

Article

Phenology of *Oenocarpus mapora* H. Karst in Low-Terrace and High-Terrace Forests of the Madre de Dios Region, Peru

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Abstract: *Oenocarpus mapora* H. Karst (*O. mapora*) is an Amazon palm with high economic and nutraceutical potential, from which the pulp and oil can be extracted. The objective of this study was to evaluate the phenology of *O. mapora* in low-terrace and high-terrace forests of the Madre de Dios Region, Peru. Two hundred sixteen individuals of *O. mapora* were monitored between June 2019 and January 2020, evaluating the presence of flower buds, open flowers, immature fruits and ripe fruits. Weighted mean analyses of the phenological pattern and correlation between climatic and phenological variables were carried out. Higher productivity mediated by a greater number of mature green leaves and bunches was observed in terrace forests located at a lower altitude. In both forest subtypes, flower buds and open flowers were continuous with a peak in July and August, respectively, during the dry season. In both habitats, unripe fruits were also continuous with a peak in September, while ripe fruits showed a peak in December and January in low-terrace and high-terrace forests, respectively, during the rainy season. Our findings show that flowering was continuous during the evaluated period, while fruiting increased during the rainy season associated with a greater number of days with precipitation.

Keywords: Amazon; Arecaceae; flowering; fruiting; forests; Peru



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1. Introduction

Phenological events in Neotropical plants are regulated by abiotic and biotic factors. Climate and soil are the most important abiotic factors that regulate plant phenology [1,2]. In tropical forests with well-defined dry and rainy seasons, the phenological patterns are highly seasonal, with precipitation and soil moisture being the main factors that induce reproductive activities [3]. In general, flowering is triggered by rains. In many tree species, more intense rains induce a greater synchronization of flowering [4]. Furthermore, in some species, fruit production increases during the rainy season [5,6].

Palm trees are abundant in the tropics and are found in almost all possible habitats, but their diversity is greatest in rainy lowland rainforests [7]. The phenological behavior of palm populations and communities is still scarce for the forests of the South American Amazon. The flowering of palm trees takes place mainly in the dry season and fruiting throughout the year but is greater in the rainy season. These phenological variations are influenced by various factors, such as the degree of seasonality, which is correlated with flowering [8].

In the Amazon, there is very little information on the flowering and fruiting processes in palm trees. Approximately, the Amazon basin is home to 151 species of palm trees [7], of which 149 species of palm trees have been reported in the Peruvian Amazon [9].

The Madre de Dios Region located to the Eastern part of Peru has an area of 85,182.63 km², which represents 6.6% of the Peruvian territory and 15.3% of the Peruvian Amazon. [10]. In this region, which presents a high biological diversity in flora and fauna [11], 42 species and 18 genera of palm trees have been identified, mainly in four forest habitats: terra firme, flood plain, terrace and premontane hills. These forests present densities ranged from 1709 to 3245 (on average 2755) palms/hectare [12].

In general, terrace forests present a lower species richness and abundance of palm trees compared to other forests in the Madre de Dios Region, Peru [12]. Within the palm trees of the Peruvian Amazon that inhabit terrace forests, *O. mapora* has received less attention. However, this palm tree has a high economic potential due to the different uses attributed to it, which is why it is highly valued by the Ashaninka population of Peru [13]. The roots and pods are attributed a medicinal and cosmetic use, the logs are used in the construction of rustic houses, the leaves for the construction of baskets and house roofs, while the fruits have a high nutraceutical potential, from which the pulp and oil can be extracted. Ripe fruits are used to make beverages that can be consumed locally or exploited commercially [14]. In tropical forests, palms can contribute more than 80% of the total biomass of the fruit fall, which constitute a “key resource” for the survival of frugivorous vertebrates and the maintenance of Neotropical rainforests [15]. In the case of *O. mapora* fruits, these have a high potential for industrial exploitation due to their high content of phenolic compounds and polyunsaturated fatty acids.

To our knowledge, this is the first study to evaluate the phenological behavior of *O. mapora* in the Peruvian Amazon. This study evaluated the hypothesis that meteorological conditions or habitat influence the phenological pattern of *O. mapora*, with higher productivity associated with lower altitudes. The objective of this research was to compare the phenological behavior and productivity of *O. mapora* in two types of habitats (low-terrace and high-terrace forests) from the Madre de Dios Region, Peru.

