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Original Article

Phenology of *Guarea macrophylla* Vahl (Meliaceae) in subtropical riparian forest in southern Brazil

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Abstract

Climate is one of the main factors that affect plant behavior. The phenology of *Guarea macrophylla* Vahl, which is a small tree used for reforestation of degraded areas, was monitored for 18 months in a riparian forest at the Schmidt Stream, Campo Bom, in the state of Rio Grande do Sul, southern Brazil. Vegetative (leaf fall and leaf flushing) and reproductive events were observed, with the latter divided into flowering (flower buds and anthesis) and fruiting (unripe, ripening and ripe fruit). Phenological events were related to temperature, photoperiod and precipitation and their seasonality was verified by circular statistical analysis. Vegetative phenophases were continuous; they were not related to climate factors and presented low intensity, emphasizing the perennial aspect of the species. Flowering occurred during spring and summer. Both flower buds and anthesis were related to temperature and photoperiod. Fruiting was constant and went through all stages of development. Unripe fruits developed during the months with the lowest photoperiod and ripen more intensely in winter, on colder days. Ripe fruit became available for dispersal in spring, in times of longer photoperiod and higher temperatures. Except for leaf fall, all other phenological events showed seasonality in their manifestation. The one-month difference between the onsets of the flowering phases observed in this study indicated that local climate changes induced the early occurrence of this phenophase.

Keywords: climate, flowering, fruiting, seasonality.

Fenologia de *Guarea macrophylla* Vahl (Meliaceae) em mata ciliar subtropical no sul do Brasil

Resumo

O clima é um dos principais fatores que condicionam o comportamento das plantas. A fenologia de *Guarea macrophylla* Vahl, arvoreta utilizada no reflorestamento de áreas degradadas, foi acompanhada durante 18 meses, em mata ciliar do arroio Schmidt, Campo Bom, RS, Brasil. Foram observados os eventos vegetativos (queda foliar e brotamento) e reprodutivos, separados em floração (botão floral e antese) e frutificação (frutos imaturos, maturando e maduros). Os eventos fenológicos foram relacionados à temperatura, ao fotoperíodo e à precipitação e a sua sazonalidade foi verificada por meio da análise estatística circular. As fenofases vegetativas foram contínuas, não se relacionaram com os fatores climáticos e apresentaram baixa intensidade, ressaltando a característica perene da espécie. A floração ocorreu durante a primavera e o verão e tanto botão floral quanto antese relacionaram-se com temperatura e fotoperíodo. A frutificação foi constante e passou por todos os estádios de desenvolvimento. Os frutos imaturos desenvolveram-se em meses com o menor fotoperíodo e maturaram mais intensamente no inverno, em dias de menor temperatura. Os frutos maduros tornaram-se disponíveis para os dispersores na primavera, em períodos com maior fotoperíodo e temperatura. Com exceção da queda foliar, todos os outros eventos fenológicos apresentaram sazonalidade em sua manifestação. O adiantamento de um mês entre as florações observadas no presente estudo indicou que as alterações climáticas locais de temperatura induziram a ocorrência antecipada dessa fenofase.

Palavras-chave: clima, floração, frutificação, sazonalidade.

1. Introduction

Seasonality of plant growth in tropical environments may be caused by the periodicity of dry seasons, although many plants present seasonal phenophases despite being located in regions where the climate is humid throughout the year (Mehltreter, 2008). In general, flowering in tropical forests coincides with increased solar radiation and decreased precipitation, while fruiting is generally associated with and concentrated in the wet season (Marques and Oliveira 2004; Munhoz and Felfili, 2007). The less seasonal the climate of an environment is, the greater the diversity of phenophases, as there are no climatic factors restricting plant development (Morellato et al., 2000). Because of its subtropical climate, the southern region of Brazil is not under the influence of climatic seasonality regulated by rainfall. The region is characterized by an absence of water stress, therefore, the phenology is mostly related to temperature and photoperiod, which have higher annual amplitudes (Bauer et al., 2012, 2014).

