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Phenology of *Annona macrophyllata* (Annonaceae) along an elevational gradient in a tropical deciduous forests of Chiapas, Mexico

Fenología de *Annona macrophyllata* (Annonaceae) en un gradiente altitudinal en un bosque tropical caducifolio de Chiapas, México

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Abstract:

Background and Aims: *Annona macrophyllata* (Annonaceae) is widely distributed in the tropical deciduous forests (TDF) of southern Mexico and Central America. TDF is an ecosystem characterized by seasonal changes determined by high precipitation. The alternation between rainy and dry seasons has favored deciduous phenological patterns in plants that inhabit this ecosystem. Describing phenological events is essential for understanding plant life cycles and the phenotypic plasticity of plants. This study aimed to evaluate the phenology of *A. macrophyllata* along an elevational gradient in the state of Chiapas, Mexico, in order to contribute to the understanding of its life cycle, phenotypic plasticity, and capacity to adapt to climatic variations.

Methods: The stages of leaf formation, flowering, fruiting, and senescence were recorded at four TDF locations in the state of Chiapas, Mexico, along an elevational gradient of 24-1300 m. Phenology was determined over an annual cycle using the extended scale of the Biologische Bundesanstalt, Bundessortenamt and Chemische Industrie (BBCH). The seasonality of the study sites was determined using data from meteorological stations of the National Water Commission of the Government of Mexico.

Key results: *A. macrophyllata* showed a deciduous habit across the entire elevational gradient. The vegetative phenology phases are seasonally separated; leaf budding occurs during the rainy season, while senescence occurs during the dry season. Reproductive phenology is exclusively associated with the rainy season; flowering occurs at the beginning of this season, and fruit development extends throughout the rainy season. At lower elevation sites (24-500 m), fruit development was completed earlier than at higher elevation sites (700-1300 m).

Conclusions: *Annona macrophyllata* shows deciduous phenology that is synchronous across the elevational gradient and independent of local climatic variations.

Key words: BBCH, dry deciduous forest, phenophases, seasonality.

Resumen:

Antecedentes y Objetivos: *Annona macrophyllata* (Annonaceae) se distribuye en bosques tropicales caducifolios (BTC) del sur de México y Centroamérica. El BTC es un ecosistema que se caracteriza por cambios estacionales determinados por la precipitación. La alternancia entre las estaciones de lluvia y sequía ha favorecido patrones fenológicos caducifolios en las plantas que habitan este ecosistema. La descripción de eventos fenológicos es fundamental para comprender los ciclos de vida y la plasticidad fenotípica de las plantas. El objetivo de este estudio fue registrar la fenología de *A. macrophyllata* en un gradiente altitudinal del BTC de Chiapas, proporcionando información sobre la especie y su entorno.

Métodos: Se documentaron los estados de foliación, floración, fructificación y senescencia en cuatro localidades del BTC del estado de Chiapas, México en un gradiente elevacional (24-1300 m). La fenología se determinó durante un ciclo anual utilizando la escala extendida Biologische Bundesanstalt, Bundessortenamt and Chemische Industrie (BBCH). La estacionalidad de los sitios de estudio se determinó con datos de las estaciones meteorológicas de la Comisión Nacional del Agua del Gobierno de México.

Resultados clave: *Annona macrophyllata* mostró un hábito caducifolio en todo el gradiente altitudinal. Las fases de la fenología vegetativa están separadas en la estacionalidad, la brotación foliar sucede durante la temporada de lluvias, mientras que la senescencia en la estación seca. La fenología reproductiva está asociada exclusivamente a la estación de lluvias, la floración se presenta al inicio de esta estación y el desarrollo de frutos se extiende en todo el periodo de lluvias. En los sitios de menor elevación (24-500 m) el desarrollo de frutos concluyó antes que en los de mayor altitud (700-1300 m).

Conclusiones: *Annona macrophyllata* muestra una fenología caducifolia sincrónica en el gradiente altitudinal e independiente de las variaciones climáticas locales.

Palabras clave: BBCH, bosque seco caducifolio, estacionalidad, fenofases.

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Introduction

Phenological variation is one of the phenotypic plasticity responses of plants to environmental changes (Bonamour et al., 2019). In plant species distributed across elevational gradients, phenological changes are primarily manifested in the flowering and fruiting periods (Exner et al., 2010; Mondino et al., 2019). The duration of the vegetative and reproductive periods are influenced by abiotic factors such as temperature, radiation, and precipitation, which vary with altitude (Cortés-Flores et al., 2019). These elevational variations generate recurring trends in the frequency and duration of phenological phases, allowing the identification of phenological patterns associated with specific environmental conditions. These phenological patterns are particularly notable in seasonal ecosystems such as tropical deciduous forests (TDF), where the alternation between the rainy season and the dry season determines the life cycles of plants (Borchert, 1999; Balvanera et al., 2000). Most species in TDF exhibit deciduous habits, synchronizing leaf budding with the onset of rain and senescence with drought. These behaviors represent phenological and physiological adaptations that allow them to survive in a climate profile with distinct seasons and prolonged periods of water deficit (Nanda et al., 2014; González-Esquinca et al., 2016; Lima et al., 2021; Pereira et al., 2024).

Although these phenological patterns have been widely documented in diverse ecosystems (Gottsberger 1989; Godoy et al., 2009; Azeez and Folorunso, 2014; Jiménez-Zurita et al., 2023; Dewi et al., 2023). Studies on TDF that analyze the effect of elevational gradients are scarce and represent a knowledge gap for characterizing widely distributed species. In contrast, in temperate forests and mountain systems, there is evidence that elevation modulates phenological patterns, although with differentiated responses depending on the life form (Ziello et al., 2009; Inouye and Wielgolaski, 2024). For instance, in herbaceous plants such as *Lupinus luteus* L. (Fabaceae) (Berger et al., 2008) and *L. polyphyllus* Lindl. (Ludewig et al., 2022), phenological cycles are shortened at low elevations. However, in tree species such as *Pinus pseudostrobus* Lind. (Pinaceae) and *Fagus sylvatica* L. (Fagaceae), phenological events are advanced and vegetative growth is prolonged in sites

of lower elevation (Viveros-Viveros et al., 2006; Dittmar and Elling, 2006; Hájková et al., 2010; Čufar et al., 2012). Regarding reproductive phenology, elevation can affect flowering patterns, and their timing is likely to shift at higher elevations, as observed in alpine species of the genus *Primula* (*P. denticulata* Sm., *P. sikkimensis* Hook., *P. capitata* Wall. Ex Duby, *P. dickieana* Watt, *P. glomerata* Pall., and *P. primulina* (Spreng.) H. Hara); Gurung et al., 2018), *Cerasus leveilleana* (Koehne) H. Ohba and *C. sargentii* (Rehder) H. Ohba (wild cherry) (Tochigi et al., 2021). Therefore, delays in early flowering periods that occur at higher elevations may partially overlap with later flowering periods at lower elevations (Tochigi et al., 2021). The latter may be relevant for important food species grown across elevational gradients, as they would maintain longer production periods, resulting in longer marketing periods.