2. Materials and Methods

2.1. Species Studied

O. mapora is a monocaule or multicaule Amazonian palm, belonging to the Arecaceae family, which has up to 10 stems, a height and diameter between 5–15 m and 4–17 cm, respectively. It can be found in primary or moderately intervened humid forests, which can be on the mainland or flooded areas. It is distributed from Central America to Northern South America, including the Amazon basin, from sea level to 1000 m of altitude [16,17]. In Peru, it is distributed along the lower Ucayali, often in swamps where *Mauritia flexuosa* L.f. inhabits. In this region, the density of *O. mapora* can reach 351 trees per hectare. In the Peruvian Amazon, *O. mapora* is called “sinami”, “sinamillo”, “ciame” or “ungurahuillo”. Generally, its fruits appear at the end of the rainy season and at the beginning of summer, when they are ripe, they are dark purple in color and can be used for making beverages [18].

2.2. Study Area

The study was carried out between June 2019 and January 2020 (in eight field trips) at the “Los Amigos” Biological Station, granted to the “Asociación para la Conservación de la Cuenca Amazónica (ACCA)”, located in the “Los Amigos” river basin in the lower Amazon rainforest of the Madre de Dios Region (12°34′06.9″–12°50′10.12″ S, 70°05′56.5″–70°40′26″ W), ranging from 200–300 m asl [19]. This area has an extension of 145,918 ha and a total perimeter of 450 km. The climate of this region is hot, humid and seasonal [20]. The dry season occurs from May to October and the rainy season from November to April [21]. The annual average temperature is 24.2 °C, with a maximum and minimum temperature of 37.9 °C and 11.3 °C, respectively. Average annual precipitation is 2648 mm, average relative humidity and minimum relative humidity are 87.6% and 29.2%, respectively [19]. According to the classification of Life Zones by Holdridge [22], the Madre de Dios Region of Peru belongs to the Transitional to Subtropical Tropical Humid Forest Life Zone (bh-T/S). In this region, the terrace forest and floodplain forest predominate.

Furthermore, it presents in its surroundings bamboo patches, primary succession forest, riparian vegetation and areas altered by artisanal gold mining [19]. The present study was carried out in two types of habitats: low-terrace and high-terrace forests (Figure 1). Terraced forests are found along rivers, adjacent to and similar to floodplains, but located outside the flood zone. The terraces are flat and originated as floodplains but have risen higher due to tectonic movements [12]. Terrace forests can be subdivided into low-terrace forest located on terraces formed during the Pleistocene and high-terrace forest located on the Pebas and Ipururo formations developed in the late Tertiary [23].