Guarea macrophylla Vahl (Meliaceae), popularly known as pau-de-arco, is a native perennial small tree commonly found in riparian forest. It is often recommended for reforesting conservation areas and its wood is used for making packaging. (Lorenzi, 2009). It also provides other non-timber forest products such as medicinal and pharmaceutical ones (Ubessi-Macarini et al., 2011). Its flowers are pollinized by beetles and moths (Silva-Junior and Pereira, 2009) and its fruits are dispersed by birds (Fadini and Marco Júnior, 2004; Prado, 2013). It is distributed across French Guyana, Argentina (Sobral et al., 2013) and in all regions of Brazil (Stefano et al., 2015). In the state of Rio Grande do Sul, it can be found in the formations of the Alto Uruguai region, on the southern hills of the Serra Geral, in the Atlantic Forest and in the northern hills of the Serra do Sudeste (Sobral et al., 2013).

In Brazil, the phenology of *Guarea macrophylla* was monitored in areas with alternating dry and wet periods, specifically in forests of the state of São Paulo (Spina et al., 2001; Bencke and Morellato, 2002; Genini, et al., 2009), in areas without a defined dry season in Paraná (Mikich and Silva 2001; Marques and Oliveira, 2004) and Santa Catarina (Vinholes et al., 2015). All of these studies evaluated the phenology of *Guarea macrophylla*, from the observation of 1 to 12 individuals within arboreal communities; therefore, the vegetative and reproductive events of this unique species were not individually emphasized.

The aims of this study were as follows: I) to describe the phenological events of a population of *Guarea macrophylla* in riparian forest; II) to examine the relationship between vegetative and reproductive events and temperature, precipitation and photoperiod, and III) to analyze the seasonality of phenophases at the population level. Phenological events were expected to be more influenced by temperature and photoperiod than by precipitation, due to the lack of alternating wet and dry periods in the subtropical regions of Brazil (Buriol et al., 2007). Since the species is perennial (Lorenzi, 2009), it is believed that only reproductive events are evidently seasonal.

2. Material and Methods

2.1. Study area and climate

The study was conducted in the municipality of Campo Bom, state of Rio Grande do Sul, in a fragment of riparian forest of approximately 10 hectares, located by the Schmidt Stream (29°39'8.66"S and 51°04'50.31"W, 25m a.s.l.). In the riparian forest, other tree species are found such as *Luehea divaricata* Mart. & Zucc. (Malvaceae), *Erythrina falcata* Benth (Fabaceae), *Parapiptadenia rigida* (Benth.) Brenan (Fabaceae), *Machaerium stipitatum* Vogel (Fabaceae), *Allophylus edulis* (A.St.-Hil. et al.) Hieron. ex Niederl. (Sapindaceae).

This area has a moist, mesothermal climate without a dry season and it is categorized as type Cfa according to the Köppen climate classification (Peel et al., 2007). According to data related to the period from June 2013 through November 2014 (18 months studied), obtained from the Campo Bom Weather Station (29º40'34.17'S and 51º03'52.99'W; 25.8 m a. s. l.), July 2013 had the lowest average temperature (12.7 °C), and the highest temperature (26.5 °C) was reached in January 2014 (Figure 1). The average temperature during this same period was 19.2 °C. In comparison, the average temperatures in June, July and August of 2014 were 1.2 °C, 2.2 °C and 3.0 °C, respectively, warmer than the same months in 2013. Over the 18 months evaluated, the accumulated rainfall was 3,184.2 mm, the minimum was recorded in May 2014 (83.8 mm) and the maximum in August 2013 (370.7 mm) (Figure 1). The monthly photoperiod obtained from the Anuário Interativo do Observatório Nacional (2014) ranged from 10.2 to 14 light hours during the period.

