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# Climate seasonality and plant vigor effects on reproductive phenology of *Potalia turbinata* (Gentianaceae) in Costa Rica

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## ABSTRACT

**Introduction:** *Potalia turbinata* (Gentianaceae) is a treelet distributed from Nicaragua to Panama. Information on its reproductive biology and phenology is lacking.

**Objective:** To describe the reproductive phenology of *P. turbinata*, morphologically characterize its fruits and seeds, and determine whether flower and fruit production correlates with climate (temperature and precipitation) and plant vigor.

**Methods:** The research took place at Tirimbina Biological Reserve in Costa Rica, January 2017–March 2019. Monthly counts of flowers and fruits were conducted on 86 plants. We used circular statistics to determine the duration and peak of flowering and fruiting. Fruit production was compared between years to describe reproductive cycles. We correlated flower and fruit abundance with climatic conditions. Plant measurements included height, basal stem diameter, leaf crop, seeds per fruit, fruit and seed dimensions, and fruit hardness. We used height, diameter, and number of leaves as proxies for plant vigor and compared plant vigor between fruiting (i.e., number of fruits) and non-fruiting plants.

**Results:** Flowering lasted 2–6 months per plant, peaking in April, while fruiting was prolonged (3–10 months), moderately peaking in August. Flower abundance was negatively correlated with precipitation, but fruiting showed no significant correlation with climate. Fruit production negatively correlated with plant height and positively correlated with basal stem diameter. Non-fruiting plants had more leaves than fruiting plants.

**Conclusions:** At the population level, *P. turbinata* flowered and fruited annually. Individuals were supra-annual, an uncommon reproductive pattern for tropical species. The correlation between flowering and lower precipitation supports possible insect pollination, though direct pollinator observations remain needed. The results concur with other studies indicating a correlation between fruit number and plant size. This investigation provides information on the reproductive phenology and fruit traits of *P. turbinata*, laying a foundation for future research into its interactions with pollinators and dispersers.

**Keywords:** flower and fruit production; Gentianaceae; treelet phenology; tropical forest; fruit morphology; Tirimbina Biological Reserve.

## RESUMEN

## Efectos de la estacionalidad climática y el vigor de las plantas sobre la fenología reproductiva de *Potalia turbinata* (Gentianaceae) en Costa Rica

**Introducción:** *Potalia turbinata* (Gentianaceae) es un arbusto distribuido desde Nicaragua hasta Panamá. La información sobre la biología de esta especie es escasa y se desconoce su fenología reproductiva.

**Objetivo:** Describir en detalle la fenología reproductiva de *P. turbinata*, caracterizar morfológicamente sus frutos y semillas, y determinar si la producción de frutos y flores se correlaciona con el clima (temperatura y precipitación) y el vigor de la planta.

**Métodos:** La investigación se llevó a cabo en la Reserva Biológica Tirimbina, Sarapiquí, Costa Rica, desde enero 2017 hasta marzo 2019. Se realizaron conteos mensuales de flores y frutos en 86 plantas. Se utilizaron estadísticas circulares para determinar la duración y el pico de las fenofases de flores y frutos. La producción de frutos se comparó entre años para describir los ciclos reproductivos. Se probó la correlación entre la cantidad de flores y frutos y la estacionalidad climática. Las mediciones de las plantas incluyeron altura, diámetro basal del tallo, número de hojas, semillas promedio por fruto, dimensiones de frutos y semillas, y dureza de los frutos. El vigor de la planta (altura, diámetro basal, número de hojas fueron variables usadas como una aproximación de vigor) se evaluó en relación con el tamaño de la cosecha de frutos.

**Resultados:** La floración duró entre 2 y 6 meses por planta, con un pico en abril, mientras que la fructificación fue prolongada (3–10 meses), con un pico moderado en agosto. La abundancia de flores se correlacionó negativamente con la precipitación, pero la fructificación no mostró una correlación significativa con el clima. La producción de frutos se correlacionó negativamente con la altura de la planta y positivamente con el diámetro basal del tallo. Las plantas sin frutos tenían más hojas que las plantas con frutos.

**Conclusiones:** A nivel de población *P. turbinata* tiene un ciclo reproductivo anual pero los individuos tienen una reproducción irregular supra-anual, un ciclo reproductivo poco común en especies tropicales.

La correlación entre la floración y menor precipitación respalda la posibilidad de polinización por insectos, aunque aún se requieren observaciones directas de polinizadores. Los resultados coinciden con otros estudios que indican una correlación entre el número de frutos y el tamaño de la planta. Esta investigación aporta información sobre la fenología reproductiva y las características de los frutos de *P. turbinata*, sentando las bases para futuras investigaciones sobre sus interacciones con polinizadores y dispersores.