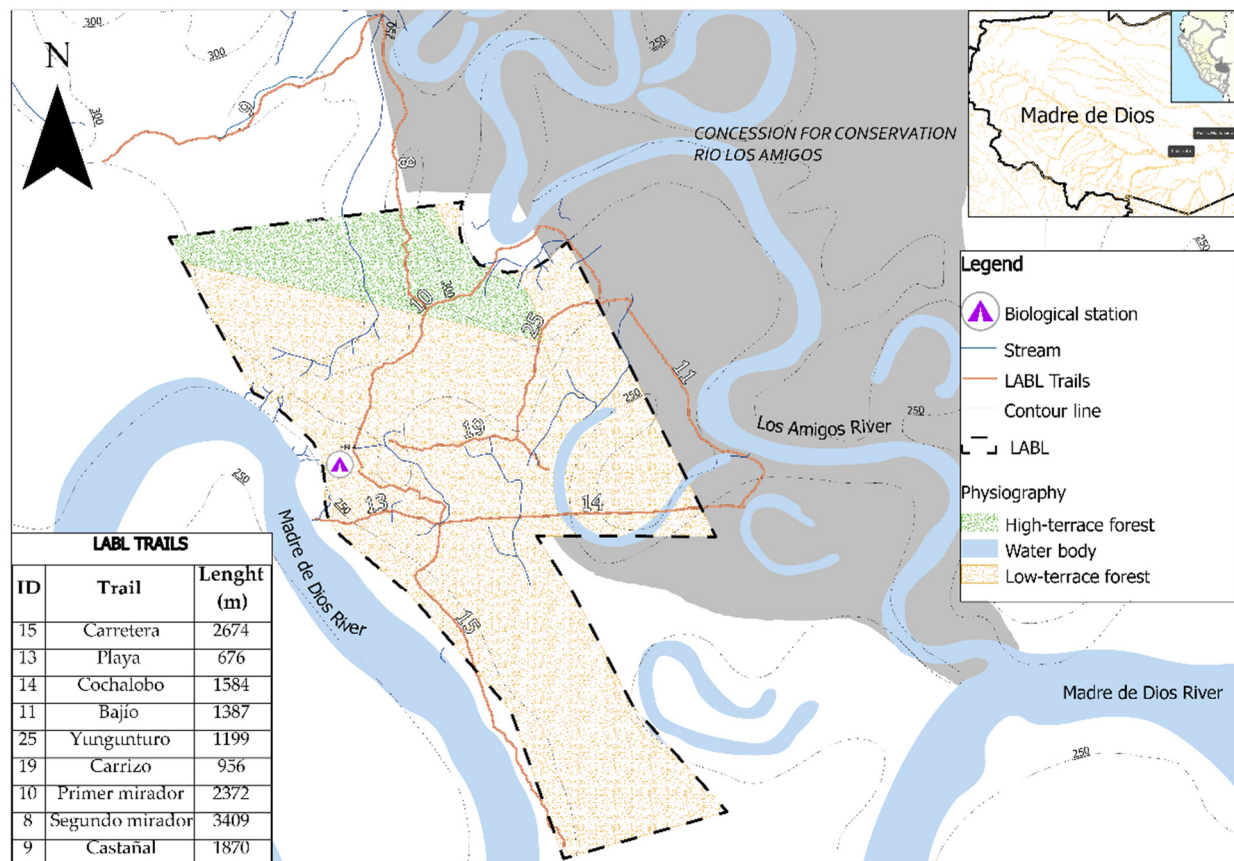


Figure 1. Location map of the study area in the “Los Amigos” Biological Station in the Madre de Dios Region, Peru. LABL: “Los Amigos” Biological Station.

2.3. Selection of Individuals

For the identification of *O. mapora* individuals, the variable transect method proposed by Foster et al. [24] was used, which allows to quickly perform vegetation evaluations. In the present study, approximately eight palm trees were evaluated for each transect. The phenological monitoring was carried out in low-terrace and high-terrace forests, in nine existing trails of the “Los Amigos” Biological Station of the Madre de Dios Region, Peru (Table 1).

Table 1. Geographical characterization of the trails evaluated in the study.

Trail	Habitat	Length (m)	Altitude (m asl)	Longitude	Latitude
Carretera	Low-terrace forest	2674	250–300	−70.094397	−12.576631
Playa	Low-terrace forest	676	250–270	−70.088417	−12.570647
Cochalobo	Low-terrace forest	1584	250–275	−70.098553	−12.570858
Bajío	Low-terrace forest	1387	250–286	−70.083242	−12.565974
Yungunturo	High-terrace forest	1199	285–300	−70.089977	−12.562769
Carrizo	High-terrace forest	956	268–300	−70.094028	−12.567466
Primer mirador	High-terrace forest	2372	250–300	−70.094459	−12.561381
Segundo mirador	High-terrace forest	3409	264–300	−70.099235	−12.547318
Castañal	High-terrace forest	1870	270–300	−70.104610	−12.551184

The individuals of *O. mapora* were selected according to Ureta et al. [21], considering: (a) individuals capable of producing flowers and fruits, (b) individuals with flowers and fruits, and (c) individuals with a crown free of infestations (lianas, epiphytes and stranglers). Likewise, for each one of the individuals of *O. mapora*, the height, number of mature green leaves and bunches per individual were recorded (Table 2).

Table 2. Main characteristics of *O. mapora* in low-terrace and high-terrace forests in the Madre de Dios Region, Peru.