2.2. Guarea macrophylla

Guarea macrophylla measures 3 to 10 meters tall. It has a short trunk, pinnate compound leaves with 2-7 pairs of leaflets and pending axillary inflorescences with rosy or red flower petals. The ripe fruit is a dehiscence pear-shaped capsule that opens lengthwise into four sections exposing from 4 to 10 bright red-orange arillate seeds (Klein, 1984; Lorenzi, 2009; Prado, 2013).

2.3. Phenology

Twenty (20) adult specimens of *Guarea macrophylla* were selected. Phenological observations were made at monthly intervals during 18 months of monitoring, starting in June 2013 and ending in November 2014, inspecting vegetative (leaf fall and leaf flushing) and reproductive

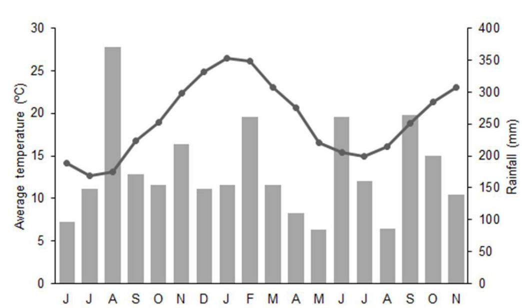

Figure 1. Monthly average temperature and accumulated rainfall, between June 2013 and November 2014, in the municipality of Campo Bom, Rio Grande do Sul.

phenophases, which considered flowering (flower buds and anthesis) and fructification, divided in: unripe fruits (green, small in size), ripening fruit (red and closed), ripe fruits (with arillate seeds exposed). To estimate the intensity of each phenological events we used (i) the Fournier intensity index (Fournier, 1974), in which data obtained are classified by a semi quantitative interval scale consisting of five categories (0 to 4), with an interval of 25% between each category, and (ii) by the activity index, a qualitative method that verifies the presence and absence of the phenophase (Morellato et al., 2010b). In order to calculate Fournier intensity index for each month, the sum of all intensity categories given to each individual was divided by the maximum sum that could be attributed to the population (total number of individuals selected multiplied by four, the highest intensity class), resulting in a ratio.

2.4. Statistical analysis

Spearman's rank correlation (r_s) was used to examine the relationship between the observed phenological patterns and the temperature, precipitation and photoperiod in the month of occurrence and in the previous month, with a 5% level of significance, using the SPSS (version 22) statistical program. Reference values used to classify correlations were the following: $0 > r < 0.3$ (low), $0.3 \leq r < 0.6$ (moderate), and $r \geq 0.6$ (strong), following Callegari-Jacques (2003). Circular statistics was employed to investigate and interpret phenological patterns (Garcia et al., 2009; Morellato et al., 2010a). Parameters were calculated via the Oriana software version 3 (Kovach, 2009). Months were converted into angles, with intervals of 30º wide. The following parameters were calculated: mean angle (μ) or mean date that referred to the time of the year around which the phenological activity of individuals is most concentrated; circular standard deviation; and vector r, which indicates the intensity of concentration (0 to 1) around the mean angle. Vector r can be considered a measure of the seasonality "degree". Rayleigh test was applied to indicate the significance ($P<0.05$) of the mean angle (Morellato et al., 2000).

3. Results

3.1. Phenology

The vegetative phenophases were continuous throughout the study, without a period of complete leaf abscission in the canopy (Figure 2). All individuals in the population sampled showed leaf fall in November 2013 and July 2014, but with low intensity (25%). The relative frequency of individuals with leaf fall ranged from 25% to 100% (Figure 2A). Plants exhibited leaf flushing every month, always with maximum frequency, but with greater intensity in individuals in October 2013 and November 2013 and October 2014, corresponding to 71%, 50% and 48%, respectively (Figure 2B). None vegetative phenophase was related to the meteorological factors analyzed in the month of occurrence and in the previous month (Table 1). There was no significant seasonality in leaf fall event, with dates distributed uniformly throughout the study. The mean angle of leaf flushing was significant and had the lowest r-value, indicating low seasonality (Table 2).