Tropical species have been less explored from a phenological perspective, despite their great diversity and ecological relevance. This is the case of *Annona* L. (Annonaceae); this genus has ecological and economic importance in tropical ecosystems. Phenology aspects have been documented for *Annona lutescens* Saff., *A. reticulata* L., *A. purpurea* Moc. & Sessé ex Dunal, *A. glabra* L., *A. montana* Macfad., *A. muricata* L., *A. squamosa* L., and *A. senegalensis* Pers. (Azeez and Folorunso, 2014; Dewi and Siti, 2015; González-Esquinca et al., 2016; Mendes et al., 2019); however, it is unknown whether phenological characteristics are conserved along elevational gradients, particularly in relation to variations in climatic factors.

A species of particular interest is *Annona macrophyllata* Donn.Sm., a deciduous tree that inhabits the TDF of southern Mexico and Central America, and whose distribution is mainly concentrated at elevations below 1300 m a.s.l. (Cruz Pineda, 2002). It is known as “papausa” or “ilama” and is considered of economic importance given its fruits appreciated for their characteristics (González-Esquinca et al., 2015). Although not as well-known as soursop (*A. muricata*), sugar apple (*A. squamosa*), or custard apple (*A. cherimola* Mill.), it can be considered a fruit species with high potential in marketing chains. Its phenological cycle shows a marked synchronization with the seasonal regime. During the rainy season, it experiences active



growth of shoots, branches, leaves, and fruits, while in the dry season, it enters a state of vegetative dormancy (Otero-Sánchez et al., 2015; González-Esquinca et al., 2016). This species has developed physiological and phenological mechanisms to avoid water stress, adjusting its growth cycle in response to soil temperature and humidity (Otero-Sánchez et al., 2006). However, how environmental factors associated with elevational gradients, such as temperature and precipitation, modulate its phenology is unknown, which limits the understanding of its adaptive plasticity in the face of variable conditions.

This study aimed to evaluate the phenology of *A. macrophyllata* along an elevational gradient in the state of Chiapas, Mexico, in order to contribute to the understanding of its life cycle, phenotypic plasticity, and capacity to adapt to climatic variations. The results provide a basis for developing strategies for the conservation, marketing, and sustainable management of this species.

Materials and Methods

Study area

The study area was located in a tropical deciduous forest across an elevational gradient between 24 and 1300 m. The study was conducted in the municipalities Tonalá (15°59'44"N 93°49'0"W; 24 m), Chiapa de Corzo (16°41'49"N 92°57'29"W; 550 m), San Lucas (16°36'47"N 92°42'58"W; 660 m), and Las Rosas (16°21'35"N 92°22'42"W; 1307 m) in the state of Chiapas, Mexico. The municipalities Tonalá and Las Rosas represent the extremes of the elevational gradient (Fig. 1). The region's climate is warm and sub-humid, with summer rainfall (AW1), and is characterized by a marked dry season (October-May) and rainy season (June-October). Average annual precipitation is 921.9 mm (García, 1988). Average annual temperature is 25.8 °C; maximum temperature is 38 °C, in exceptionally warm years.

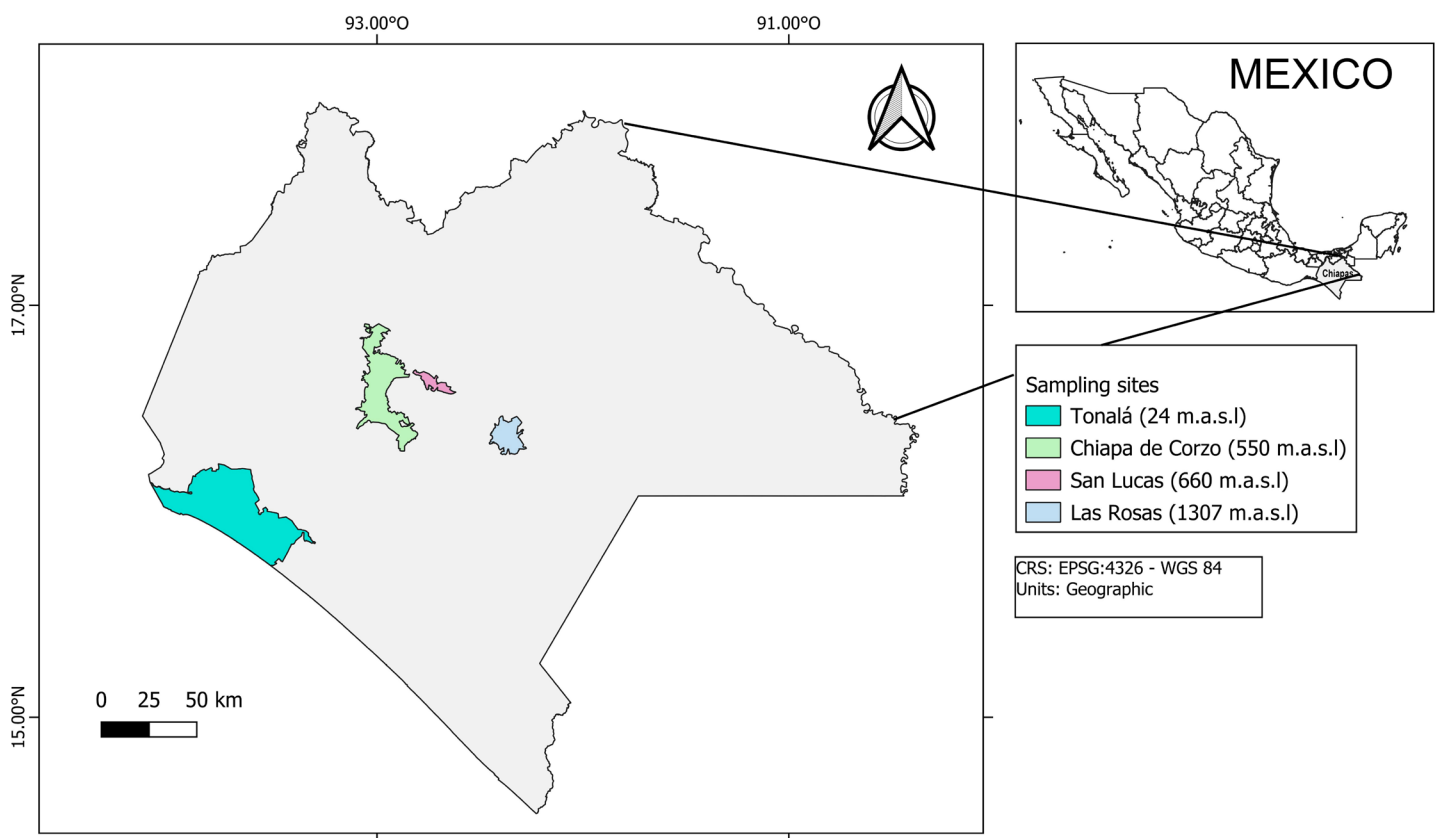


Figure 1: Study area in tropical deciduous forests of Chiapas, Mexico, along an elevational gradient with the presence of *Annona macrophyllata* Donn.Sm. Sampling sites: Tonalá, Chiapa de Corzo, San Lucas, and Las Rosas.



