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Phenological patterns from two sympatric subspecies of the palm *Geonoma cuneata* (H. Wendl. ex Spruce) and their gall inductor *Contarinia geonomae* (Gagné)

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Abstract: *Geonoma cuneata* is a variable species with eight subspecies and one of two palms worldwide with a gall record. In this species, staggered flowering has been suggested as a possible mechanism to explain its reproductive isolation from sympatric subspecies. In this study, we examined the phenology of two *G. cuneata* subspecies and their gall inductor, *Contarinia geonomae*, in the Caribbean lowlands of Costa Rica. For 207 consecutive weeks, we monitored the phenology of 79 *G. cuneata* individuals and recorded the outcomes of 434 inflorescences in terms of abortions, fruit, and gall success. We analyzed phenological patterns, checked for seasonality and synchrony, and evaluated the effects of precipitation and temperature on each phenophase. The reproductive outcomes of the two subspecies were compared in terms of abortions of the inflorescences and the development of fruits or galls in the infructescences. Both subspecies were mainly seasonal and showed a clear overlap in all phenophases during the four years of study. However, seasonality and synchrony were very well marked in *G. cuneata* subsp. *cuneata* whereas *G. cuneata* subsp. *procumbens* was characterized by lower synchrony and higher abortion rates. Emergent inflorescences were influenced by average temperature, while flowering was influenced by monthly rainfall and average temperature. Moreover, the peak flowering occurred just after the end of the dry season, whereas ripe fruits peaked at the end of the rainy period. Ripe fruits showed higher levels of synchrony and were the only phenophase in which the mean date did not differ among subspecies. This was partly explained by the higher number of abortions and lower fruiting success of individuals flowering outside the peak period. Instead, such individuals are more likely to have infructescences with galls and higher loads. Flowering convergence did not support phenology as a mechanism of reproductive isolation. However, an extended combination of time from flowering to fruiting in both subspecies benefits the gall inductor by providing an extended period of oviposition and adult emergence.

Keywords: Arecaceae, Cecidomyiidae, gall ecology, palm ecology, species coexistence

Resumen: *Geonoma cuneata* es una especie de palma muy variable con ocho subespecies reconocidas. También es una de las únicas dos especies de palmas a nivel mundial con un registro de un inductor de agallas. En la especie, la floración escalonada ha sido sugerida previamente como un posible mecanismo para explicar el aislamiento reproductivo entre subespecies creciendo en simpatría. En este estudio, examinamos la fenología de dos subespecies de *G. cuneata* y su inductor de agallas *Contarinia geonomae* en las tierras bajas del Caribe de Costa Rica. Durante 207 semanas consecutivas seguimos la fenología de 79 plantas de *G. cuneata* y registramos los resultados de 434 inflorescencias en términos de abortos y éxitos en la fructificación y producción de agallas. Analizamos los patrones fenológicos, revisamos la estacionalidad, la sincronía y evaluamos el efecto de la precipitación y la temperatura en cada fenofase. También comparamos el comportamiento de ambas subspecies en términos de los abortos de las inflorescencias y el desarrollo de frutos o agallas en las infrutescencias. Ambas subspecies mostraron un comportamiento primordialmente estacional y un claro traslape en todas sus fenofases durante los cuatro años de estudio. No obstante, la estacionalidad y la sincronía fueron muy marcadas en *G. cuneata* subsp. *cuneata* mientras que *G. cuneata* subsp. *procumbens* se caracterizó por poseer una menor sincronía y mayores tasas de abortos. La temperatura promedio influyó en la producción de inflorescencias, mientras que la floración estuvo influenciada por la precipitación mensual y la temperatura promedio. Adicionalmente, el pico de floración ocurrió al final de la época seca, mientras que el pico de frutos ocurrió al final de la época lluviosa. Los frutos maduros mostraron los niveles más altos de sincronía y fueron la única fenofase en la que la fecha promedio nunca diferio entre subespecies. Esto fue en parte explicado por el mayor número de abortos y menor éxito en la fructificación de los individuos que florearon fuera del periodo pico. Esos mismos individuos también mostraron mas posibilidades de poseer infrutescencias con agallas y en mayor cantidad. El traslape en la floración no respalda la fenología como un mecanismo de aislamiento reproductivo. Sin embargo, el periodo combinado de floración y fructificación en ambas subespecies beneficia al inductor de agallas al incrementar el periodo de ovoposición y emergencia de adultos.