**Palabras clave:** producción de flores y frutos; Gentianaceae; fenología de arbustos; bosque tropical; morfología de frutos; Reserva Biológica Tirimbina.

## INTRODUCTION

Phenology refers to the study of life cycle events and the seasonal timing of each event for individuals, populations, species, and communities (Rathcke & Lacey, 1985). Plant reproductive phenology includes the timing and patterns of flowering and fruiting (Engel & Martins, 2005; Boyle & Bronstein, 2012; Numata et al., 2022). Reproductive phenological events are influenced by abiotic factors such as precipitation and temperature, ecological interactions with pollinators and dispersers (Pires et al., 2018), as well as phylogenetic and genetic constraints (Wright & Calderon, 1995; Fenner, 1998; Wilczek et al., 2010; Du et al., 2020). Investigating the phenological strategies and life cycles of plants provides insights into their reproduction and survival (Rathcke & Lacey, 1985) as well as their interactions with herbivores and other animals which use the plants (van Schaik et al., 1993). Detailed information on reproductive phenology is still lacking for many tropical plant species.

Phenological patterns are more variable in tropical wet forests than temperate and tropical dry forests as the environment supports flowering and fruiting year-round (Opler et al., 1980; Boyle & Bronstein, 2012). Variation in tropical plant phenology is reflected in their diverse patterns that include subannual (reproducing more than once per year), annual (reproducing once a year), continuous (flowering and fruiting all year), and supra-annual cycles (one reproductive cycle over more than one-year) (Newstrom et al., 1994). Temperate plant species are more seasonal and predictable than tropical species and often closely follow temperature, precipitation, and light diel cycles (Ting et al., 2008). In a tropical dry forest, where water stress influences reproductive phenology, tree species tend to flower in response to seasonal rainfall, with dry-season flowering linked to drought-resistant species (Lasky et al., 2016).

Precipitation influences productivity and seasonality in tropical environments (Brearley et al., 2007). Many studies report that fruiting intensity and peaks increase with precipitation in tropical rainforests (Mendoza et al., 2017; Dunham et al., 2018), and in Costa Rica, understory species show a fruiting peak in the second half of the year during the rainier period (Opler et al., 1980; Boyle & Bronstein, 2012). Understory species have irregular flowering in rain forests, but more commonly, shrubs show higher flower production during the less rainy period at the beginning of the year (Opler et al., 1980).

Plant flowering and fruiting are often influenced by plant size because larger plants can allocate more resources for reproduction (Ollerton & Lack, 1998; Fernández Otárola et al., 2013), and investigating the relationship between plant size and fruit production provides insight about the strategies implemented by the plant (e.g., resource allocation and size at reproductive maturity). Larger plants tend to have more and/or larger fruits (Herrera, 1993). A study on the legume *Lotus corniculatus* showed that larger plants produced more fruits and had lower seed predation (Ollerton & Lack, 1998). In a wet tropical forest of Costa Rica, 17 tree species showed the same pattern, with larger plants producing more fruits; tree size also predicted whether a plant reproduced (Minor & Kobe, 2019). A study in a lowland conifer forest investigated the effect of plant size, plant age, site factors, and canopy density on flower and fruit production of nine understory shrubs; the study stated that plant size (closely followed by plant age) was the main factor in predicting flower and fruit quantities (Wender et al., 2004).

The family Gentianaceae comprises 16 genera and 30 hermaphroditic species in Costa Rica (Sánchez, 2010). These species predominantly consist of herbs, although there are some shrubs, trees, mycoheterotrophs, and epiphytes (Sánchez, 2010). *Potalia turbinata* Struwe & V. A. Albert is an understory treelet and the only species of the genus in Costa Rica. Flowers of *P. turbinata* have been observed from March to May, and fruits in May, July, September, and December (Struwe & Albert, 2004). There is currently no formal description of the phenology of this plant or the other eight species in the genus (Frasier et al., 2008).

Information on the reproductive phenology of *P. turbinata* would facilitate the study of their use by floral visitors and frugivorous species. *Potalia turbinata* is known to be utilized by bats; for instance, *Vampyriscus nymphaea* uses its leaves to build conical tents as refuge and feeding sites (Villalobos-Chaves et al., 2016). Tent construction may reduce flower production by limiting the foliar area exposed to the low light in the forest understory (Rodríguez-Herrera et al., 2018). Describing the phenology of *P. turbinata* establishes a foundation for further studies on the dynamics of its interactions with associated fauna.