Phenological characterization

In each site, 10 adult *Annona macrophyllata* trees that had fruited at least once and were in good phytosanitary condition were selected. Individuals were located in a dispersed manner within each sampling locality, avoiding spatial clustering to ensure representative coverage of the site. Although no measurements of diameter at breast height, tree height, or canopy size were recorded, all selected individuals were mature trees exhibiting clear reproductive capacity. Plants were numbered and observed every two months from February 2022 to January 2023. This sampling frequency was selected to characterize the main phenological transitions while ensuring logistical feasibility across sites over an annual cycle. Phenophases were recorded through direct observation and photographic documentation. Although this interval allows detection of general seasonal patterns, short-lived phenophases or rapid transitions between stages may have been underrepresented and not adequately detected.

The vegetative and reproductive stages were characterized using the modified and extended “Biologische Bundesanstalt, Bundessortenamt und Chemische Industrie” (BBCH) scale described by Hess et al. (1997). This scale is a standardized decimal coding system that describes the phenological development of plants through major growth stages (0-9) and secondary stages that subdivide the major growth stages into more specific development phases. For this study, the following growth stages were used: leaf development (BBCH 1), leaf senescence and the onset of dormancy (BBCH 9), flowering (BBCH 6), and fruiting (BBCH 7 and 8).

Characterization of precipitation and temperature across the elevational gradient

The seasonality of the study area was determined using precipitation and temperature data from 2022 obtained from the meteorological stations of the National Water Commission (CONAGUA, 2022), affiliated with the Ministry of Environment and Natural Resources of the Government of Mexico. The stations geographically and altitudinally closest to the study sites were selected: Tres Picos (Tonalá), Acala CFE (Chiapa de Corzo), Villa de Chiapilla (San Lucas), and Villa las Rosas. Seasonal patterns were identified by

constructing ombrothermic diagrams using monthly precipitation and mean temperature data for 2022, following the Gaussen criterion ($P=2T$). According to this criterion, dry periods occur when precipitation is less than twice the mean temperature ($P<2T$). This analysis allowed for the delineation of the dry and rainy seasons in the study locations.

Statistical and multivariate analyses

Kendall correlation analyses were performed to evaluate the relationship between phenophases and the elevational gradient. This non-parametric method was selected due to the ordinal nature of the phenological data (BBCH scale) and observed deviations from normality and homoscedasticity assumptions required for parametric tests.

Climatic variables (maximum temperature, mean temperature, minimum temperature, mean precipitation, and elevation) were evaluated using Principal Component Analysis (PCA) to explore patterns of environmental variation among sampling sites and stations. The analysis was based on a standardized environmental data matrix, where variables were scaled to eliminate differences in measurement units. The interpretation of climatic gradients was based on the first two principal components.

Differences in climatic conditions between stations were evaluated using an Analysis of Similarity (ANOSIM) based on the Euclidean distance. This non-parametric test was selected due to observed deviations from multivariate normality in the dataset, making it appropriate for the analysis of ecological data.

To assess the direct relationship between phenological stages and environmental variables, a Canonical Correspondence Analysis (CCA) was performed using phenological stages as response variables and elevation, maximum temperature, minimum temperature, and mean precipitation as explanatory variables. Prior to the analysis, collinearity among environmental variables was evaluated using variance inflation factors (VIF), and highly correlated variables were excluded to improve model stability and interpretability. Mean temperature, although initially considered to describe overall climatic variation, was excluded from the CCA due to high collinearity with other temperature variables. The significance of the CCA model and the



contribution of individual environmental variables were assessed using permutation tests (999 permutations). The analysis was based on a response matrix of phenological stages and an environmental matrix including elevation the selected explanatory variables.

Additionally, Pearson correlation analyses were conducted to examine the relationships between elevation and climatic variables. Prior to these analyses, assumptions of normality and homocedasticity were evaluated; however, given the robustness of Pearson correlation to moderate deviations from normality and the exploratory nature of this analysis, this method was considered appropriate.

Although the dataset includes repeated observations of the same individuals over time, mixed-effects models were not applied, because the primary objective of this study was to identify general patterns of association between phenological stages and environmental gradients, rather than to model individual temporal variation. Moreover, the ordinal nature of the phenological variables and the

multivariate structure of the data are more appropriately addressed using ordination techniques.

All statistical analyses were performed in R (version 4.2.1; R Core Team, 2022), using the base *stats* package for correlation analyses, *FactoMineR* and *factoextra* for PCA, and *vegan* for ANOSIM and CCA.

Results

Seasonal characterization along the elevational gradient

Monitoring precipitation and temperature during the phenological study identified well-defined seasonal patterns, with variations across the elevational gradient. The ombrothermic precipitation-temperature diagram for 2022 showed a seasonal pattern in all study sites. The highest rainfall was concentrated between May and September, identifying a five-month rainy season with monthly accumulations between 70 and 500 mm (Fig. 2). In contrast, the dry season extended from October to April, characterized



Figure 2: Ombrothermic diagram of the municipalities Tonalá, Chiapa de Corzo, San Lucas, and Las Rosas, Chiapas, Mexico, for the year 2022. Monthly records of average temperature (dots and dashed lines) and precipitation (bars) obtained from CONAGUA (2022) meteorological stations are shown. The scale was adjusted following the Gausson criterion ($2 \text{ mm of precipitation} = 1^\circ \text{C}$), where periods in which precipitation is less than twice the average temperature ($P < 2T$) indicate dry conditions.



by considerably lower rainfall. During the rainy season, average temperatures indicated that Tonalá (24 m) and Chiapa de Corzo (550 m) had the warmest conditions, with values close to 28 °C. Conversely, at the higher-elevation locations of San Lucas (660 m) and Las Rosas (1307 m), average temperatures remained below 25 °C during the analyzed period.

In contrast, the dry season included the period from October to April, with low rainfalls at all sites, particularly between January and April, with accumulated rainfall of less than 36 mm. During this period, thermal behavior was similar to the rainy season. Tonalá and Chiapa de Corzo maintained warmer temperatures (26–29 °C), while San Lucas and Las Rosas continued to record values below 25 °C.