The population demonstrated a discontinuity in the first flowering, with a one-month interval between each of them (Figure 3). The flowering onset occurred in October, when all trees had flower buds followed by anthesis in November (95% of these trees). After one month, the flower buds reoccurred in in January and February (45% and 35% frequency, respectively) (Figure 3A), with open flowers in February and March (60% and 15%, respectively) (Figure 3B). The second flowering began in September 2014, with 80% of the population showing flower buds; in November, 90% had open flowers. The intensity of flowering event fluctuated between occurrences, but it was always below 50%. The phenophase of flower buds was strongly related to photoperiod and moderately related to temperature in the month of occurrence. Anthesis was moderately related to photoperiod and temperature in the month of occurrence and in the previous month (Table 1). No flowering event correlated with precipitation. The mean angle of flower buds and anthesis was significant and the high degree of seasonality was denoted by the elevated value of vector r (Table 2).

Unripe fruits only failed to occur in October, November and December, however, the relative frequency of the population ranged from 20% to 100% in the remaining months. In January and February, all trees showed unripe fruits, although the intensity has not exceeded 31% in any month in which the event occurred (Figure 4A). There was a moderate negative relationship between this phenophase and the photoperiod in the month of occurrence (Table 1).

Only in January, ripening fruit were not observed, despite being constant over the-study period with relative frequency in the population ranging from 15% to 100%.

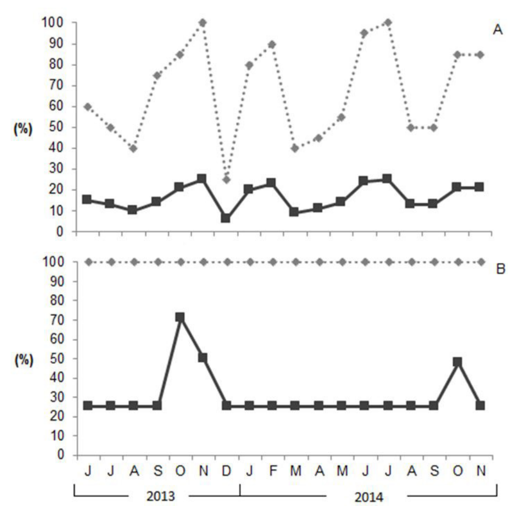

Figure 2. Vegetative events of *Guarea macrophylla* between June 2013 and November 2014, in a fragment of riparian forest located by the Schmidt Stream in Campo Bom, Rio Grande do Sul. (A) leaf fall; (B) leaf flushing. Activity (dashed line) and Intensity (continuous line) Index.

Table 1. Spearman's rank correlations (r_s) between the phenological events of *Guarea macrophylla* and temperature, photoperiod and precipitation in the month of occurrence (0) and in the previous month (1), in a fragment of riparian forest located by the Schmidt Stream in Campo Bom, Rio Grande do Sul.