Keywords: Arecaceae, Cecidomyiidae, ecología de agallas, ecología de palmas, coexistencia de especies

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Introduction

Arecaceae, with approximately 2600 species, is one of the most diverse monocot families (Christenhusz & Byng, 2016) and one of the most abundant groups in Neotropical humid forests (Staggemeier et al., 2017; Muscarella et al., 2020). In these areas, several canopy species have been classified as hyperdominant (ter Steege et al., 2013), whereas some lineages of the subfamily Arecoidae are particularly diverse and dominant in the understory (Cano et al., 2022). These hyperdiverse genera are often formed by highly related or poorly defined complexes of sympatric subspecies (Roncal et al., 2012; Bacon et al., 2022). As such, a key question in palm ecology is determining the mechanisms that allow these taxa to coexist and the ecological implications for interacting fauna.

Different flowering phenologies have been proposed to explain the coexistence of highly related plants (Martin et al., 2007; Pascarella, 2007; Spriggs et al., 2019: Pereira et al., 2022). However, the phenology of most tropical palms remain unknown, with few studies focusing on dominant species (Mendes et al., 2017; Pedroso et al., 2021), species useful to humans (Silva & Scariot, 2013), or species that are in danger of extinction (Martínez et al., 2021). Although palm phenological behavior can be highly variable (Henderson, 2002), seasonal and synchronized flowering (De Steven et al., 1987; Ibarra-Manríquez, 1992; Castro et al., 2007; Genini et al., 2009) and continuous flowering throughout the year (Martén & Quesada, 2001; Genini et al., 2009) are the most common behaviors. In palms, flowering phenology is often shaped to increase reproductive success based on pollinator behavior and climatic conditions. Continuous flowering has been reported to increase pollination chances in environments with unpredictable weather conditions, such as high rainfall (Martén & Quesada, 2001), and mostly in bee-pollinated species (Henderson et al., 2000). In contrast, seasonal flowering is common in areas with climate seasonality (De Steven, 1987; Mendes et al., 2017), among specific weevil-pollinated species (Henderson et al., 2000; Carreño-Barrera et al., 2020), and as a mean to attract and satiate pollinators (Bruno et al., 2019).

Although few studies have focused on the phenology of closely related palms, there is evidence that flowering phenology plays an important role in sympatric palm coexistence and divergence (Savolainen et al., 2006; Carreño-Barrera et al., 2020). Early tropical studies at the community level found that staggered flowering was common among some genera (De Steven et al., 1987; Henderson et al., 2000), and has promoted more recent phenological studies on sympatric species (Bruno et al., 2019; Chan & Chua, 2019; Carreño-Barrera et al., 2020). For instance, differences in the temporal patterns of flowering among four *Ceroxylon* species in Colombia were shaped as a mechanism to avoid pollination competition while maintaining viable pollinator populations (Carreño-Barrera et al., 2020). Ultimately, such differences in flower phenology could drive reproductive isolation by limiting gene flow between related taxa (Savolainen et al., 2006; Barfod et al., 2011). There is a clear case of speciation in sympatry between the two species of *Howea*, which are reproductively isolated by flowering phenological differences (Savolainen et al., 2006; Papadopulos et al., 2019). However, an overlap in flowering among sympatric palm species is also common (Bruno et al., 2019; Chan & Chua, 2019). Several biotic and abiotic conditions and phylogenetic constraints have been identified as possible barriers preventing phenological differences (Davies et al., 2013; Park et al., 2022). Indeed, the flowering behavior within a genus of palms can be highly variable. For example, in *Geonoma,* continuous (Henderson, 2000; Martén & Quesada, 2001) and seasonal flowering with different degrees of synchrony (Henderson, 2000; Borchsenius, 2002) have been reported. This genus is one of the most diverse, widespread, and abundant species from of palms in the Neotropics, often with polymorphic species and subspecies growing sympatrically (Henderson, 2011; Loiseau et al., 2019). For such taxa in sympatry, flowering biology and phenology have been suggested as possible reproductive isolation factors (Borchsenius et al., 2002; Borchsenius et al., 2016). However, there are very few phenological studies on this genus, and none have compared the same species in different geographical areas. In addition, the ecological implications of the phenological patterns of sympatric palms on interactive fauna have rarely been addressed.