Principal Component Analysis (PCA) detected differences between the rainy and dry seasons at all evaluated sites (Fig. 3). The first two principal components of PCA explained 83.9% of the total data variability. The first principal component (PC1) explained 63.2% (eigenvalue=3.16) of the variance and grouped the different temperature metrics, with mean temperature showing the highest loading ($r=0.97$), followed by minimum ($r=0.93$) and maximum temperature ($r=0.90$), while elevation showed a negative association with this axis ($r=-0.69$). PC2, which explained 20.7% (eigenvalue=1.04), was strongly and positively associated with precipitation ($r=0.96$), indicating that this variable mainly defines this component. In general, PCA confirms that the months of January, February, March, and

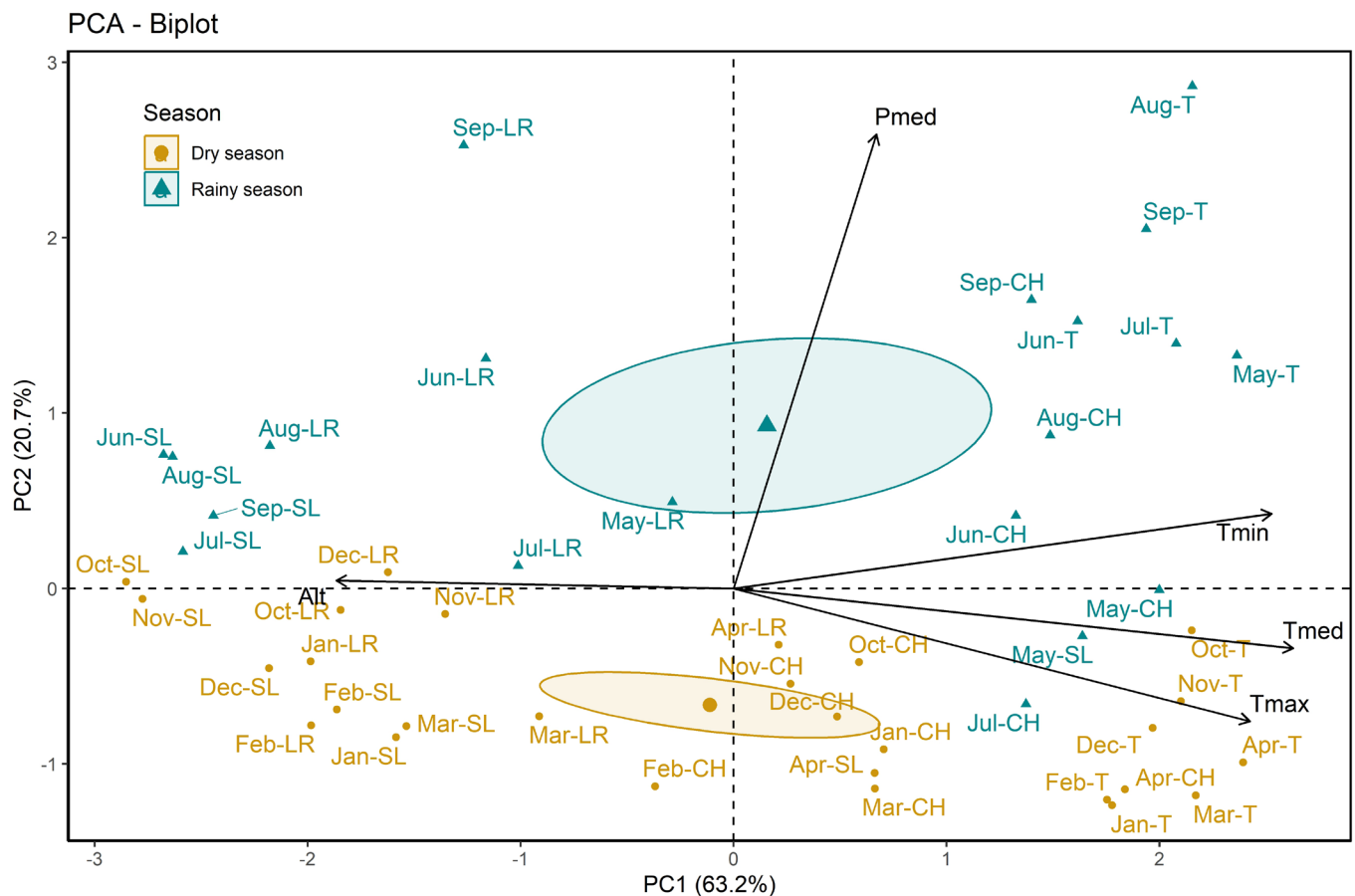


Figure 3: Principal component analysis of environmental variables for the year 2022, in the tropical deciduous forests of Chiapas, Mexico. T (Tonalá); CH (Chiapa de Corzo); SL (San Lucas); LR (Las Rosas). Environmental variables: Pave (average precipitation); Tmin (minimum temperature); Tmax (maximum temperature); Tmea (mean temperature); and Alt (altitude).



April are the most evident period of the dry season, while the period from June to September is the most evident period of the rainy season. At some sites, May and July, when located in the center of the graph, could indicate a transition from drought to rain, while from October to December, transition from rain to drought. The vectors indicating magnitude and direction show that average temperature exerts the greatest influence on seasonal behavior, and rainfall to a lesser extent, while elevation presents a negative correlation with the other variables analyzed.

PCA also showed that seasonal differentiation is consistent along the elevation gradient. This elevational

seasonal constancy was confirmed by a Euclidean distance-based analysis of similarity (ANOSIM), which detected a significant separation between the dry and rainy seasons ($R=0.152$; $p=0.003$).

Canonical Correspondence Analysis (CCA) revealed a significant relationship between phenological stages and environmental variables (permutation test, $F_{4,43}=2.72$, $p=0.002$). The first canonical axis (CCA1) explained 62.3% (eigen value=0.43) of the total variation, while the second axis (CCA2) explained 23.6% (eigen value=0.16) (Fig. 4). Among the environmental variables analyzed, maximum temperature ($p=0.001$) and mean precipitation ($p=0.002$),

