
Source: Authors.

Figure 7. Carrasco Phytophysiology: Activity Index for Precipitation, Temperature and Humidity in the years 2019 and 2020, Northeastern Brazil.



Source: Authors.

Figure 8. Phytophysiology Humid Forest: Activity Index for Precipitation, Temperature and Humidity in the years 2019 and 2020, Northeastern Brazil.



Source: Authors.

3.3 Fruiting

The fruiting of *C. langsdorffii* occurred annually for the Cerradão, Carrasco and Humid Forest physiognomies. Regarding the time range in months of this phenophase in the different areas, the Cerradão, Carrasco and Humid Forest manifested the short, intermediate and long forms, with the latter recorded only in 2020 in the different phyto-physiognomies.

The Cerradão had fruit from February to May in 2019, with peak synchrony in February with 100% of individuals (Figure 9A). In 2020 it occurred from February to July, with the highest peak recorded in March at 90%, showing high synchrony (Figure 9B). The circular statistics for 2019 and 2020 revealed Mean Vector (μ) equal to 65.104° and 109.909° respectively, which indicates high activity in February 2019 and March and April 2020 (Table 1).

The Length of Mean Vector (r) in 2019 and 2020 was equal to 0.823 and 0.585 respectively, the Median was 60° and 120° , and the Rayleigh Test (p) equal to 0.00007 and 0.0001 respectively, with seasonality for the two years analyzed (Table 1). The fruits showed significant positive correlation of Activity Index in 2019 with precipitation ($r_s = 0.64$; $p = 0.0241$) and humidity ($r_s = 0.75$; $p = 0.0048$) and negative with temperature ($r_s = -0.533$; $p = 0.0743$) (Table 2) (Figure 6). For the Intensity

Index there was significant positive correlation in 2019 with precipitation ($r_s = 0.68$; $p = 0.0136$) and humidity ($r_s = 0.69$; $p = 0.0121$) and significant negative correlation in 2020 with temperature ($r_s = -0.60$; $p = 0.0377$) (Table 3) (Figure 2).

For the Carrasco in 2019 fruiting occurred from January to April, with a peak in January, with 90 % of individuals exhibiting the phenophase (Figure 9C). In 2020 individuals were observed fruiting throughout the year, with the highest peak occurring in February and from June to August, with 80% of individuals fruiting (Figure 9D). The circular data revealed for 2019 and 2020 Mean Vector (μ) equal to 31.918° and 162.808° respectively, which indicates high activity in January 2019 and June 2020 (Table 1).

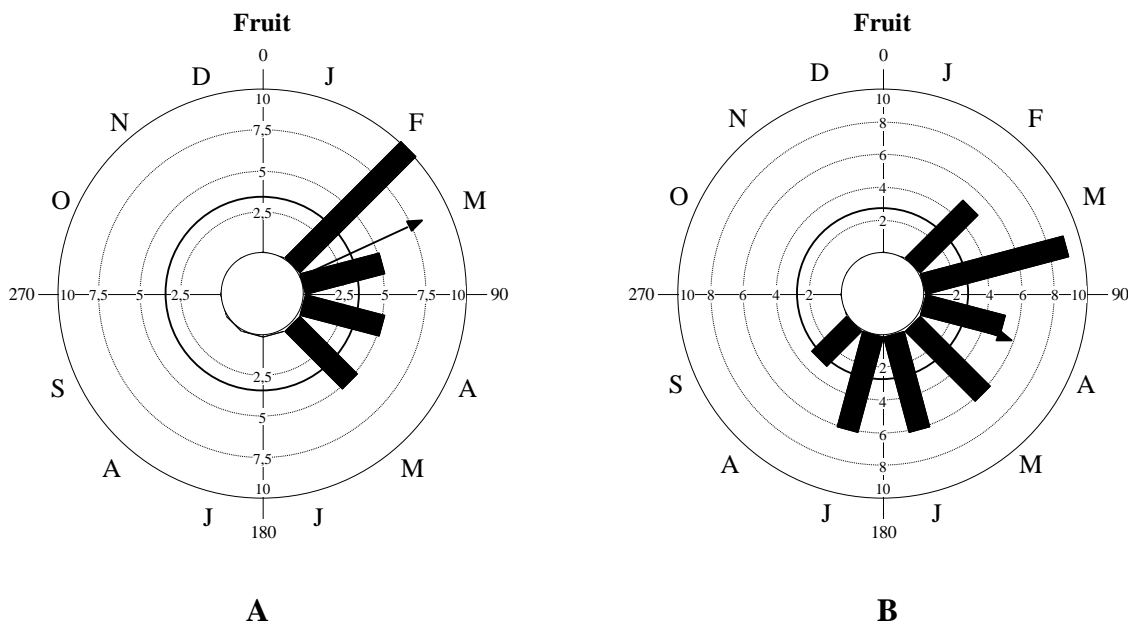
The Length of Mean Vector (r) in 2019 and 2020 was equal to 0.875 and 0.178 respectively, the Median was 30° and 150° , and the Rayleigh Test (p) equal to $8.51E-09$ and $9.00E-02$ respectively (Table 1). There was no seasonality for the two years analyzed. The fruits manifested significant positive correlation of Activity Index in 2019 only with precipitation ($r_s = 0.66$; $p = 0.0187$); there was no significant negative correlation with any of the observed variables (Table 2) (Figure 7).