The aim of this study was: 1) to describe the reproductive phenology of *P. turbinata* and the morphological characteristics of its fruits and seeds, 2) to determine whether rainfall and temperature correlate with flower and fruit production in the population, and 3) to evaluate if plant vigor (height, basal stem diameter, and number of leaves) correlates with fruit production. We expected *P. turbinata* to adjust its phenology to maximize reproductive success. Since this species is likely insect-pollinated (Rincón et al., 1999), we predict that it will flower during the early months of the year when precipitation decreases and conditions are more favorable for insect pollinators (Janzen, 1967). On the contrary, we expected that fruiting occur with the onset of heavier rains in the latter half of the year, as happens in many insect-pollinated plants in rainforests. Temperature exhibits minimal variation throughout the year and should not correlate with either of the phenophases (flowering and fruiting). We expected plant vigor to correlate with fruit production.

## MATERIALS AND METHODS

**Study site and species:** We conducted this study at the Tirimbina Biological Reserve (hereafter Tirimbina), Heredia province, Costa Rica (10°25' N; 84°47' W). Tirimbina includes 345 ha mostly covered by mature rain forest (Holdridge et al., 1971). The mean annual temperature and precipitation are 24.3 °C and 3 777 mm respectively, with an elevation of 180–220 m asl (Ley-López & Avalos, 2017). The rainy season occurs from May through November, while the dry season extends from December through April.

*Potalia turbinata* is endemic to Central America and has a restricted and patchy distribution in southeastern Nicaragua, northeastern Costa Rica, and northeastern Panama (Struwe & Albert, 2004; Sánchez, 2010). Its habitat ranges from sea level to 700 m (Sánchez, 2010). This species is a pachycaul understory shrub or treelet with a height up to 4.5 m. The leaves are simple, 30–75 cm long and 7.5–18 cm wide, oblanceolate, and grouped distally on branches (Sánchez, 2010). The flowers are produced on a compact corymbose-cymose inflorescence, with up to 30 flowers that vary in color from white, yellow, pale green, yellow-green, or green (Struwe & Albert, 2004; Sánchez, 2010). The green fruits are turbinate with a transverse ring and may darken slightly as they mature (Sánchez, 2010).

**Phenology:** We located, marked, and quantified *P. turbinata* plants in a high-density area along the Ajillo trail (ca. 805 m long), including all individuals within 10 m on either side of the trail. We sampled monthly from January 2017 to March 2019, covering a total of 27 months. A total of 83 *P. turbinata* plants were sampled in 2017, increasing to 86 in 2018 and at the beginning of 2019. Sampling frequency may affect the interpretation of phenological patterns. For tropical trees, it is advised to sample every two weeks, but if monthly sampling is chosen, a minimum of 25 trees are recommended (Morellato et al., 2010). Fournier and Charpantier (1975) comment that monthly observations are appropriate to obtain a good representation of tree phenology; particularly in species that phenological phases change slowly as is the case of *Potalia turbinata* that changes slowly from flowering to fruiting and fruit maturation (Rodríguez-Herrera, unpubl.). Hence, we considered monthly sampling appropriate.

During each survey, we counted flower buds, flowers in anthesis, and fruits for each plant, rather than per inflorescence. The number of inflorescences was not recorded. Immature and mature fruits were grouped together due to difficulty in distinguishing their development conditions because of the lack of conspicuous changes in color or size. To classify the different reproductive stages of the plant, the reproductive structures were classified as flower buds if plants had unopened flowers, flowering if at least one flower was open, and fruiting if they had fruits at any stage of development. A plant could have more than one reproductive stage at a time.

The CircStat package (Berens, 2009) was used to determine the circular mean and the value of the vector-r for each phenophase. Vector-r varies between 0 and 1, where values closer to 1 indicate a strong seasonality (i.e., a defined peak), and values closer to 0 indicate low or absence of seasonality. To determine if the circular distribution was seasonal, we applied the Rayleigh test (Zar, 1999). This information facilitated the determination of the duration, peak, and frequency of the flower and fruit phenophases at the population level. Data from 83 plants from 2017 and 2018 were combined in this analysis.

We implemented a Student's t-test to compare fruit production between 2017 and 2018 to assess interannual variability as basal information on the annual variation in resources for animals. Fruit production data were log-transformed to improve normality. Normality was assessed using the Shapiro-Wilk test, and variance homogeneity was tested using Levene's test. Fruit production is defined as the maximum number of fruits observed on each plant at a given census rather than cumulative fruit output over the entire reproductive season. This method was chosen because cumulative fruit counts were not feasible in our monthly sampling design, and the maximum observed count provides a standardized comparison across individuals and years.