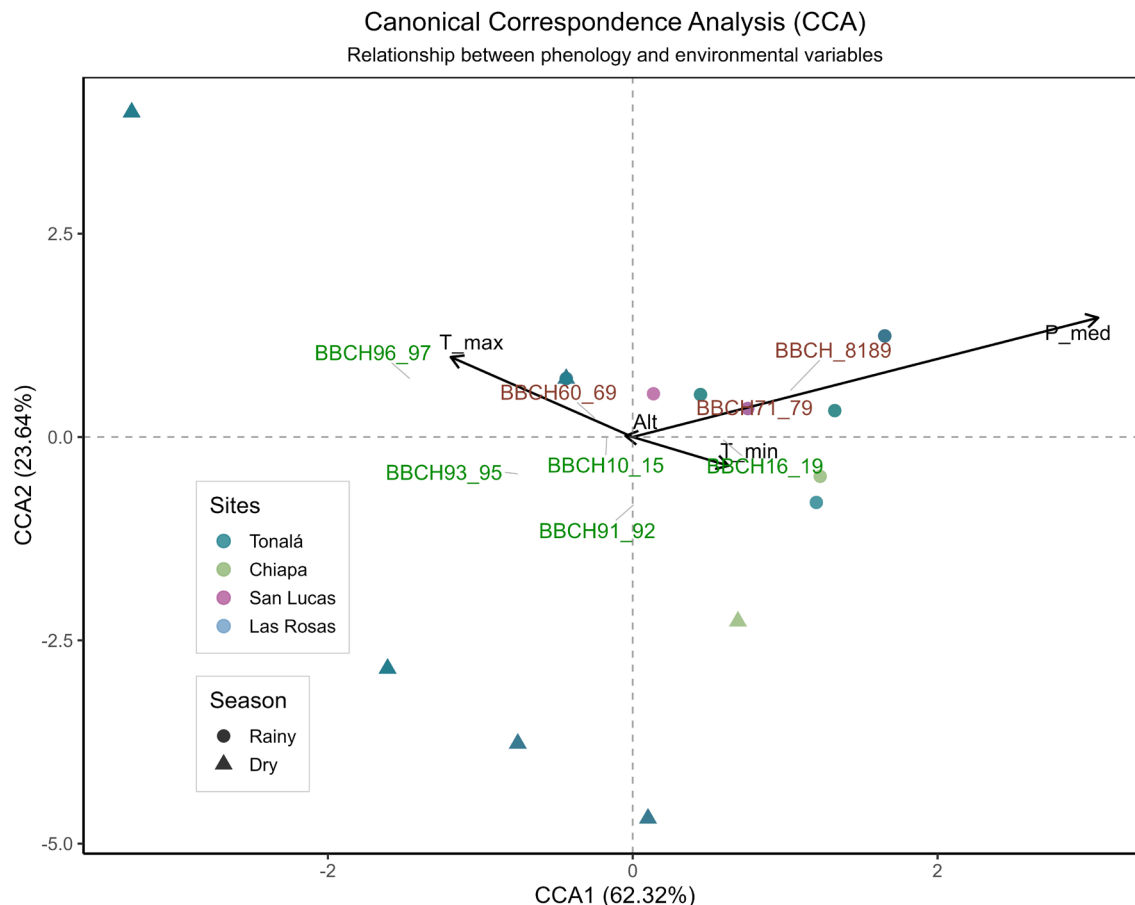


Figure 4: Canonical Correspondence Analysis (CCA) showing the relationship between environmental variables recorded during 2022 and the phenological stages of *Annona macrophyllata* Donn.Sm. in Tropical Dry Forest in the municipalities Tonalá, Chiapa de Corzo, San Lucas and Las Rosas, Chiapas, Mexico. Environmental variables: P_{med} (mean precipitation), T_{min} (minimum temperature), T_{max} (maximum temperature), and Alt (elevation). Phenological stages according to the BBCH scale: BBCH10_15 (first leaves unfurled), BBCH16_19 (leaves reach their final varietal size), BBCH91_92 (shoots complete their development, foliage still green), BBCH93_95 (leaves begin to discolor and fall), BBCH96_97 (50-100% of leaves fallen or discolored), BBCH60_69 (flowering), BBCH71_79 (fruit formation), and BBCH_8189 (fruit ripening). The ellipses represent 95% confidence intervals for the rainy and dry seasons. The vectors show the influence of environmental variables on phenology.



showed significant contributions to the ordination, while minimum temperature showed a marginal effect ($p=0.063$). In contrast, elevation did not show a significant independent effect on the model ($p=1.000$).

The ordination diagram indicated that reproductive phenophases, particularly flowering and fruit development, were associated with higher precipitation and, to a lesser extent, with minimum temperature, while vegetative processes such as leaf development and senescence tended to occur under different climatic conditions along the seasonal gradient, rather than a direct association with a single climatic factor.

Pearson correlation analyses showed negative relationships between elevation and temperature variables. Altitude was negatively correlated with minimum temperature ($r=-0.611$, $p<0.001$) and maximum temperature ($r=-0.425$, $p=0.003$), indicating that temperature decreases with increasing elevation. Conversely, the relationship between elevation and mean precipitation was weak ($r=-0.117$, $p=0.429$), indicating that, unlike temperature, precipitation does not depend on the elevational gradient in the study area.

However, PCA identified two atypical records during the rainy season: San Lucas in May (29 °C, 154 mm) and Chiapa de Corzo in July (28 °C, 55 mm), which were located within the dry conditions quadrant (October-April), suggesting a possible alteration of the usual seasonal pattern in these locations (Fig. 3). Taken together, these analyses reveal a marked climatic seasonality in the study area, with a rainy season from May to September and a dry season from October to April. This environmental framework provides the context for interpreting the phenological patterns observed along the elevational gradient.

Vegetative phenology

The vegetative development of *A. macrophyllata* includes a stage of active leaf growth followed by a dormancy period. Budding began at the end of the dry season (March-April; Fig. 5A), followed by leaf development throughout the rainy season (Fig. 5B), while senescence progressively occurred during the dry season (Fig. 5F-H), with partial foliage retention (Fig. 5H).

Regarding leaf development: leaf regrowth coincided with the end of the dry season (April) and the beginning of the rainy season (May) across the entire elevational gradient. At lower-elevation sites (24-660 m), leaf development reached its final stage (BBCH16_19) once the rainy season was established (June; Fig. 6A-C). In contrast, at Las Rosas (1307 m), this phenological stage occurred in July (Fig. 6D), with slight elevational lag of approximately one month.

In Tonalá (24 m) and Chiapa de Corzo (550 m), individuals maintained green foliage (BBCH91) from the rainy season until the beginning of the dry season (September-November). In San Lucas (660 m) and Las Rosas (1307 m), green foliage was maintained only during the first two months of the dry season (October-November), showing a one-month reduction in the duration of this leaf period (BBCH91_92) compared to lower-elevation sites before the beginning of senescence.

The first signs of senescence (BBCH93_95) were recorded almost simultaneously across the entire elevational gradient during the first months of the dry season (Fig. 6). During the intermediate phase of the dry season (November-January), leaf turgor loss, progressive chlorosis development, and leaf color were observed, from green to yellow and then to brown. Leaf abscission increased as the drought intensified, reaching its peak in months with virtually no rainfall (February-March), when individuals presented between 50% and 90% defoliation (BBCH96_97).

The regrowth-senescence cycle followed a similar pattern at all sites; although complete leaf development was reached during the rainy season, the peak time presented a slight lag. At the highest elevation site (1307 meters above sea level), this development was completed in the last rainy month (August), while in lower elevation sites, it was reached two months earlier, at the beginning of the rainy season (June). In general, the vegetative phenology of *A. macrophyllata* was closely associated with climatic seasonality, with slight temporal lags along the elevational gradient.

Reproductive phenology

Annona macrophyllata showed temporal variations in its reproductive phenology along the elevational gradient.