Here, we present four-year weekly phenological data for two sympatric subspecies of *Geonoma cuneata* (*G. cuneata* subsp. *cuneata* and *G. cuneata* subsp. *procumbens*) and their gall inductor *Contarinia geonomae*, from the Atlantic lowlands of Costa Rica. This species was selected for two reasons. First, *G. cuneata* is one of the few subspecies in which a previous phenological study showed staggered flowering (Borschsenius, 2002), allowing for comparisons in different geographical areas. Second, there are only two palm species with a gall record (Gagné et al., 2018). Estimates have shown that there could be up to 211,000 gall-inducing species worldwide (Espírito-Santo & Fernandes, 2007). However, the vast majority of this gall-inducing insect species remain undescribe and knowledge about their ecology and relationship with their host remain unknown. Galls are highly specific meaning that they should synchronize their life cycle with their host phenology (Mopper, 2005; Pfeffer et al., 2018). In *G. cuneata*, galls are formed on the infructescences, making it easy to detect their phenology and relationships with both subspecies. Such case is uncommon since galls very rarely develop on flowers, fruits or seeds (Butterill & Novotny, 2015; Mendonça & Stiling, 2018; Gätjens-Boniche et al., 2021).

Our work mainly aimed to describe and compare the phenological behavior of the two *G. cuneata* subspecies in terms of flowering and fruiting patterns and as gall hosts. Specifically, we aimed 1) to determine whether the phenophases of both subspecies overlap or were seasonal, and if so, whether they correlated with precipitation or temperature; 2) to determine if there were differences between both subspecies in terms of inflorescence production and the proportion of inflorescences that produced fruits, galls, or aborted fruits; and 3) to determine the gall inductor phenology and its relationship with both palm subspecies. We hope to provide data to help understand the basic ecology of sympatric palm taxa and their relationships with the interacting fauna.

Methods

Study site

The study was conducted at Tirimbina Biological Reserve (TBR, 10°25'N; 84°47'W, 3777 mm, 24.3 °C), Sarapiquí, Heredia, Costa Rica , between September 2014 and August 2018. The TBR protects 345 ha of mature lowland rainforests, with most of the reserve covered by primary or old secondary forests. The area is relatively flat (180–220 masl) with several small creeks and hillsides crisscrossing the reserve. Yearly average temperature and precipitation during the study period were 24.6 °C and 4288 mm, respectively (TBR, meteorological station).