We tested for correlation (Pearson's correlation) between monthly 24-hour average precipitation and temperature with monthly total numbers of flowers and fruits in the population during the study period. To account for potential time-lagged effects of climate seasonality on the reproductive phenology, we tested for correlations with 0-, 1-, 2-, and 3-month offsets of meteorological data. Climate data with records for the duration of the study were obtained from a local weather station at Tirimbina. This analysis helps determine whether climatic factors such as rainfall or temperature act as cues for triggering flowering and fruiting, potentially influencing pollination success and seed dispersal.

**Plant morphological traits:** We recorded the morphological measurements for 81 plants in January 2019. We measured the height of each plant from the ground to the top of the apical meristem, basal stem diameter at 10 cm above ground, and recorded the number of fully developed leaves per plant. Three plants had modified leaves in 2018, presumably altered by tent-roosting bats. These leaves were included in the study as they were still living and attached to the plant. Additionally, these plants had already initiated their reproductive cycles before leaves were modified.

In addition to the plant vigor traits, we measured fruit and seed characteristics. Fruits with well-developed transverse rings were collected from plants near the study area to measure their morphological characteristics (2–10 fruits per plant), such as weight (OHAUS Scout Pro scale, model SPE 123), length, and width at the widest point of each fruit's transverse ring. A total of 185 fruits from 27 plants were collected (19 in August 2017, 106 in October 2017, and 60 in November 2018), and fruit hardness was determined for 132 fruits. Fruit hardness, defined as the strength required to perforate the exocarp and mesocarp and access the seeds, was estimated using a penetrometer with a 2 mm chisel (Chatillon, model DPPH-100). The chisel was aligned perpendicular to the fruits' transverse rings. We weighed 150 seeds from 30 fruits collected from 10 plants, with five seeds taken per fruit, using a precision lab scale (Sartorius, model GMBH 2842), and measured their length, width, and thickness. Fruit and seed dimensions were measured with a dial caliper (SPI, model 31-414-6).

**Plant vigor effects on fruit production:** To evaluate the effect of plant vigor on fruit production of *P. turbinata*, we used a general linear model with fruit production per plant as the response variable and height, basal stem diameter, and number of leaves as explanatory variables. The explanatory variables were standardized (mean-centered and scaled by standard deviation) to allow for interpretation of model coefficients on a common scale. This analysis focused on data from the 2018 reproductive season because vigor traits from the previous year were incomplete. Additionally, we tested whether plant vigor traits differed between fruiting and non-fruiting plants using a general linear model, with each trait as a response variable and reproductive status (fruiting vs. non-fruiting) as the explanatory variable. Since a minimum reproductive size has not been formally established for *P. turbinata*, no size threshold was applied to exclude potential juveniles among the non-fruiting plants. Additionally, individuals at the minimum recorded height and basal stem diameter in our dataset were observed fruiting. All statistical analyses were conducted in R v.4.0 (R Core Team, 2024).

## RESULTS

**Phenology:** Flower buds began in February, with a peak in March (Fig. 1A). Records of open flowers began in March and peaked in April (Fig. 1B), about a month after the flower-bud peak. Fruit production was prolonged, starting in April and continuing until February of the following year, with peak production occurring in May, July, and August (Fig. 1C); June 2018 was not sampled, and this may have affected the fruiting pattern observed in Fig. 1C. Flower bud and flower production were highly seasonal, with a significant unimodal pattern (Fig. 1A, Fig. 1B). However, fruit presence showed a more prolonged, barely seasonal pattern (Fig. 1C). The onset of the different floral stages did not vary between the two sampling years.

The presence of fruits lasted for up to 10 months from the initial detection of the fruiting phase until all fruits had either fallen from the plants or been removed. The fruiting period of individual plants averaged 7 months with a range of 3 to 10 months. Flower bud and flower presence per plant ranged from 2 to 6 months.

The number of plants flowering each year varied up to 369%. There were 13 flowering plants in 2017, 48 in 2018, and 20 by March 2019. All plants that flowered in 2017 and 2018 produced fruits; observations in 2019 ended before the fruiting phase. Nine plants (69.2 %) flowered subsequently from 2017 to 2018, and 18 plants (37.5 %) from 2018 to March 2019. Four plants that produced flowers in 2017 also produced flower buds in 2019, three of which flowered all three years. .

Fruit production was significantly lower in 2017 than 2018 (28.15 ± 21.24 SD versus 43± 27.16 SD: t = -2.07, df = 56, p = 0.043). The number of fruits per plant at the peak count ranged between 10 to 81 in 2017, and 4 to 136 fruits in 2018. The mean value of the peak count of fruits per fruiting plant during the study was 39.67 (± 26.53 SD) and for flowers it was 29.94 (± 21.81 SD). The number of flowers observed per plant ranged from 2 to 107. The maximum fruit count across the population was 344 fruits in June 2017 and 1667 in May 2018. Flower buds and flowers considered together had a maximum count across the population of 543 in 2017 and 1658 in 2018, both in March.