Parameter	Low-Terrace Forest (<i>n</i> = 84)	High-Terrace Forest (<i>n</i> = 132)
Height (m)	10.52 ± 2.93	11.95 ± 1.89 *
Number of mature green leaves per individual	8.07 ± 1.40	7.84 ± 1.35 *
Number of bunches per individual	1.55 ± 0.67	1.42 ± 0.60 *

* Differences between groups were evaluated using the Mann Whitney U test., *p* < 0.05.

2.4. Reproductive Phenology, Rainfall and Temperature

Two hundred sixteen individuals of *O. mapora* (84 and 132 in low-terrace and high-terrace forests, respectively) were directly monitored monthly with binoculars [25] by two people for a period of eight months from June 2019 to January 2020. For each individual, the total number of the following phenophases was recorded monthly: (1) Unopened inflorescences (flower buds), (2) Open inflorescences (open flowers), (3) Green inflorescences (unripe fruits) and (4) Ripe inflorescences (ripe fruits) (Figure 2).

The rainfall and temperature data were obtained from the meteorological station “Monitoring Center 1” located in the low-terrace forest in the “Los Amigos” Conservation Concession, Madre de Dios Region, Peru. In the study area, there is another meteorological station located at a distance of 3.5 km from “Monitoring Center 1”; however, it did not record complete data for this period.

As shown in Figure 3, during the study period, a rainfall between 85–551 mm (212 mm on average) was observed. Rainfall had a unimodal behavior, with a maximum peak in December with 551.20 mm. The number of days with precipitation varied between 4 and 31 days (17 days on average). The climate was warm with an average temperature ranged between 25.69 to 29.52 °C (27.87 °C on average), while the maximum and minimum temperatures varied between 33.47 to 38.10 °C and 17.39 to 23.00 °C, respectively.



Figure 2. (A) *O. mapora* in its natural habitat, (B) Flower bud, (C) Open flower, (D) Unripe fruits and (E) Ripe fruits.

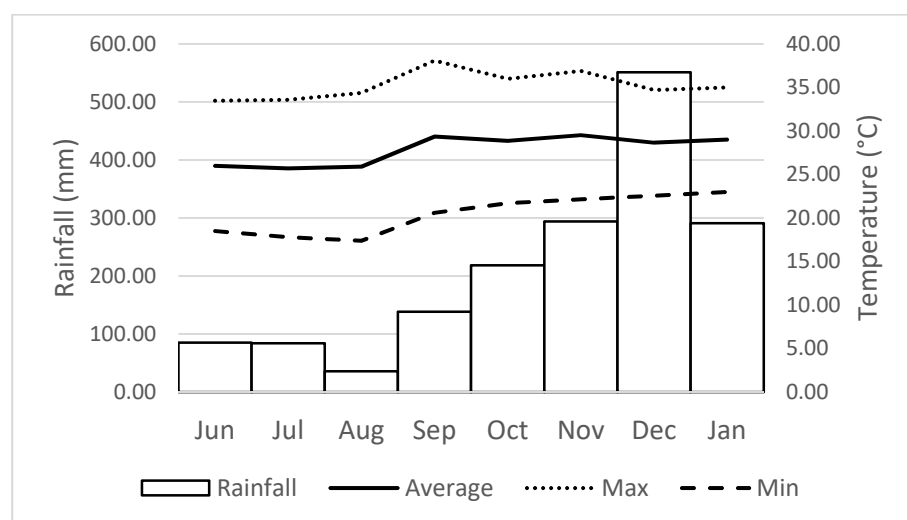


Figure 3. Rainfall and monthly temperature between June 2019 to January 2020 in the Madre de Dios Region, Peru. Months are represented by their first three letters. Max: Maximum, Min: Minimum.

2.5. Biometric Characteristics of the Fruits

Each bunch of *O. mapora* produced between 500 and 700 fruits. From five individuals of *O. mapora* from low-terrace and high-terrace forests, 223 fruits from different positions

along the rachis were selected to evaluate their biometric characteristics. For each of the fruits, the length, width and weight of the fruit were recorded.