In the Humid Forest fruits were observed from January to May in both 2019 and 2020 (Figure 9 E and F). 90 % of the individuals fruited from February to May and 10 % in January (Figure 9 E and F). The difference observed between the two years studied was that in 2020, 90 % of the individuals had the phenophase in June and July (Figure 9 F).

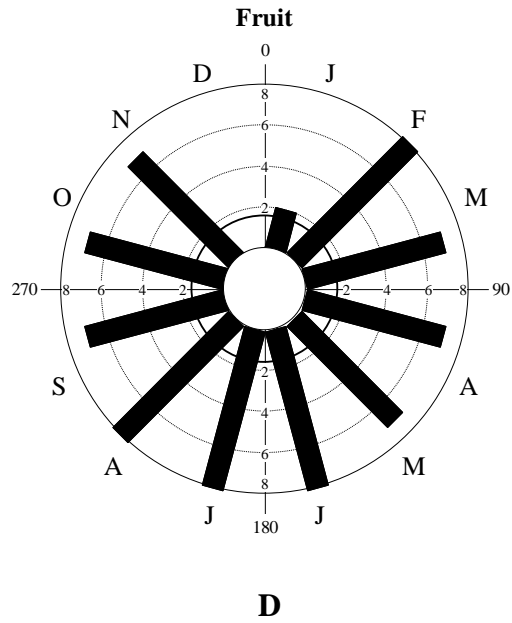
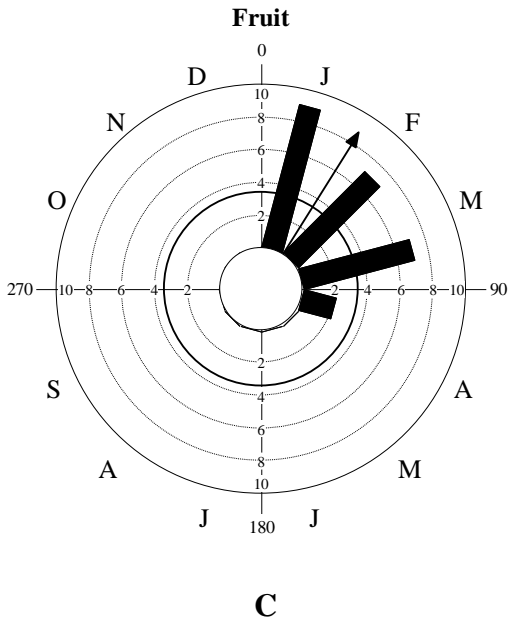
For the circular statistics in the years studied (2019 and 2020), it was recorded that Mean Vector (μ) was equal to 73.179° and 88.295° respectively, which indicates high activity in March 2019 and between March and April 2020 (Table 1). The Length of Mean Vector (r) in 2019 and 2020 was equal to 0.821 and 0.731 respectively, the Median was 60° and 90° , and the Rayleigh Test (p) was equal to $4.63E-11$ and $3.58E-11$ respectively (Table 1). The data show that there was no seasonality in this phenophase. There was significant positive correlation of Activity Index (Table 2) (Figure 8) and Intensity (Table 3) (Figure 4) for 2019 with precipitation ($r_s = 0.7216$; $p = 0.008$) ($r_s = 0.74$; $p = 0.0051$) and humidity ($r_s = 0.7614$; $p = 0.004$) ($r_s = 0.71$; $p = 0.0086$) respectively. Moreover, in 2020 the Activity Index showed a positive correlation with humidity ($r_s = 0.5632$; $p = 0.0565$) (Table 2) (Figure 8).