The number of flowers in the population correlated negatively with monthly precipitation (r=-0.442, p=0.040), so the number of flowers increased when precipitation decreased. However, the number of fruits did not correlate with precipitation (r=0.359, p=0.101). Flowering remained negatively correlated with precipitation at a 1-month offset (r=-0.451, p=0.040), but this relationship weakened at 2-month (r=-0.087, p=0.709) and 3-month offsets (r=-0.046, p=0.842). Fruit production did not correlate significantly with precipitation at any offset

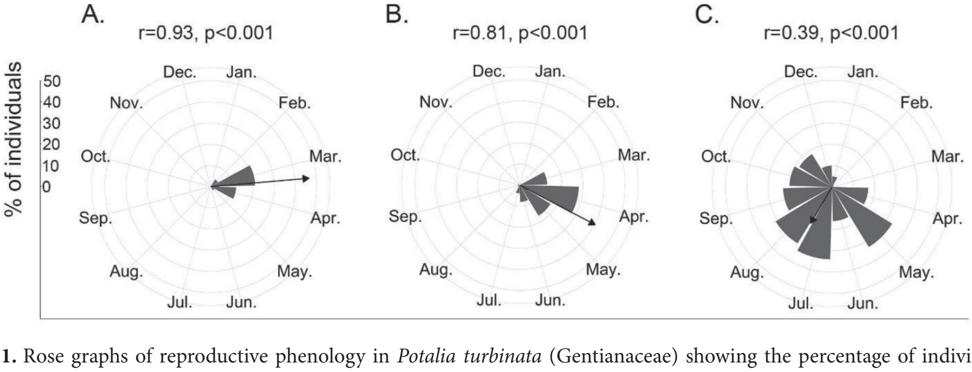

**Fig. 1.** Rose graphs of reproductive phenology in *Potalia turbinata* (Gentianaceae) showing the percentage of individuals with: **A.** flower buds, **B.** open flowers, and **C.** fruits. The arrow indicates the circular mean, and its length represents the value (0-1) of the vector-r (greater length equals greater seasonality). P-values for the Rayleigh test indicate a clear seasonality of the three reproductive stages.

**Table 1**

Descriptive values of plant vigor, fruit, and seed traits of *Potalia turbinata* (Gentianaceae).

| Plant vigor traits | Height (cm) | Basal Stem Diameter (cm) | Number of Leaves |
|---|---|---|---|
| Mean ± SD | 245.7 ± 80.4 | 3.2 ± 0.8 | 16.9 ± 6.2 |
| Range | 60–450 | 1.9-5.1 | 4–38 |

| Fruit traits | Weight (g) | Length (mm) | Width (mm) | Hardness (N) |
|---|---|---|---|---|
| Mean ± SD | 2.7 ± 0.5 | 18.9 ± 1.1 | 21.3 ± 1.6 | 44.6 ± 8.1 |
| Range | 1.4–3.9 | 16.0–21.5 | 16.1–24.7 | 16.0–68.0 |

| Seed traits | Seeds per Fruit | Weight (mg) | Length (mm) | Width (mm) | Thickness (mm) |
|---|---|---|---|---|---|
| Mean ± SD | 36.2 ± 7.3 | 13.8 ± 2.8 | 4.8 ± 0.4 | 2.9 ± 0.3 | 1.4 ± 0.2 |
| Range | 11.0–46.0 | 1.3–20.4 | 3.6–5.6 | 1.8–3.8 | 0.8–1.9 |

(all p>0.1). Flowering (r=0.017, p=0.939) and fruiting (r=-0.170, p=0.449) did not correlate with temperature which had a 24-hour average monthly temperature of 25.5 °C, with a narrow range from 22.4 to 31.7 °C during the study. Correlations with temperature were non-significant across all offsets (all p-values>0.1).

**Plant morphological traits:** Table 1 summarizes the measurements of the plants, fruits, and seeds. Of the 81 plants measured in January 2019, 55.6% had fruited in 2018.