Study species

Geonoma cuneata is an understory palm species reaching between 1–3 m, easy to distinguish in the TBR from other *Geonoma* species because of its spike-like inflorescence with a conspicuous peduncular bract (Fig. 1). The palms are distributed from Nicaragua to Peru. However, it consists of a complex of eight subspecies with different geographic distributions, several of which often grow sympatrically (Henderson, 2011). In the TBR, there are two subspecies: *G. cuneata* subsp. *cuneata* (*Gcc*) and *G. cuneata* subsp. *procumbens* (*Gcp,* Fig. 1). The former has opaque, entire, and bifid or pinnate leaves, whereas the latter has shiny pinnate leaves with numerous pinnae (up to approximately 25). Nonetheless, a few plants exhibited intermediate characteristics, making

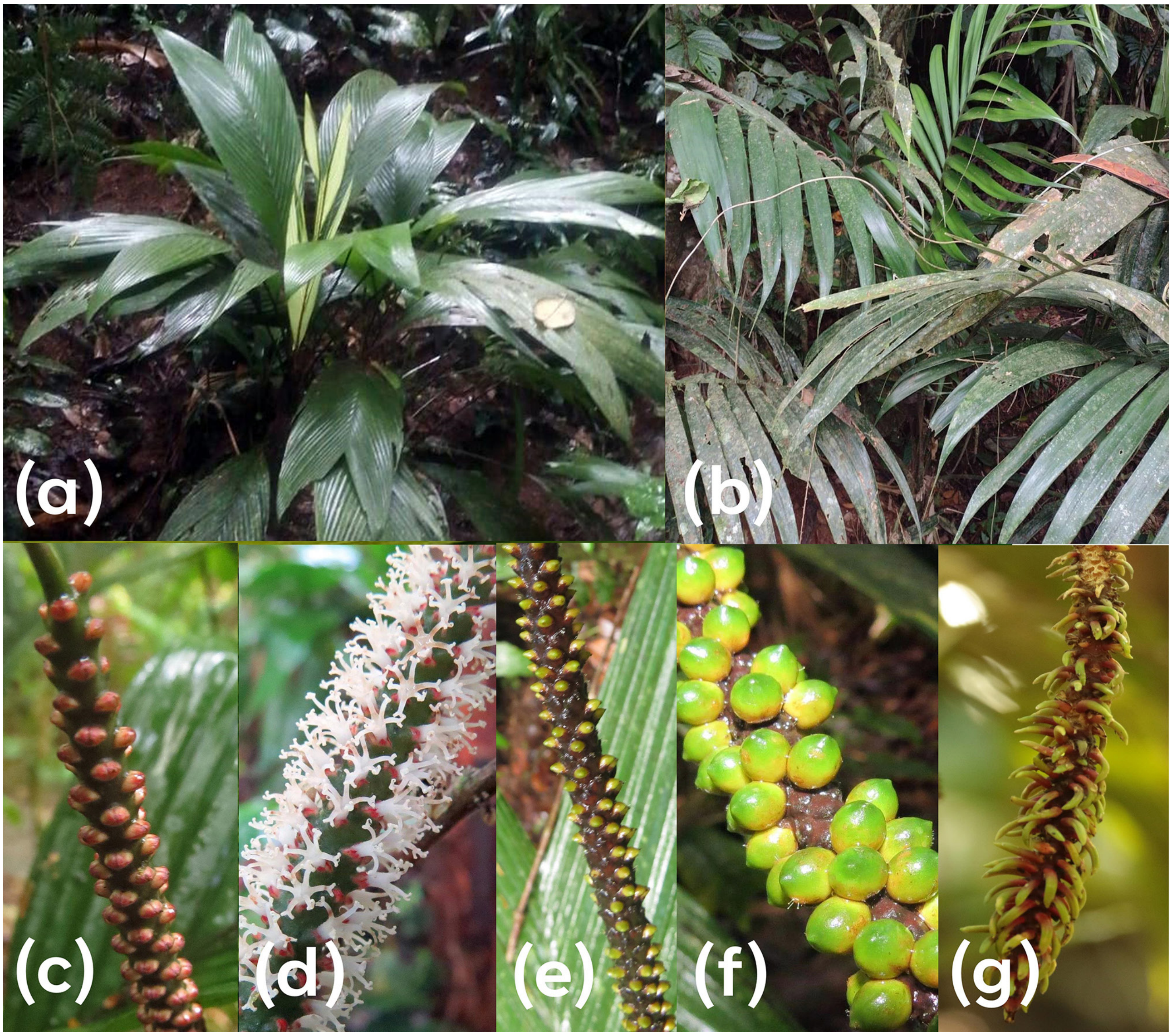

Fig. 1. *Geonoma cuneata* subsp. *cuneata* (a), *G. cuneata* subsp. *procumbens* (b), and different phenological stages: peduncular bracts (c), flowers (d), early unripe fruits and immature galls (e), unripe fruits at their maximum size (f), and immature galls at their maximum size (g), at Tirimbina Biological Reserve, Heredia, Costa Rica. Photos: ERV and JMLL

it difficult to assign them to a particular subspecies. Individuals with intermediate characteristics where not take it into account for this study. In the TBR, *Gcc* is relatively common across the entire forest, with an estimated density of 128 individuals/ha. In contrast, *Gcp* is scarce, with a density of 8.3 individuals/ ha, and often grows in waterlogged soils. The species is protandrous, and once flowers have fallen, the infructescence can produce fruits, galls (or both), or be aborted (Fig. 1). Both a detailed description of the flowering biology of *G. cuneata* (Borchsenius, 2002), and a complete description of the gall inductor *Contarinia geonomae* (Gagné et al., 2018) could be found elsewhere.

Field observations