Figure 9. Circular histograms of individual frequencies of peak fruiting dates of *Copaifera langsdorffii* Desf. in areas of *Cerradão*, *Carrasco* and Humid Forest in Chapada do Araripe, Northeastern Brazil. The bars represent the frequencies of individuals with phenophase for the two years of observation (January 2019 to December 2020). The arrow points to the average date (mean angle) and the arrow length corresponds to the r value (degree of seasonality), ranging from 0 to 1. For details of the analysis, see Table 1.

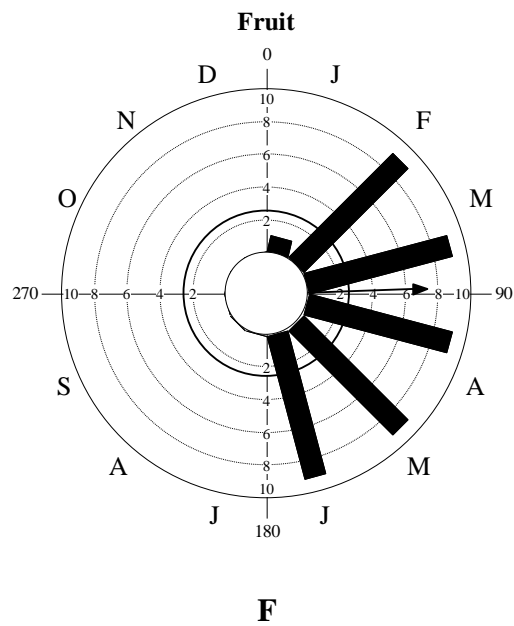
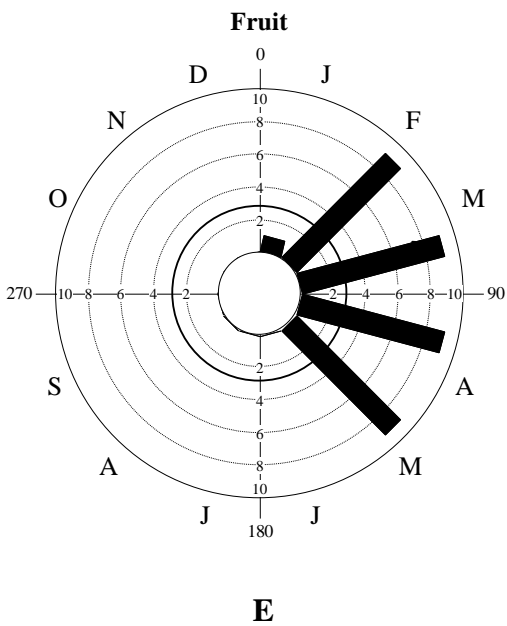
A - Fruit *Cerradão* 2019
B - Fruit *Cerradão* 2020



C - Fruit Carrasco 2019
D - Fruit Carrasco 2020



E - Fruit Humid Forest 2019
F - Fruit Humid Forest 2020



Source: Authors.