**Plant vigor effects on fruit production:** Among the analyzed plant vigor traits, basal stem diameter showed a strong positive correlation with fruit production (Table 2). In contrast, taller plants were associated with lower fruit production (Table 2; Fig. 2). Of these variables, only the number of leaves was significantly

**Table 2**

Results of a GLM on the effect of plant vigor traits on fruit production in *Potalia turbinata* (Gentianaceae).

| Factor | Estimate | S.E. | t-value | P-value |
|---|---|---|---|---|
| Intercept | 42.91 | 2.95 | 14.53 | <0.001 |
| Height | -12.51 | 4.24 | -2.95 | 0.005 |
| Diameter | 26.24 | 4.23 | 6.21 | <0.001 |
| No. leaves | 4.51 | 3.00 | 1.50 | 0.140 |

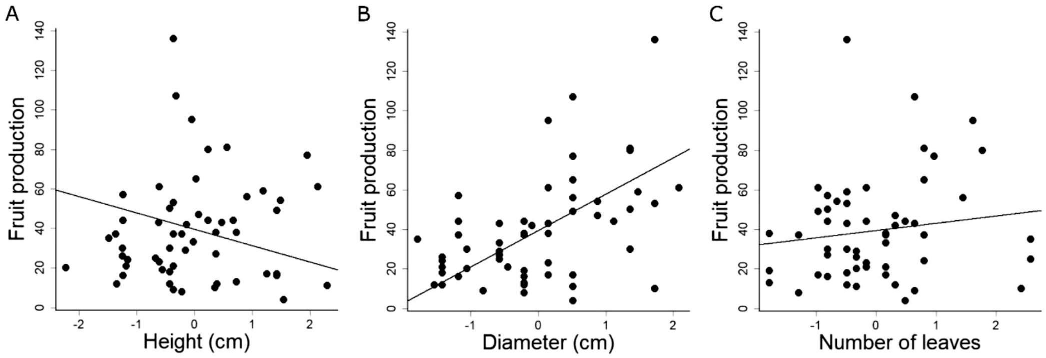

**Fig. 2.** The relationship between **A.** plant height, **B**. basal stem diameter, and **C.** number of leaves with fruit production in plants of *Potalia turbinata* (Gentianaceae) in Costa Rica.

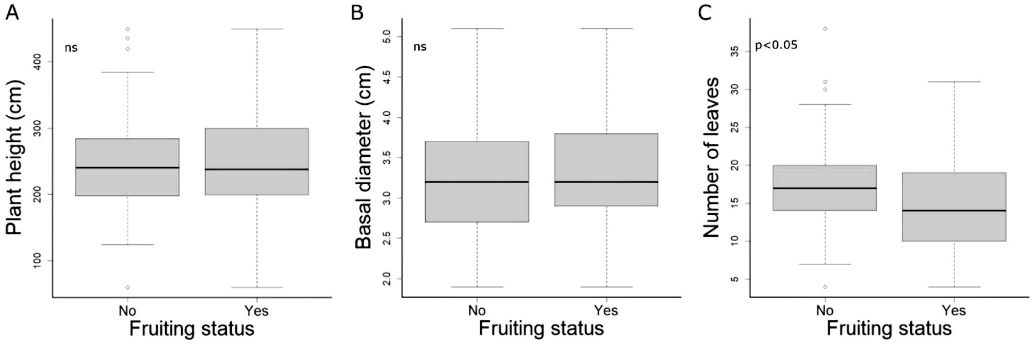

**Fig. 3.** Comparison of plant vigor traits between fruiting plants and non-fruiting plants of *Potalia turbinata* (Gentianaceae) in Costa Rica. Data from the year 2018: **A.** height, **B.** basal stem diameter, and **C.** number of leaves.

higher in non-fruiting plants (p=0.007); the other two variables did not differ between fruiting and non-fruiting plants (Fig. 3).

## DISCUSSION

**Phenology:** Phenological patterns in flowering and fruiting often differ between individual and population levels (Sakai et al., 2005; Fenner, 1998). In contrast, a study at La Selva (20 km from Tirimbina) analyzing 226 treelets and shrubs across 35 species found that despite some individual variation, phenological patterns at the individual level generally reflected those of the population (Boyle & Bronstein, 2012). *Potalia turbinata* exhibited lower consistency between individual and population-level phenology. As a population, *P. turbinata* followed an annual phenological pattern, but differed at the individual level with a small fraction of the individuals exhibiting annual patterns, while the majority were supra-annual.

Many species follow an annual cycle at La Selva in accordance with precipitation fluctuation, similar to the documented pattern in *Potalia turbinata* at the population level (Sakai, 2001). At the individual level at La Selva, subannual phenological patterns were predominant, followed by annual patterns, while continuous and supra-annual strategies were rare (Newstrom et al., 1994; Sakai et al., 2005), making *P. turbinata* a notable exception at the individual level. This suggests that *P. turbinata* individuals may require longer recovery periods between reproductive events, potentially due to resource limitations or other ecological constraints.