In August 2014, we randomly selected and tagged 53 individuals of *Gcc* and four from *Gcp* across the trails of the TBR. Owing to the low abundance of *Gcp,* additional focal searches for this subspecies were performed until February 2015. Thereafter, we had 56 *Gcc* plants and 23 *Gcp* plants. Field observations were done weekly from September 3, 2014, to August 29, 2018 (207 consecutive weeks). Each week, we categorized the phenological stage of each palm according to the inflorescence that emerged. The following categories were used (Fig. 1): 1. infertile (without inflorescences), 2. emergent inflorescences (the first moment an inflorescence was observed), 3. peduncular bracts (from inflorescence appearance to bud opening); 4. masculine flowers; 5. feminine flowers; 6. post-flower (from the fall of the last flower until the appearance of fruits, galls, or abortion of the inflorescence); 7. unripe fruits (fruits that have not reached their final size or remain green), 8. ripe fruits (purple and dark fruits), 9. immature galls (galls that have not reached their maximum size and remain green); 10. mature galls (full-size dark galls at their full size). Because anthesis lasts for less than a week, the completion of flowering could occur between the two censuses. In these cases, the flowering period was assigned as the observation period. Categories 1–6 were categorical and exclusive to each inflorescence (although, in rare cases, a single inflorescence could harbor masculine and feminine flowers simultaneously). Then, each inflorescence was cataloged as aborted (inflorescences in which no galls or fruits developed and fell after a few days) or "fruit or gall successful" (when ripe fruits or galls were grown, disregarding the number). For gall and fruit loads (categories 7–10), we estimated the proportion of fruits and galls that developed in each infructescence based on the total number of flower scars found in the rachillae.