4. Discussion

Leaf presence patterns, flowers and fruits of *C. langsdorffii*: vegetative and reproductive strategies and the influence of abiotic factors

Individuals from more arid sites (Carrasco and Cerradão) showed leaf fall earlier than the humid area (Humid Forest). They also exhibited a longer duration of leaf loss when compared to the wetter site population. The main differences between populations were related to leaf fall, which starts earlier in populations from more arid sites, as described by Goulart *et al.* (2005) for populations of *Plathymenia reticulata* Benth. (Fabaceae). The intensity and duration of leaf fall are directly related to water availability in the environment (Liu *et al.*, 2016; Silveira *et al.*, 2013; Walker *et al.*, 1995), varying among populations as shown here. During the dry season there is a greater incidence of solar radiation with an increase in evapotranspiration, which, combined with water deficit, promotes limitation of stomatal opening to reduce transpiration, damaging the photosynthetic apparatus and reducing water use efficiency (Franco, 1998; Lemos-Filho, 2000; Meinzer *et al.*, 1999).

Thus, deciduousness during periods of hydric limitation is an important strategy developed to reduce this stress through leaf loss, which prevents even more pronounced transpiration and dehydration in this period (Borchert, 1980; Reich and Borchert, 1984). In addition, reduced transpiration is an important mechanism for returning internal water levels in the plant (Borchert, 1980; Reich and Borchert, 1984).

The research revealed a reasonable diversity of flowering patterns and strategies in *C. langsdorffii* among the Cerrado, Carrasco and Humid Forest phyto-physiognomies of Northeastern Brazil.

The flowering pattern of *C. langsdorffii* can be considered regular, or seasonal, and also annual, according to the classification of Newstrom *et al.* (1994). This is because flowering occurred at similar periods in the three areas analyzed, with peaks in the months of December and January in the cycles analyzed.

Higher temperatures are determinants in the induction of flowering (Ziparro and Morellato, 2007), which in the case of *C. langsdorffii* correlated positively and significantly in the three study areas. Liebsch & Mikich (2009), Cascaes *et al.* (2013) and Roberts *et al.* (2015), have indicated a seasonal pattern of flowering, especially when there is a transition from cooler to higher temperatures. These abiotic factors may also be related to the presence of pollinators, dispersers and predators, which exert a strong direct influence on phenological behavior (Morellato *et al.*, 1989; Rocha *et al.*, 2020).

Precipitation has been suggested as the primary cause of variations in the onset and duration of seasonal reproductive environments (Borchert *et al.*, 2004; Petit, 2001). The lower stress levels that plants from wetter sites are subjected to allow for rapid recovery after the drought period (Toledo *et al.*, 2012) allocating resources to flower production. In addition, more time for seed development generates larger and more vigorous seeds (unpublished data), important characteristics for seedling development in competitive environments (Leishman, 2001; Souza and Fagundes, 2014; Yanlong *et al.*, 2007).

Fruiting occurred annually and showed a positive and significant correlation in activity with precipitation in the three areas analyzed and with humidity in the Cerradão and Humid Forest. Seasonality was only shown in the Cerradão phyto-physiognomy. *C. langsdorffii* presented fruits during the rainy season for the Cerradão, Carrasco and Humid Forest phyto-physiognomies, with the exception only of the year 2020 in Carrasco and Humid Forest where individuals were observed with fruits in both the rainy and dry periods. Griz & Machado (2001) observed that the rainy season was the most common factor in fruit production in tropical regions, especially in Tropical Dry Forests.

According to phenological studies made with *C. langsdorffii*, it is possible to affirm that it has a vegetative and reproductive development, as well having periods of irregular flowering and fruiting phenophases, in terms of occurrence, intensity and length, depending on the study area. In this study, flowering occurred when the species had the fewest leaves; as in the Cerrado of São Paulo-Brazil, flowering occurred just after leaf fall. In contrast, in Oliveira *et al.* (2017) the flowering of *C. langsdorffii* occurred after the budding phenophase. The flowering of the population of this same species studied in the

Cerrado of Minas Gerais-Brazil was considered regular annual, since it flowered at the same time during the study period (1999-2001) (Freitas and Oliveira, 2002). In the Semi-deciduous Forests, *C. langsdorffii* was classified as supra-annual, possibly related to the existence of a biennial or triennial pattern (Dias and Oliveira Filho, 1996; Pedroni et al., 2002).

The study showed that populations of *C. langsdorffii* adjust phenological behavior according to the environmental conditions of each population; this characteristic may contribute significantly to the breadth of a species' niche, which could explain the success of *C. langsdorffii* in a range of different habitat types in its wide geographic distribution. Furthermore, the phenotypic plasticity observed in all populations studied for their vegetative phenology, especially for leaf fall, in terms of adjustments to the onset and duration modulated by water availability, is an important factor for the persistence of the species in the face of future climate change.