Several factors influence fruit and seed production, including resource allocation, floral herbivory, and effective pollination (Cunningham, 2000). Insufficient resource accumulation in certain plant species can lead to a supra-annual fruiting pattern, as these plants require longer periods to replenish between fruiting years (Fenner, 1998). Boyle and Bronstein (2012) mentioned light variation, rainfall, and nutrient availability as possible factors affecting flowering and fruiting patterns; although, in their study, precipitation was not an influencing factor. Other contributing factors to variation include competition and herbivory (Sakai et al., 2005). Cunningham (2000) studied an understory plant and found that floral herbivory was the main limiting factor on fruit production followed by the proportion of flowers visited by pollinators. Genetics may also influence plant phenology, flowering, and fruiting (Wilczek et al., 2010; Tang, et al., 2016). Abiotic and biotic factors may control plants with conservative genomes to a lesser extent (Fenner, 1998).

The average annual fruit production in *Potalia turbinata* was significantly lower in 2017 than in 2018, highlighting interannual variation in reproductive output. This variation further suggests that resource availability and environmental factors may have a stronger influence on fruit production than floral herbivory, which was not observed during this study. While we described flowering and fruiting patterns, future research could examine additional reproductive metrics, such as fruit set and seed viability, to better understand reproductive success in *P. turbinata*.

Tropical plants tend to have longer fruiting periods, averaging four months (Jordano, 1992). *Potalia turbinata* is one example of an extremely lengthy fruiting period at the population level (ten months) and at the level of individual plants (approximately seven months). In this study, immature and mature fruits were considered together due to difficulty in distinguishing the categories because of cryptic color and size changes. Immature fruits in early development present an underdeveloped transverse ring. In future studies, to avoid ambiguity while deciding whether fruits are immature or mature, color could be measured and the diameter of the fruit ring across the months could be considered. Though it would be more demanding in the field, a higher resolution of the timing of phenological events could be achieved, such as a more precise timing of fruit maturation. Additionally, the start of fruit dispersal could be used as an indicator of fruit maturity.

*Potalia turbinata* only had one flowering period per year at Tirimbina. Flowering took place at the beginning of the year (lower precipitation) and fruiting at the middle to second half of the year (higher precipitation), which is consistent with flowering and fruiting tendencies reported by Opler et al. (1980) of treelets and shrubs in Costa Rican tropical wet forests. Flowering periods were shorter for supra-annual species and tended to occur in the dry season more than for annual or subannual plants (Bawa et al., 2003), which is similar to *P. turbinata* with a population level flowering period of four to five months during a period of less rainfall.

Flowering in the dry season may influence pollination success in *P. turbinata* by aligning reproductive timing with seasonal changes in pollinator availability. Tree and shrub species pollinated by bees, butterflies, flies, and wasps tend to reach their peak flowering during the dry season in Venezuela (Ramírez, 2006). All flowering plants of *P. turbinata* successfully produced fruits and exhibited pronounced flowering seasonality. Plants with high flowering synchrony are more likely to reproduce successfully, as they attract more pollinators (Bruno et al., 2019). Successful cross-pollination, autonomous self-pollination, and apomixis are possible mechanisms contributing to seed development. While *P. turbinata* had strong flowering seasonality, its pollination strategy remains uncertain. Rincón et al. (1999) suggested that the species may be insect-pollinated, but no direct observations confirm this. Further research is needed to identify pollination strategies and explore the environmental factors influencing fruit production in *P. turbinata*.

Though the onset of the rainy season was not a significant determinant in the *P. turbinata* fruiting cycle, the flowering significantly correlated with less rain which in turn led to the presence of fruit during the rainy months. Seed germination facilitation is one factor that may influence fruiting occurring during the rainy season (Garwood, 1983). The lack of correlation between temperature and flowering and fruiting may be a consequence of the little, non-seasonal variation in this environmental variable.

The timing of flowering and fruiting of *P. turbinata* in this study overlapped with herbarium collected phenological information. Sánchez (2010) states that flowers are found from March to June, while Struwe and Albert (2004) mention March to May and specify fruiting observations in May, July, September, and December. This investigation further detailed the reproductive phenophases by examining their full extension and patterns.

**Plant morphological traits:** The plant height of *P. turbinata* plants in this study is consistent with the values reported by Struwe and Albert (2004). The number of flowers was previously reported as up to 30 per plant (Struwe & Albert, 2004), but we observed a range beyond that number. We also documented a larger stem diameter at 3.21 cm, compared to 14 mm, and fruit size was slightly larger in this study (16–22 x 16–25 mm compared to 10–14 x 11–18 mm). However, Struwe and Albert (2004) collected measurements from dry material which could lose 10–15 % of its mass. Sánchez (2010) described the seeds as 4–5.5 mm which is in accordance with our findings. Additionally, we provided novel data on the number of seeds, weight, width, and thickness, as well as fruit hardness.