Phenological event	Month	Temperature	Photoperiod	Precipitation
Leaf fall	0	r_s=0.07 *P*=0.778	r_s= –0.004 *P*=0.987	r_s=0.28 *P*=0.258
	1	r_s=0.04 *P*=0.873	r_s=0.004 *P*=0.985	r_s= –0.01 *P*=0.957
Leaf flushing	0	r_s=0.18 *P*=0.476	r_s=0.35 *P*=0.149	r_s=0.23 *P*=0.351
	1	r_s=0.04 *P*=0.875	r_s=0.17 *P*=0.494	r_s=0.28 *P*=0.252
Flower buds	0	**r_s=0.51 *P*=0.029**	**r_s=0.61 *P*=0.007**	r_s=0.39 *P*=0.113
	1	r_s=0.29 *P*=0.235	r_s=0.45 *P*=0.058	r_s=0.08 *P*=0.749
Anthesis	0	**r_s=0.53 *P*=0.024**	**r_s=0.49 *P*=0.043**	r_s=0.16 *P*=0.529
	1	**r_s=0.50 *P*=0.033**	**r_s=0.52 *P*=0.024**	r_s=0.21 *P*=0.400
Unripe fruits	0	r_s= –0.31 *P*=0.207	**r_s= –0.49 *P*=0.037**	r_s= –0.04 *P*=0.885
	1	r_s=0.09 *P*=0.732	r_s= –0.30 *P*=0.221	r_s= –0.42 *P*=0.087
Maturing fruits	0	**r_s= –0.83 *P*<0.001**	**r_s= –0.70 *P*=0.002**	r_s= –0.03 *P*=0.896
	1	**r_s= –0.85 *P*<0.001**	**r_s= –0.83 *P*<0.001**	r_s= –0.04 *P*=0.870
Ripe fruits	0	r_s=0.25 *P*=0.311	**r_s=0.47 *P*=0.046**	r_s=0.19 *P*=0.460
	1	r_s= –0.13 *P*=0.602	r_s=0.13 *P*=0.593	r_s=0.43 *P*=0.073

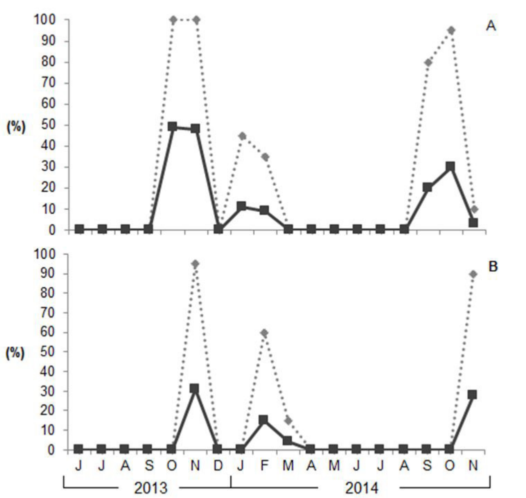

Figure 3. Flowering of *Guarea macrophylla* between June 2013 and November 2014, in a fragment of riparian forest located by the Schmidt Stream in Campo Bom, Rio Grande do Sul. (A) flower buds; (B) anthesis. Activity (dashed line) and Intensity (continuous line) Index.

In the months of maximum frequency, the intensities of this phenological event did not exceed 53% (Figure 4B). This phenophase was strongly and negatively related to the temperature and photoperiod in the month of occurrence and in the previous month (Table 1).

Ripe fruits were observed between September and December de 2013, ranging from 30% to 80% of the individuals in the population demonstrating the phenophase. In 2014, the onset of this phenophase was observed in August (10% of the population) and continued until November (30%). Thus, the intensity of the event in these months ranged from 3% to 30% in individuals (Figure 4C). This phenological event was moderately related to photoperiod in the month of occurrence (Table 1).

The mean angle of unripe and ripening fruits was significant and presented low value of vector r, indicating low seasonality (Table 2). The mean angle of ripe fruits was significant and the high degree of seasonality was indicated by the elevated value of vector r (Table 2).

4. Discussion

The continuous pattern, the low intensity of vegetative events and the simultaneous occurrence of leaf fall and leaf flushing of *Guarea macrophylla*, make the perennial aspect of the species evident. In the same region of Rio Grande do Sul, this leaf change behavior has also been demonstrated in other zoochoric species monitored under the same climatic conditions, such as *Myrsine coriacea* (Sw.) R. Br., *M. guianensis* (Aubl.) Kuntze, *M. lorentziana* (Mez.) Arechav. (Bauer et al., 2012), *Ocotea pulchella* (Nees) Mez, *Myrcia brasiliensis* Kiaersk e *Psidium cattleyanum* Sabine (Bauer et al., 2014). In environments with little seasonality regarding precipitation, as in this study, Jackson (1978) suggested that the continuous behavior of these vegetative phenophases for perennial species may be the most advantageous strategy for the plants, since this enables the photosynthetic rate to be sustained throughout the year and allows the old leaves to persist until the nutrients are translocated. Since the vegetative phenophases constitute a continuous event, there is less dependence on rainfall (Singh et al., 2006).