Some species may present variations in phenology depending on the environment and region where they are located. This occurs because the type of soil and climate variations in each region are factors that influence not only the period, but also the intensity of phenological events of plant species, so that different results can be found (Silvério and Lenza, 2010), as can be observed for *C. langsdorffii* in this study. In addition, this phenological variation can cause events to correlate in different ways with climatic variables (Silva, 2016). Examples of this kind were also found for *C. langsdorffii* (Fabaceae) by Fagundes *et al.* (2016) and for other Brazilian savanna species, such as *Roupala montana* Aubl. (Proteaceae) and *Davilla elliptica* A. St.-Hil. (Dilleniaceae) by Silvério & Lenza (2010).

Copaifera langsdorffii exhibits large intraspecific trait metamer variation elevated across a climatic gradient, as well as the ability to modify these traits in response to different climatic conditions (Souza et al., 2018). Such characteristics may explain the species' success in a variety of habitats, with a wide geographic distribution in the Cerrado, Atlantic Forest, and Caatinga (Souza et al., 2018). Populations from environments with greater interannual climatic heterogeneity could be better suited to cope with future climate change because of their xerophytic characteristics and their higher levels of phenotypic plasticity (Souza et al., 2018).

5. Conclusion

Variations in precipitation, temperature and humidity in the Cerradão, Carrasco and Humid Forest areas of the Chapada do Araripe influence the phenology of *Copaifera langsdorffii*, confirming that climate change alters the phenological events of this species.

Copaifera langsdorffii presented a semi-deciduous vegetative phenological strategy, with the largest quantity of leaves recorded mainly from the end of the rainy season to the beginning of the dry season in the Cerradão, Carrasco, and Humid Forest areas. The temperature negatively influenced the presence of leaves; in other words, the higher the temperature, the fewer the number of leaves, while precipitation showed a positive relationship only in the Cerradão, with no influence in the other areas. Humidity only interfered positively in the Carrasco. Thus, precipitation and humidity seem to influence the phyto-physiognomies differently.

The flowering of *Copaifera langsdorffii* showed an annual pattern, with one cycle per year in the Cerradão, Carrasco, and Humid Forest areas. Both the highest number of individuals and the highest number of flowers per individual occurred in the rainy season in all three areas. Temperature exerted an influence only in the Carrasco for this phenophase, where high temperatures probably favor flowering in this phyto-physiognomy, while humidity positively favored the number of flowering individuals for the Cerradão. In the Humid Forest the environmental factors did not manifest any influence on this phenophase.

Copaifera langsdorffii showed an annual fruiting pattern for the Cerradão, Carrasco and Humid Forest of the Chapada do Araripe. For the fruits, variations were registered among the phyto-physiognomies with regard to the greatest peaks with the presence of this phenophase, as well as the number of fruits per individual.

In the Cerradão the highest peaks occurred during the rainy season, whereas in the Carrasco it occurred during the rainy and dry seasons, and in the Humid Forest during the rainy season and the beginning of the dry season. This is probably related to the differences in soils of the different phyto-physiognomies, as well as to the variations in abiotic factors of these different locations that characterize each environment.

It was recorded that precipitation positively influenced fruiting in the Cerradão, Carrasco, and Humid Forest, except for the amount of fruit per individual in the Cerradão, which was negatively influenced. Humidity influenced this phenophase positively in the Cerradão and Humid Forest, both for the greater number of individuals and for the greater number of flowers per individual, while in the Carrasco it also influenced it positively, but only for the greater number of flowers per individual. The temperature manifested influence only on the intensity of the individuals, which is the quantity of flowers per individual, with negative influence and only for the Carrasco.

Therefore, the vegetative and reproductive patterns of *Copaifera langsdorffii* are seasonal for the Cerradão, Carrasco and Humid Forest areas, with the sole exception of fruiting, which is influenced by environmental seasonality only in the Cerradão.

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Note: All figures must be black and white.

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