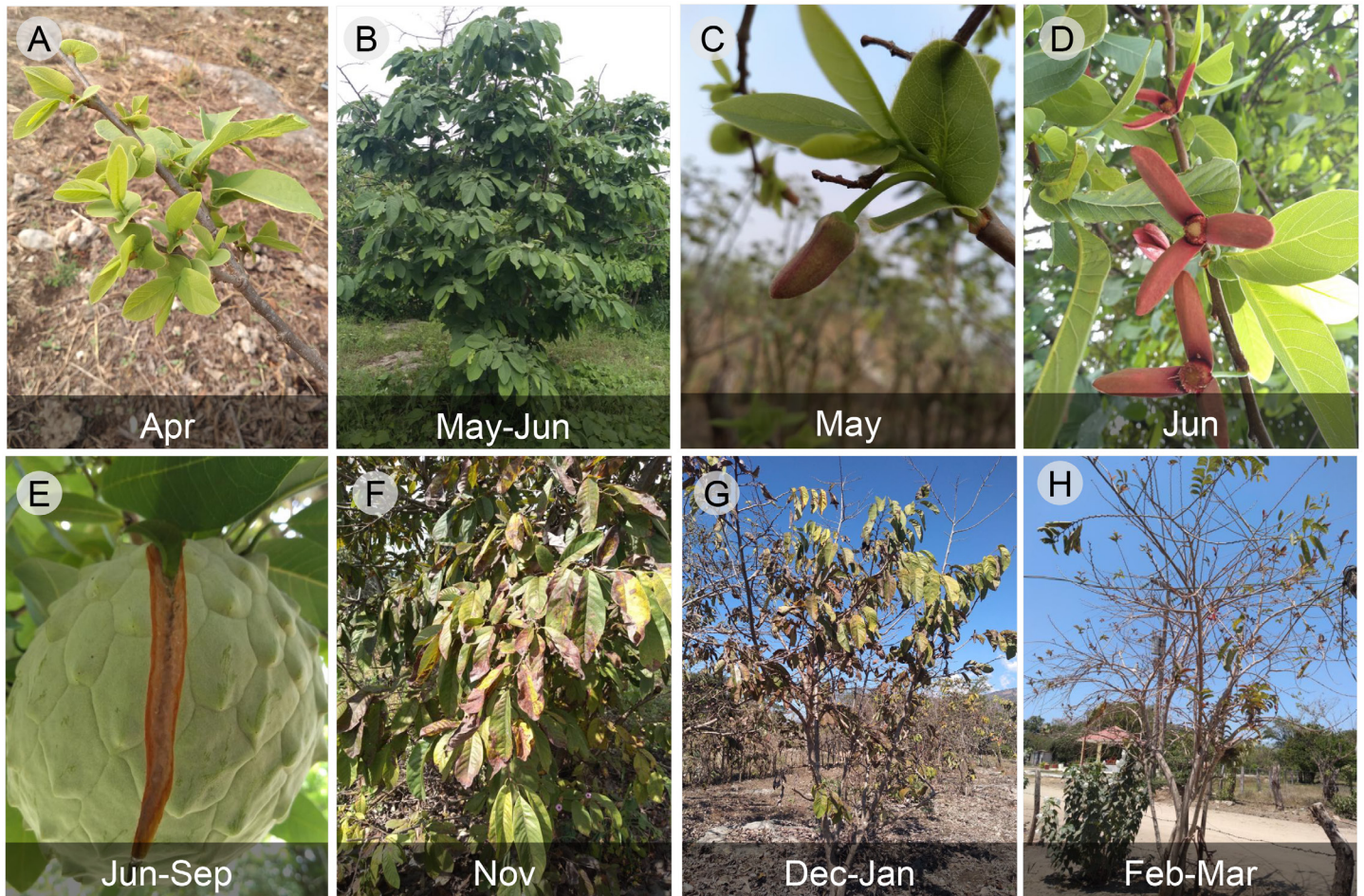


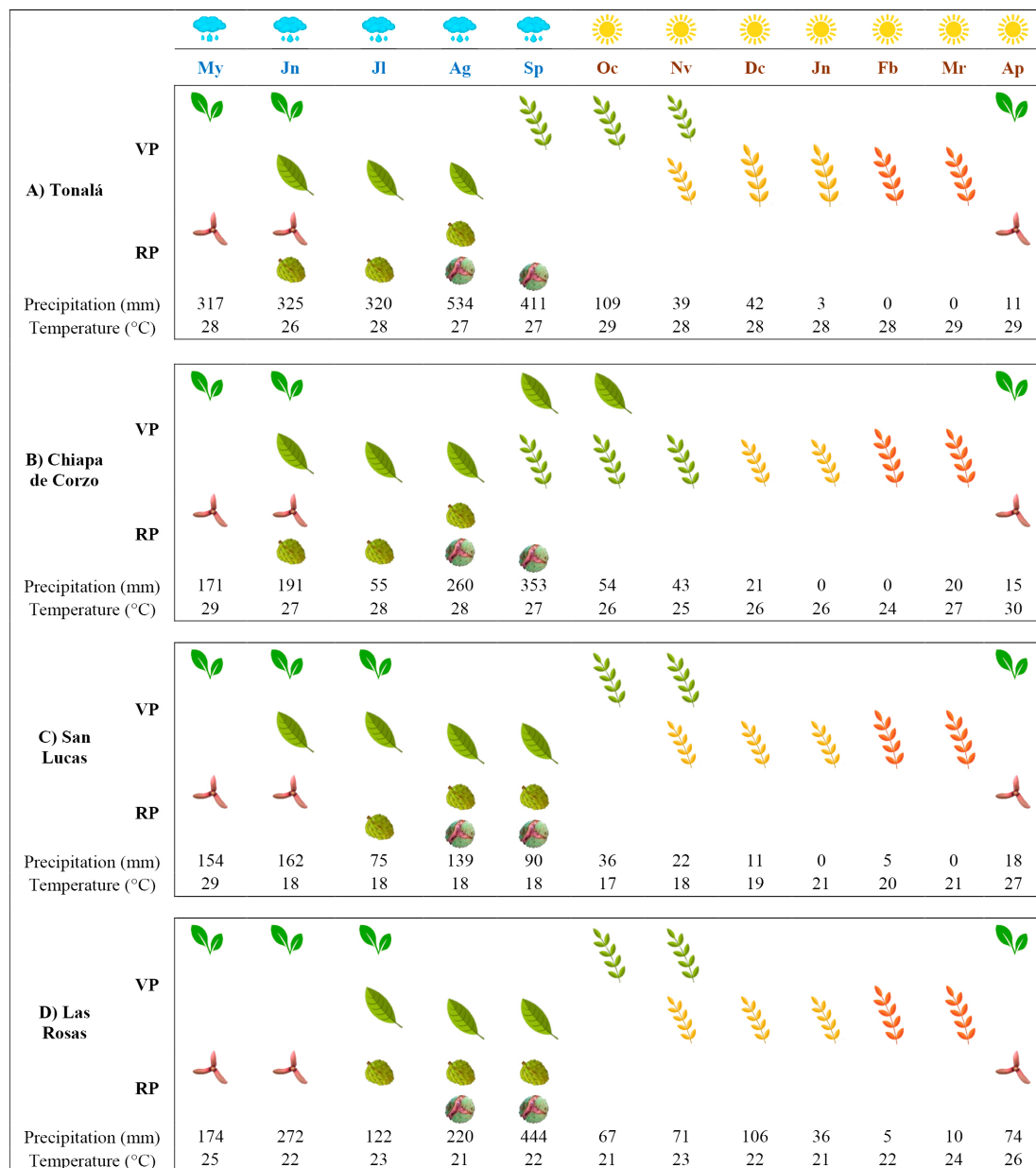
Figure 5: Developmental stages of *Annona macrophyllata* Donn.Sm. A. first leaves; B. leaves and branches at final size; C. flower bud; D. flowers and new leaves; E. fruits; F. beginning of senescence; G. senescent branches; H. tree with 90% defoliation.