Plant and fruit morphological traits are noteworthy for further investigations involving fruit consumption or seed dispersal mechanisms of *P. turbinata*. The seeds of Neotropical woody species are primarily dispersed by vertebrates (Howe & Smallwood, 1982), and the size of the seeds influences whether they are ingested (Sebastián-González, 2017, Ong et al., 2021). Smaller seeds are more likely to be swallowed by a disperser and pass through the digestive tract; larger seeds (> 12 mm) tend to only be swallowed by large vertebrates including primates, tapirs, and peccaries (Fuzessy et al., 2018). Seed weight and length can influence whether a seed is swallowed or dropped as well as which frugivores act as dispersers. Large-seeded fruits are less likely to be consumed by birds, bats, and small mammals (Fuzessy et al., 2018), although bats and small sized rodents have been observed dispersing large-seeded fruits by synzoochory (Melo et al., 2009; Ong et al., 2021). *Potalia* seeds are small and numerous, suggesting they are likely dispersed through gut passage, as observed in *Carollia perspicillata* dispersing *Potalia amara* seeds (Lobova et al., 2009). Bats have also been observed removing fruits of *P. turbinata* (Salazar, unpubl.). Further investigation into *Potalia* seed dispersal is warranted due to a lack of information.

Fruit hardness may also affect fruit consumption as there is a limit to the hardness that can be handled by different species. Dumont (1999) documents changing behaviors of phyllostomid bats when they consume fruits of varying hardness and indicates that some species have morphological traits that aid in consumption. Additional studies on *P. turbinata* could contribute information on animal diets, particularly regarding fruit hardness.

**Plant vigor effects:** The height of fruiting plants of *P. turbinata* was negatively correlated with fruit production, while basal stem diameter showed a positive correlation with fruit production. These findings partially align with previous studies reporting that tree size is often positively associated with reproductive output or influences initial reproductive activity (Herrera, 1991; Susko & Lovett-Doust, 2000; Fernández-Otárola et al., 2013). A study at La Selva Biological Station of approximately 2,000 trees from 17 species showed that the number of fruits produced could be predicted by plant size (Minor & Kobe, 2019). This trend has also been shown in other plants such as a cactus species studied by Bustamante and Búrquez (2008), which had higher flowering intensity and plant fecundity in larger plants.

The amount of light available through canopy gaps may influence plant size (Wender et al., 2004). Competition can also affect plant size, and increased plant growth usually correlates with more access to resources; crowding affects the plant reaching its maximum potential size and in turn, affects its crop size or fecundity (Tracey & Aarssen, 2011). Fig tree fruit production may be influenced by the amount of time the trees are able to restore nutrients between reproductive cycles (Huang et al., 2019), which is another factor along with plant size that could be considered in future studies on *P. turbinata*.

The number of leaves did not correlate with fruit production in *P. turbinata* when analyzing only fruiting plants, indicating that leaf number does not directly influence the number of fruits. However, there was a significant difference in leaf number between fruiting and non-fruiting plants, with non-fruiting plants having more leaves, while fruiting plants had fewer. This pattern suggests an inverse relationship between leaf production and fruiting, potentially driven by resource allocation trade-offs. This finding aligns with studies showing a balance between vegetative growth and reproductive effort. Wheelwright (1986) found that fruit production and new leaf production in the same year were negatively correlated in 12 of 15 studied tree species of the Lauraceae family in Monteverde, Costa Rica. In most species, vegetative growth and reproduction were negatively associated, which may explain why *P. turbinata* fruiting plants exhibited fewer leaves. This suggests that resource allocation toward fruit production may come at the expense of vegetative growth. In trees, vegetative growth (leaf production) and reproductive development (flower and fruit production) are closely linked (Borchert, 1983). The extent and drivers of this potential trade-off in *P. turbinata* remain unclear.

Previously, specific phenological information was lacking for the genus *Potalia* apart from knowing in which months flowering and fruiting herbarium specimens were collected. We found that *P. turbinata* produces flowers and fruits annually at the population level with varying patterns at the individual level. Higher flower abundance coincides with drier months, as predicted. The initial expectation of the fruiting phenophase correlating with rainfall was not supported. Fruit production of *P. turbinata* correlates with plant size (height and diameter), concurring with predictions. The information gathered serves as a foundation for further investigations on *P. turbinata*. Next steps include identifying pollinator and disperser interactions with the plant and the abiotic factors that influence phenological strategies.

**Ethical statement:** The authors declare that they all agree with this publication and made significant contributions; that there is no conflict of interest of any kind; and that we followed all pertinent ethical and legal procedures and requirements. All financial sources are fully and clearly stated in the acknowledgments section. A signed document has been filed in the journal archives.

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