It is possible that the low concentration of leaf flushing in a specific period required less energy to be expended in storing and protecting resources than with synchronous species, which produce new leaves once or twice a year (Coley and Kursar, 1996). Moreover, the presence of leaf flushing in all the months may lower the

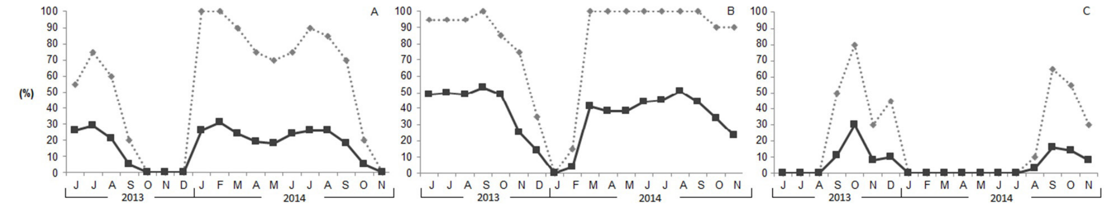

Figure 4. Fruiting of *Guarea macrophylla* between June 2013 and November 2014, in a fragment of riparian forest located by the Schmidt Stream in Campo Bom, Rio Grande do Sul. (A) unripe fruits; (B) ripening fruits; (C) ripe fruits. Activity (dashed line) and Intensity (continuous line) Index.

Table 2. Results of circular statistical analysis testing for the occurrence of seasonality on phenological events of *Guarea macrophylla* in a fragment of riparian forest located by the Schmidt Stream in Campo Bom, Rio Grande do Sul.

	Phenological events						
	Leaf fall	**Leaf flushing**	**Flower buds**	**Anthesis**	**Unripe fruits**	**Ripening fruits**	**Ripe fruits**
Observations (N)	200	323	137	50	217	376	51
Mean angle (μ)	252.07º	288.33º	21.01º	34.68º	160.26º	221.77º	306.14º
Mean date	-	30 Sep.	30 Oct.	15 Dec.	22 May	23 Jul.	15 Oct.
Circular standard deviation	123.55º	122.25º	40.44º	55.26º	96.03º	82.09º	34.79º
Length of mean vector (r)	0.10	0.10	0.78	0.63	0.24	0.36	0.84
Rayleigh test (*P*)	0.136	0.03	<0.001	<0.001	<0.001	<0.001	<0.001

likelihood of excess leaf predation of a single individual by phytophagous organisms (Morellato et al., 1989). However, plants have other defenses against herbivores beyond the phenological mechanisms (Ângelo and Dalmolin, 2007). *Guarea macrophylla* has four types of flavonoids in its leaves (Pereira et al., 2012) and these secondary metabolites are responsible, in part, for protecting against herbivores (Gould and Lister, 2006). However, insects were observed feeding on the mature leaves of some individuals of the monitored population.

Higher intensities of leaf renewal coincided with the onset of flowering, occurring very close to each other. These simultaneous events indicate that the immediate transfer of resources to a growing body is more energy efficient than storing such resources for translocation at a later time (Chapin 3rd et al., 1990). Furthermore, in places where no water stress occurs, the flowering peak is expected to coincide with the emergence of leaves and both phenophases occur in the period with the longest photoperiod (Marques and Oliveira, 2004). The flowering of *Guarea macrophylla* started to develop when triggered by the increase in temperature and photoperiod. According to Stevenson et al. (2008), the further from the equatorial region, the greater the relationship between the phenophases of tropical plants and solar radiation.