2.6. Data Analysis

The mean date for all phenological variables was calculated using the weighted average date of occurrence, which is the arithmetic mean of all the dates on which the occurrence was observed, weighted by its abundance on each date [26,27]. This analysis was carried out with the R software version 4.0.4. Differences in the intensity of the different phenological variables between low-terrace and high-terrace forests were evaluated using the non-parametric Mann-Whitney U test. Furthermore, to evaluate the association between the climatic and phenological variables, the monthly mean of each climatic variables was correlated with the monthly average per individual of each phenological variable using the Spearman method. These results were considered significant at $p < 0.05$ and $p < 0.01$.

3. Results

3.1. Plant Height and Mature Green Leaves

As shown in Figure 4 and Table 3, the different phenological variables evaluated showed variation in their intensity in low-terrace and high-terrace forests. In the high-terrace forest, the palm trees presented a significantly higher average height compared to the low-terrace forest ($p < 0.05$). In both forest subtypes, no significant differences were found in the height of *O. mapora* depending on the season.

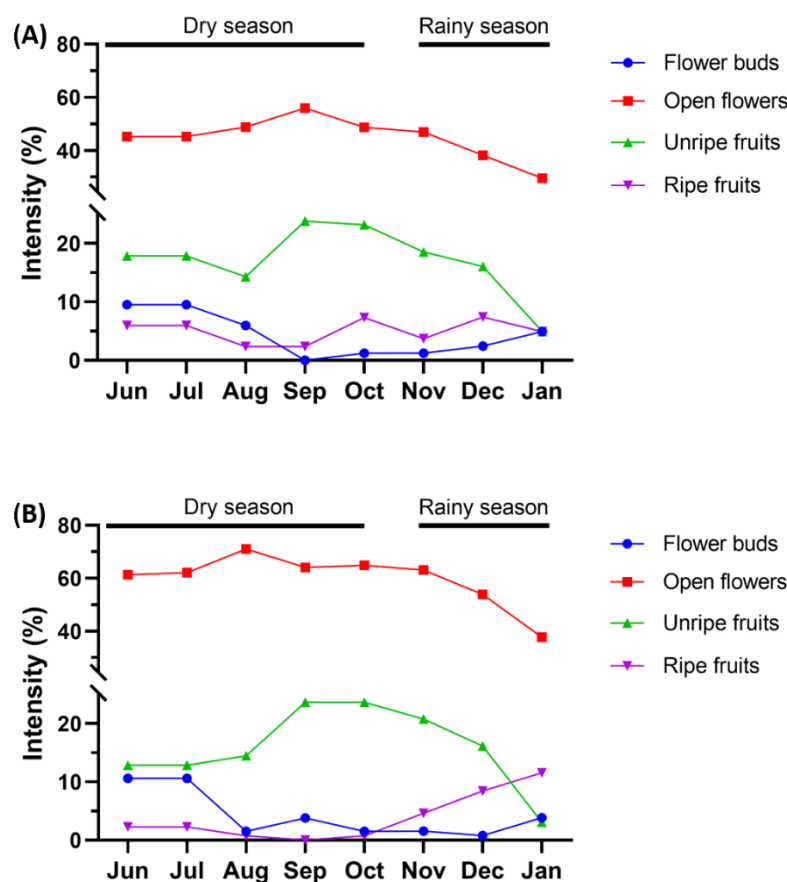


Figure 4. Intensity of phenophases of *O. mapora* for low-terrace (A) and high-terrace forests (B) of the Madre de Dios Region, Peru.

Table 3. Weighted mean of phenological variables in low-terrace and high-terrace forests of the Madre de Dios Region, Peru.

Habitat	Mature Green Leaves	Bunches	Flower Buds	Open Flowers	Unripe Fruits	Ripe Fruits
Low-terrace forest						
Mean date	222 (10 August 2019)	223 (11 August 2019)	182 (1 July 2019)	231 (19 August 2019)	244 (1 September 2019)	226 (14 August 2019)
High-terrace forest						
Mean date	222 (10 August 2019)	224 (12 August 2019)	184 (3 July 2019)	231 (19 August 2019)	254 (11 September 2019)	185 (4 July 2019)

Data were expressed in Julian days.