This species exhibits almost simultaneous flowering onset across elevations, although the duration of this phenophase varies among sites. Fruit development begins first in lower elevation sites (Tonalá and Chiapa de Corzo) and almost a month later in higher elevation sites (San Lucas and Las Rosas).

Flowering began simultaneously with the end of the drought (late April) and the onset of rains (early May) at all sites (Fig. 6). Full flowering (BBCH 65) was recorded in May in Chiapa de Corzo and Tonalá (Fig. 6B, D), while in San Lucas and Las Rosas in June (Fig. 6A, C). During observations, flowers were at various stages: some were just beginning

their development, others were halfway their final size or already in their male reproductive sexual phase (fully open), and some had lost petals.

Fruit development (BBCH 71-74) began when the rainy season was already established in Tonalá and Chiapa de Corzo in June (Fig. 6A, B), while in San Lucas and Las Rosas in July (Fig. 6C, D). Fruits in various stages of development were observed on the same tree. Final size (BBCH 75-79) was reached during the rainy season (between August and September). Ripening began in late August, with visible changes in pulp color; consequently, fruits reached consumption maturity (BBCH 81-85) at the end of the rainy



SYMBOLS

Vegetative phenology (VP)		Reproductive phenology (RP)	
BBCH 10-15	First leaves unfolded	BBCH 60-69	Flowering
BBCH 16-19	First leaves fully expanded	BBCH 71-79	Development of fruit
BBCH 91-92	Shoot growth completed; foliage still fully green	BBCH 81-89	Maturity of fruit
BBCH 93-95	Leaves begin to discolour and fall		
BBCH 96-97	50-100% of leaves discoloured or fallen		

Figure 6: BBCH coding phenogram of the vegetative and reproductive phenology of *Annona macrophyllata* Donn.Sm. at different elevations, based on field observations during the 2022 annual cycle. Precipitation and temperature values recorded during the study are included. A. Tonalá: 24 m a.s.l.; B. Chiapa de Corzo: 550 m a.s.l.; C. San Lucas: 660 m a.s.l.; D. Las Rosas: 1307 m a.s.l.



season (September), with white or pink pulp, depending on the species variety (Fig. 5E).

The Kendall correlation analysis for the senescence and fruiting stages of *A. macrophyllata* in relation to elevation showed no statistically significant patterns. Regarding senescence, weak negative correlation was observed ($\tau=-0.236$), suggesting that senescence tends to occur slightly earlier at higher elevations; however, this relationship was not significant ($p\text{-value}=0.6547$) and is therefore not a determining factor. On the other hand, fruiting had strong positive correlation ($\tau=0.816$), indicating that the phase tends to be delayed at higher altitudes, and although this trend is notable, it was not statistically significant ($p\text{-value}=0.1213$). Both statistically significant trends may be due to the influence of other environmental factors not considered in the study, such as soil water availability or the duration of light-dark cycles.

Finally, the onset of leaf regrowth and flowering showed strong phenological synchronization, regardless of elevation, as these events occurred at the same time at all study sites. This suggests that both processes are less influenced by elevational differences, compared to other phenophases, such as leaf development or senescence, and could be regulated by broader seasonal climatic factors, particularly temperature.

The vegetative and reproductive phenophases of *A. macrophyllata* followed a consistent seasonal pattern along the elevational gradient, with slight differences in timing between sites.

Discussion

Climatic seasonality is a determining factor in plant phenology in tropical dry forests (TDF), where the alternation between rainy and dry seasons regulates vegetative and reproductive processes. The results showed that the climatic seasonality along the elevational gradient coincides in length, with a seven-month rainy season (May-September) and a five-month dry season (October-April), showing a slight difference regarding the regularity of seasons, which generally consist of six months (Balvanera et al., 2000). Both seasons have peak periods: August and September for the rainy season, and February, March, and

April for the dry season. A decrease in temperature was recorded with increasing elevation, following the expected thermal gradient. Thus, Tonalá (24 m) and Chiapa de Corzo (550 m) had warmer temperatures compared to San Lucas (660 m) and Las Rosas (1307 m). This seasonal alternation largely determines the phenological patterns of the ecosystem's predominantly deciduous plant species (Pereira et al., 2024).

In this seasonal context, *A. macrophyllata* exhibited a phenological pattern typical of deciduous trees in TDF, with leaf decay beginning during the first months of the dry season and vegetative-reproductive reactivation synchronized with the onset of rainfall. This vegetative behavior is consistent with previous studies that documented six-month leaf decay periods (October-April), associated with decreased soil moisture at the onset of drought (Otero-Sánchez et al., 2015; González-Esquinca et al., 2016). In many deciduous species, this strategy is accompanied by the storage of water, carbohydrates, and nutrients in roots and woody tissues during unfavorable periods, which subsequently favors the rapid production of new leaves and reproductive structures when favorable environmental conditions are restored (Pineda-García et al., 2011; Vega-Ramos et al., 2024).

The reproductive development of *A. macrophyllata* coincided with the rainy season (May-September). Flowering began before the first rains (April) at all elevations and fruit development occurred during the months of greatest water availability, a behavior that has also been reported for other populations of the species (Otero-Sánchez et al., 2015; González-Esquinca et al., 2016). This temporal synchronization between reproductive processes and rainfall is common among TDF species, since humid conditions favor fruit growth, seed maturation, and the establishment of new individuals (Borchert, 1999; Zimmerman et al., 2007).

Although fruit ripening showed a homogeneous pattern across the elevational gradient, culminating in the last rainy months (August-September), the onset of fruit development tended to occur earlier in lower-elevation sites. This difference could be associated with the warmer conditions typical of these areas, which can accelerate physiological



processes related to plant growth (Bahuguna and Jagadish, 2015). In many plant species, the development rate is influenced by the thermal time accumulation, commonly expressed in growing degree days (Parthasarathi et al., 2013).

Warmer environments allow plants to accumulate these thermal units more rapidly, which could accelerate developmental processes such as fruit formation. This mechanism could explain the earlier onset of fruit formation observed at lower elevation sites (Parthasarathi et al., 2013; Fotouo Makouate and Zude-Sasse, 2025). Importantly, both varieties (pink and white) presented identical reproductive phenology. These phenological patterns are consistent with previous studies conducted across similar elevational gradients. González-Esquinca et al. (2016) reported that in populations located at 464 m (Julián Grajales, Chiapas, Mexico), *A. macrophyllata* begins flowering with the first rains (May-June) and bears fruits during the rainy season (June-October). Otero-Sánchez et al. (2015) observed phenological pattern similar to that of this study at 630 m (Iguala, Guerrero, Mexico), with flowering during the driest months (April-May) and fruiting during the rainy season (May-October).