The second flowering (September 2014) of the population monitored in this study occurred one month earlier than the first occasion in 2013 on which the phenological event was observed. This time difference between the periods of flowering is associated with the milder winter of 2014, which was on average 2.1 °C warmer than the previous year. Moreover, according to the Instituto Nacional de Meteorologia (INMET, 2014), temperatures in winter (June, July and August) of 2014, for the majority of the state of Rio Grande do Sul, were above the historical average for this state. Thus, the observations showed that temperature was the key factor in flowering, since plants with the same photoperiod, which had no changes throughout the duration of monitoring, flowered earlier after the milder winter. Changes in phenological events can indicate important variations in the climate during a particular monitoring period (Pereira et al., 2008) and, among the abiotic factors that influence plants, temperature is the key factor in triggering certain phenophases such as leaf flushing and flowering (Hannah, 2011).

It can be seen that *Guarea macrophylla* maintained the same pattern in manifesting open flowers in seasonal and non-seasonal environments regarding precipitation. This phenological event occurred in the study of Bencke and Morellato (2002) during the wet season and in months with at least 200 mm of rainfall. Similarly, in this study there were also larger total volumes of rainfall in the months in which anthesis occurred. Flower buds and anthesis were seasonal events in the area studied, occurring in spring and summer, respectively. This synchronized flowering in individuals may be related to the fact that plants, in general, are pollinated more often when flowers appear in months with strong light (Tachiki et al., 2010).

The ripening of fruit in individuals comprised all stages of development during the period sampled. The continuous occurrence of the phenophase in plants suggests that the environmental conditions, in locations with little seasonality, present no restrictions on fruit development (Talora and Morellato, 2000), even though several abiotic factors analyzed, for example temperature and photoperiod, influenced the triggering of this phenological event.

The inverse relationship between the intensity of the onset of development of unripe fruits and the increased photoperiod, and between the ripening fruits and the photoperiod and temperature, indicates that the triggering for most individuals presenting these phenophases occurs in the season in which there are fewer daylight hours (winter). Studies show that variations of 3.5 hours of light over one year, together with temperature changes, induce physiological responses in plants in southern Brazil (Marques et al., 2004; Marchioretto et al., 2007). These two climatic variables are highly correlated, varying during the year towards the same direction and it becomes difficult to separate them from the effects observed in plants (Marchioretto et al., 2007; Athayde et al., 2009). Although there were significantly low concentrations of unripe and ripening fruits, both phenophases were seasonal events, occurring in autumn and winter, respectively, with an interval of two months between them. This synchronization strengthens the affinity of these events with the coldest season and shortest photoperiod.

As reported by van Schaik et al. (1993), fruiting of tropical plants does not show a clear pattern when analyzed according to latitude. Comparing the results of our study with others, it can be observed that the period in which *Guarea macrophylla* produces ripe fruits follows a latitudinal gradient, providing its seeds to fauna in distinct periods. In the state of Santa Catarina, ripe fruits appear in November, from January to April (Vinholes et al., 2015). In the state of Paraná, they have been observed from April to October (Mikich and Silva, 2001) and from May to September (Marques and Oliveira, 2004). In the state of São Paulo, they can be found from July to September (Bencke and Morellato, 2002). Additionally, Ting et al. (2008) observed that global fructification patterns are related to climate variations.

5. Conclusion

The seasonal pattern evidenced by reproductive events indicated that even plants growing under non-seasonal climate might present seasonal phenophases. Temperature and photoperiod acted as triggers for the onset of reproductive events of these plants. Flowering required heat and increased photoperiod unlike fruit ripening, which occurred in a cooler period and with fewer hours of daylight. Subsequently, the opening of fruits with exposure of arillate seeds happened when the temperature and photoperiod rose. There is a complementarity in the ripening period of fruits of *Guarea macrophylla* evidenced by the comparison of our study, which occurred in more southern latitude, with those by other authors in the southeast of Brazil.

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