In low-terrace and high-terrace forests, the number of mature green leaves and bunches per individual presented a mean date in August, in the middle of the dry season (May to October). In both habitats, the number of mature green leaves was stable throughout the evaluated period, with a significantly higher number of mature green leaves in the low-terrace forest compared to the high-terrace forest ($p < 0.05$). Likewise, throughout the study, the average number of bunches per individual was higher in the low-terrace forest compared to the high-terrace forest ($p < 0.05$).

As shown in Table 4, in the low-terrace forest, the climatic variables (minimum temperature, rainfall and numbers of days with precipitation) showed a positive correlation with the height of the palm tree ($p < 0.05$). On the other hand, in the high-terrace forest, minimum temperature, rainfall and numbers of days with precipitation showed a negative correlation with average height of the palm tree ($p < 0.05$).

Table 4. Spearman's correlation coefficients (Rs) between monthly phenological variables and environmental factors in low-terrace and high-terrace forests of the Madre de Dios Region, Peru.

Variables	Habitat	Temperature			Rainfall	Number of Days of Precipitation
		Average	Maximum	Minimum		
Height	Low-terrace forest	0.526	0.451	0.801 *	0.801 *	0.743 *
	High-terrace forest	−0.761 *	−0.638	−0.896 **	−0.896 **	−0.722 *
Number of Mature Green Leaves	Low-terrace forest	−0.552	−0.552	−0.430	−0.381	−0.173
	High-terrace forest	0.401	0.250	0.451	0.375	0.315
Number of Bunches	Low-terrace forest	0.132	0.419	−0.180	−0.036	−0.277
	High-terrace forest	−0.073	0.146	−0.073	0.146	0.012
Flower Buds	Low-terrace forest	−0.790 *	−0.946 **	−0.443	−0.515	−0.090
	High-terrace forest	−0.181	−0.361	−0.253	−0.422	−0.194
Open Flowers	Low-terrace forest	0.144	0.419	−0.563	−0.443	−0.789 *
	High-terrace forest	−0.048	0.262	−0.619	−0.500	−0.766 *
Unripe Fruits	Low-terrace forest	0.407	0.539	−0.132	0.036	−0.283
	High-terrace forest	0.482	0.711 *	0.024	0.241	−0.182
Ripe Fruits	Low-terrace forest	−0.277	−0.337	0.337	0.410	0.612
	High-terrace forest	0.108	−0.193	0.687	0.615	0.861 **

* $p < 0.05$, ** $p < 0.01$.

3.2. Flowering and Fructification

During the study period, no large temperature fluctuations were observed. Between June to August, a lower average temperature was observed (25.69 to 25.98 °C), while between July to January an increase in the average temperature was observed (28.65 to 29.52 °C). Likewise, during the rainy season, from November to January, a significant increase in rainfall was observed, ranging from 291 to 551.20 mm.

Regarding flowering phenology, flower buds were continuous in low-terrace and high-terrace forests, with a mean date in July, peaking in June; while open flowers were also continuous in low-terrace and high-terrace forests, with a mean date and peaking in August, at the end of the dry season (May to October). When comparing the flowering pattern between both forest subtypes, the number of open flowers was significantly

higher in the high-terrace forest compared to the low-terrace forest ($59.76 \pm 10.09\%$ and $44.85 \pm 7.36\%$, respectively, $p < 0.05$).

Likewise, in the low-terrace forest, average and maximum temperature showed a negative correlation with flower buds ($p < 0.05$), while numbers of days with precipitation showed a negative correlation with open flowers ($p < 0.05$).

Fruiting phenology showed a continuous pattern for unripe fruits in low-terrace and high-terrace forests, with a mean date and peaking in September, at the end of the dry season. Ripe fruits were also continuous in the low-terrace forest, with a mean date in August, peaking in December; while in the high-terrace forest, ripe fruits peaked in January with a mean date in July. In both forest subtypes, a higher occurrence of ripe fruits was observed in the middle of the rainy season (November to April). The ripe fruits had a length, width and weight of 18.9 ± 1.0 mm, 17.8 ± 0.9 mm and 3.9 ± 0.5 g, respectively.