Discrepancies in flowering times among sites could be attributed to phenotypic plasticity in response to local environmental signs or to interannual variability in climate patterns, a common phenomenon in tropical species adapted to environmental gradients (Satake et al., 2022). This adaptive pattern has been documented in other TDF species, such as *Bursera simaruba* (L.) Sarg. and *Diospyros cuneata* Standl., which stand out as models of adaptation to this ecosystem (Valdez-Hernández et al., 2010). Similarly, *Lysiloma acapulcense* (Kunth) Benth. which adjusts its flowering according to available soil moisture (Camacho-Moreno et al., 2017), evidences the phenological plasticity mechanisms that TDF species develop to cope with environmental variability.

In TDF, there are generally two temporal strategies for the reproductive stage; species that reproduce during the rainy season and others during the dry season (Kushwaha et al., 2011). Both strategies can be found in Annonaceae that inhabit TDF; while *A. macrophyllata* coincides with *Annona purpurea* and *Sapranthus campechianus*

(Kunth) Standl. in reproductive synchronization during the rainy season (González-Esquinca et al., 2016; Chong-Rodríguez, 2020); *Annona reticulata* and *Annona lutescens* share reproductive strategies (flowering/fruiting) in dry months (Castro-Moreno et al., 2013; González-Esquinca et al., 2016). Although all five species show rainfall-triggered leaf patterns, *A. lutescens* and *A. reticulata* exhibit greater drought resistance, suggesting distinct climatic requirements and adaptive strategies within the family (González-Esquinca et al., 2016).

Annona macrophyllata shares reproductive and vegetative phenology with other botanical families that inhabit TDF, such as Burseraceae (*Bursera simaruba* and *Bursera tomentosa* (Jacq.) Triana & Planch.), in which adaptive convergence was observed, with rainfall-synchronized reproductive phenology and similar deciduous patterns (Hernández-Rodríguez et al., 2021). In contrast, *Pithecellobium dulce* (Roxb.) Benth. (Fabaceae) exhibits divergent strategies, fruiting during decreased rainfall and reducing leaf regrowth with increased temperature (Bulhão and Figueiredo, 2002; Cárdenas-Henao et al., 2015). These differences highlight the coexistence of several phenological strategies in the same ecosystem, possibly related to ecological and evolutionary factors.

Furthermore, although there are no specific studies on the effect the elevational gradient on the phenology of Annonaceae, research on other TDF species suggests that elevation can influence phenological responses through its effects on temperature and other environmental conditions. For example, in *Enterolobium cyclocarpum* (Jacq.) Griseb. (Fabaceae), a characteristic TDF species, differential phenotypic adaptation has been documented according to elevation (800-1350 m), showing a later vegetative development in lowland areas (Mora, 1990). Similarly, in *Pinus pseudostrobus* (Pinaceae), a species typical of temperate montane forests, faster growth patterns have been recorded at lower elevations (Viveros-Viveros et al., 2006). Likewise, in *Lupinus* spp. (Fabaceae), a dominant herbaceous species of montane grasslands and scrublands, phenological cycles shorten and delay significantly with increasing elevation (Reeves et al., 1977; Ludewig et al., 2022). These studies coincide with differences in leaf phenology



observed in *A. macrophyllata*, where leaf development occurred earlier at low elevations (24–607 m), suggesting that warmer conditions favor earlier growth, while increasing elevations promotes slower development (Zhang et al., 2010).

However, the onset of leaf regrowth and flowering were temporally synchronized along the elevational gradient, with no differences among elevations, suggesting that elevation does not exert a significant effect on these phenological processes in *A. macrophyllata*. However, elevation can act as an integrating factor that modulates environmental variables such as temperature and precipitation. Nevertheless, multivariate analyses indicated that phenological stages were primarily associated with these climatic variables, rather than with elevation as an isolated factor. This suggests that it is the environmental conditions resulting from the elevational gradient, and not elevation itself, that may exert the greatest influence on phenological responses. This interpretation is reinforced by observations in *A. macrophyllata*, where leaf regrowth and flowering appeared synchronized along the gradient, indicating that when underlying climatic variables, such as temperature, are homogenized, the apparent effect of elevation disappears.

Other environmental factors, not considered in this study, such as soil moisture or photoperiod, can also perform important regulatory functions, in seasonally dry ecosystems (Seghieri et al., 2009; Lima et al., 2021). Recent studies on tropical trees highlight that, in dry and warm seasons, water stress and photoperiod dominate the induction of processes such as leaf senescence (Lima et al., 2021; Meng et al., 2021; Wang et al., 2025).

Beyond their ecological relevance, the phenological patterns described in this study also have practical implications for the management of *A. macrophyllata*. Slight elevational differences in the onset of fruit development may contribute to a gradual fruit availability among producing locations. Because fruit development begins earlier at lower elevations and later at higher sites, this increasing elevational difference may slightly extend the regional harvest period. This pattern could benefit producers, considering the short post-harvest life of fruits, which requires

timely harvesting and distribution (Valle-Guadarrama et al., 2012).

In several communities in Chiapas, particularly in San Lucas and Las Rosas, papaya cultivation represents an important seasonal economic activity; therefore, knowing the timing of reproductive stages can support better planning of harvesting practices and local marketing strategies.

Furthermore, the phenological information generated in this study can contribute to ecological restoration and reforestation initiatives in TDF. Knowledge of flowering and fruiting periods can facilitate the collection of viable seeds and the propagation of native species, essential steps in restoration programs (Thomas et al., 2014). Furthermore, the synchronization of reproductive processes with the rainy season suggests that seedling establishment may be favored when sowing coincides with periods of higher soil moisture. Consequently, the incorporation of native fruit species such as *A. macrophyllata* into restoration or agroforestry programs could contribute both to ecosystem recovery and the generation of local socioeconomic benefits.

Overall, the diversity of phenological strategies in TDF reflects ecosystem resilience, although their long-term persistence likely depends on the complex interaction between phenotypic plasticity and natural selection processes.

Conclusion

Annona macrophyllata exhibits phenological plasticity in response to environmental variations associated with the elevational gradient in the tropical deciduous forests of Chiapas, synchronizing its reproductive stages with the rainy season to maximize the use of available water resources, while its deciduous habit optimizes water conservation during drought. This pattern is consistent in both varieties (white and pink), which maintain phenological synchrony regardless of microclimatic fluctuations observed along the gradient.

The results of this study provide a framework for understanding the adaptive capacity of *A. macrophyllata* in the face of climate change scenarios, highlighting its potential as a model for ecophysiological studies in seasonal



tropical ecosystems and opens new perspectives for evaluating its potential use in reforestation and ecological restoration programs in the region. In addition, it provides the opportunity for the growth of this fruit species under various conditions, expanding sites and harvest periods.

Author contributions

Conceptualization: TJSS, RCO, IDC, ARGE; Formal analysis: TJSS, RCO, IDC, ARGE; Methodology: TJSS, IDC; Writing – original draft: TJSS, RCO, IDC, ARGE, MCM; Writing – review & editing: TJSS, RCO, IDC, ARGE, MCM.

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Data availability statement

The dataset supporting the findings of this study has been deposited in SciELO Data and can be accessed at: <https://doi.org/10.48331/SCIELODATA.5EHC2W>.

Declaration of Artificial Intelligence Use

Artificial intelligence (AI) tools were used to support text editing, including translation and improvement of the wording.

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