No statistically significant differences were observed in the flowering pattern and unripe fruits between low-terrace and high-terrace forests. Throughout the study, the presence of ripe fruits were higher in the low-terrace forest compared to the high-terrace forest, although statistically significant differences were not observed.

Furthermore, in the high-terrace forest, the maximum temperature was positively correlated with unripe fruits ($p < 0.05$), while the number of days with precipitation showed a negative and positive correlation with open flowers and ripe fruits, respectively ($p < 0.05$).

4. Discussion

4.1. Plant Height and Mature Green Leaves

In plants, the height of an individual is correlated with its reproductive ability because larger individuals have a greater potential for obtaining the resources necessary for their reproduction [28]. In some palm species such as *Butia*, *Geonoma*, and *Chamaedorea*, height is associated with higher fruit or leaf productivity [29–31]. Particularly in *B. capitata*, the number of mature green leaves associated with its aerial foliar biomass and photosynthetic potential, represents a good indicator of its productivity. A higher productivity was found in a younger population composed of shorter individuals compared to older and taller individuals. An increase in height followed by the senescence of the palm tree would explain the decrease in the production of leaves and fruits [31]. Likewise, growth rates of a plant may decline with altitude because the intensity of competition for light decreases at a higher altitude [32]. According to these findings, in the present study, in the low-terrace forest compared to the high-terrace forest, *O. mapora* individuals presented a lower height. However, these individuals showed higher productivity represented by an increased number of mature green leaves and bunches, which would indicate that similar to *B. capitata* [31], productivity in *O. mapora* could be associated with the number of mature green leaves.

4.2. Flowering and Fructification

In many tropical species, the phenological behavior varies between geographic regions, and may be related to habitat and climatic conditions [33]. There are few studies on the reproductive phenology of palms of the genus *Oenocarpus* in South America. Some studies carried out in other *Oenocarpus* species, such as *O. bataua*, have reported a lack of synchrony between the individuals of a population in regions where there is no greater variation in climatic factors or it responds to endogenous factors [34,35].

A study in which the reproductive phenology of *O. bataua* was evaluated for four years in the forests of the Colombian Andes reported different peaks of flowering and fruiting during the evaluated period, observing a lack of synchrony between and within individuals. Likewise, due to the climatic conditions in which there was no greater fluctuation in temperature and rainfall during the evaluated period, no effect was observed on the onset or frequency of phenological events [34]. Furthermore, in a study carried out on the phenology of *O. bataua* in two forest types: occasionally and periodically flooded, in the Chocó Biogeographic Region of Colombia, a synchrony was not observed in the occurrence of the different phenological phases evaluated: flower bud, unfertilized inflorescence,

fertilized inflorescence, infrutescence with immature fruits, infrutescence with ripe fruits and dry bunches. Similarly, there was no significant association between precipitation and the occurrence of phenophases, so its phenological cycle seems to respond to endogenous factors and/or to ecological-evolutionary relationships [35].

Another study carried out in eight species of palm trees (*Euterpe precatoria*, *Oenocarpus bataua*, *Iriarteia deltoidea*, *Mauritia flexuosa*, *Bactris gasipaes*, *Astrocaryum murumuru*, *Socratea exorrhiza* and *Attalea phalerata*) in the Amazon rainforest of Bolivia, found that the phenology was variable according to the climate seasonal of the Amazonian forest of Hondo River, observing a decrease in the occurrence of flowers and fruits during the dry season. In the case of *O. bataua*, long asynchronous flowering and short synchronous fruiting were observed. The presence of flowers occurred throughout the rainy season (December to February), while the presence of immature fruits was observed throughout the year. The presence of ripe fruits was recorded mainly in the dry season (June to August) and lasted until the transition from the dry to rainy season (March to May) [36].

Some studies show that flowering begins at the end of the dry season, probably because palm tree seeds have the ability to germinate quickly when water and nutrients are available in the rainy season [37]. Likewise, the availability of fruits is related to a period of greater intensity of rains [38].

In the present study, during February to May 2020, complete data on the phenology of *O. mapora* could not be recorded. However, a previous study carried out between July 2005 and May 2008 in two localities of the Madre de Dios Region, Peru, such as Tampo-bata and “Los Amigos”, in which the dry and rainy seasons occur in the same periods as our investigation, reported in general that seven arborescent palms (*Mauritia flexuosa*, *Socratea exorrhiza*, *Euterpe precatoria*, *Oenocarpus bataua*, *Iriarteia deltoidea*, *Astrocaryum murumuru* and *Attalea butyracea*) that inhabit these areas, flowering occurred during the rainy season while fruiting occurred during the transition from dry to rainy season. Particularly in “Los Amigos”, located on the banks of the Madre de Dios and Los Amigos rivers, some palm trees such as *A. butyracea* showed an annual flowering and fruiting pattern. Other palms of the genus *Oenocarpus*, such as *O. bataua*, presented a sub-annual to continuous flowering pattern with maximum productivity peaks of 40% in the rainy season, while fruiting showed a continuous pattern, with peaks that varied between 60% and 80% throughout the rainy season [21]. There is no evidence on the phenological behavior of *O. mapora* in Amazonian rainforests.

During the present study, the lower Amazon rainforest of the Madre de Dios Region of Peru presented a warm climate, however, during the winter months between June to August, the lowest minimum temperature was recorded (on average 17.90 °C), which favored the formation of flower buds during these months. According to this finding, in the low-terrace forest a negative correlation was observed between flower buds with the maximum temperature and average temperature. Previous studies show that flowering is stimulated at low temperatures close to 17 °C but is reduced when the temperature is increased to 24 °C [39,40].

Furthermore, an increase of approximately 4 °C in the average temperature was observed during the spring months between September to December. During this period, in both low-terrace and high-terrace forests, this increase in average temperature is consistent with an increase in the presence of open flowers in August. A previous study shows that an increase in temperature from 20 °C to 30–35 °C, in the presence of light, is required for a rapid flower opening, observing a full opening in the presence of light and high temperatures [41]. According to these findings, a lower intensity in the abundance of open flowers was observed in the low-terrace forest, where the climatic conditions for the present study were recorded. However, altitude has an effect on phenological behavior through air temperature, causing a decrease in temperature of approximately 0.6 °C per 100 m [42], which would produce a lower minimum temperature in the high-terrace forest, driving a greater abundance of open flowers.

Comparing the two subtypes of forests evaluated in the present study, no differences were observed in the fruiting pattern, with the exception of the occurrence of ripe fruits, whose peak in low-terrace and high-terrace forests was at the beginning and middle of the rainy season, respectively.

During the evaluated period, an increase in rainfall was observed from November to January. Interestingly, an increase in the number of ripe fruits was associated with a greater intensity of rainfall and number of days with precipitation. However, in the high-terrace forest, the occurrence of ripe fruits significantly correlated with the number of days of precipitation, observing a trend in the association with rainfall. Probably, a greater availability of water in the soil mediated by a greater number of days of precipitation would be important in palm trees that grow in flooded soils such as *O. mapora*. According to this, the aptitude of this Amazon palm was associated with a greater availability of water observed during the middle of the rainy season [43].

The study of the vegetative and reproductive phenology of *O. mapora* is of great interest to understand the ecosystem and availability of resources in the Peruvian Amazon. In this sense, this palm has a high economic potential as a nutraceutical and is also part of the diet of several Amazonian herbivores, which favors its distribution and density in the Amazon forests of the Madre de Dios Region, Peru.

5. Conclusions

During our study, climatic conditions in the lower Amazon rainforest of the Madre de Dios Region, Peru, caused the flowering of *O. mapora* to be observed throughout the evaluated period, while fruiting increased from the middle of the rainy season. Flowering was influenced by temperature and type of habitat, while fruiting was associated with an increase in the number of days with precipitation. Furthermore, depending on the habitat, terrace forests located at higher altitudes had a lower average palm height, as well as a lower number of mature green leaves and bunches per individual, probably due to greater senescence and lower productivity of the palm trees. However, long-term studies are required to evaluate the effects of habitat and inter-annual climatic variation on flowering and fruiting events of this important southeastern Peruvian Amazon palm.

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