Data analysis

General phenology and seasonality

We used circular statistics to determine the presence of seasonality and compared whether there were differences in the phenophases between the subspecies (Morellato et al., 2000). In this analysis, the times of the year were converted into angles (in our case, months at intervals of 30°). The mean angle and its significance were calculated and converted back to the mean date. The mean angle indicates the central tendency of the data. The length of the mean vector r (which ranges between zero and one) provides the degree of frequency concentration around the mean. It defines the degree of seasonality (an r of one indicates that all data are concentrated around one angle and therefore shows the highest seasonality). To test the significance of seasonality, we applied the Rayleigh test to each phenophase. This test considers the null hypothesis that there is no seasonality and that all variables are distributed uniformly throughout the year. We used the monthly percentage of plants with emergent inflorescences, the presence of flowers, unripe and ripe fruits, and mature galls as phenological variables. We compared the mean direction of the phenophases that showed seasonality between subspecies using a non-parametric Watson-William test (F). In this analysis, we hypothesized that the mean vectors of the two subspecies were not significantly different. The rejected hypothesis indicated that the analyzed phenophase was asynchronous between species. A generalize logistic model was conducted to analyze the influence of climate variables (monthly sum of precipitation and monthly average temperature in each examined period) on observed phenophases. Each species' phenophase was treated as an individual model, with phenological activity as the dependent variable and climate variables as the independent variables. Each examined period was added to model as categorical data. Model was run with negative binomial distribution family using the MASS package (Venables & Ripley, 2002). The model diagnostic was made using DHARMa package (Hartig, 2022). Pseudo R^2 was calculated using Cohen's method (Cohen et al., 2002). The analyses were performed in R (Development Core Team, v. 4.2.1, 2014) using the "circular" package (Agostinelli & Lund, 2017) and with the demo version from the software Oriana (Kovach Computing Services, Wales, UK).

Comparisons between subspecies

We used a Mann–Whitney U test to assess whether there were differences between the subspecies in average inflorescence production and the average number of infructescences that successfully produced fruits per individual. We ran a Fisher's exact chi-squared test, or a chi-squared test to examine whether the proportion of infructescences that developed fruits, galls, or aborted, differed between the subspecies each year. Because a single infructescence can harbor both galls and fruits, we performed a chi-square test for each category by considering only the success of each category (e.g., the proportion of inflorescences that developed ripe fruits in *Gcc* versus the proportion of inflorescences that developed ripe fruits in *Gcp*). Similarly, we compared the success of each category of plants flowering outside the peak flowering period (between October and April for the first year and between October and May for all other years) against plant flowering during the peak period using chi-squared tests. Furthermore, we tested whether the average gall load differed among subspecies and between plants flowering outside the peak period and other plants using a Mann–Whitney U test. In all cases, we hypothesized that there would be no differences in infructescence outcome between populations or flowering periods. Linear regression was used to assess whether the proportion of galls affected the proportion of fruits in the inflorescences.

Results

General phenology and seasonality: During the four years of the study, *Gcc* and *Gcp* overlapped in all phenophases. However, both subspecies differed in terms of the mean date of several phenophases and the degree of seasonality (Table 1, Fig. 2). *Geonoma cuneata* subsp. *cuneata* showed strong seasonality ($p < 0.001$; $r > 0.5$). Seasonality was much weaker in *Gcp,* which, despite showing statistically significant results, had r values less than 0.50 in more than half of the phenophases (Table 1). This variation was due to longer and less synchronized phenophases and reflected higher standard errors from the mean angle (Table 1, Fig. 2).

The fertility cycle started with the peak of inflorescence emergence in May–June for *Gcc* and between February and May for *Gcp*. It ended between October and December, with a peak of ripe fruit for both subspecies (Table 1, Fig. 2). Except for 2017–2018, the peak of inflorescence emergence was asynchronous between the subspecies (Tables 1 and 2, Fig. 2). During the four years of study the flowering peak occurred between late June and August and differed for both subspecies during the years 2015–2016 and 2016–2017 (Tables 1 and 2). Most of the plants flowered between May and October. However, sporadic flowering was observed year-round, especially in *Gcp*, which showed low flowering r values, with the exception of 2017–2018 (Table 2). Ripe fruits and, to a lesser extent, unripe fruits showed the highest r values among all phenophases for both subspecies (Table 1). In all the years, unripe fruit peak occurred between September and October, whereas the ripe fruit peak

Table 1 Circular statistical analysis of the different phenophases of *Geonoma cuneata* subsp. *cuneata* and *G. cuneata* subsp. *procumbens* in September 2014–August 2018 at Tirimbina Biological Reserve, Heredia, Costa Rica

	Period									
	Sep 14–Aug 15					Sep 15–Aug 16				
	Emergent inflorescences	Flowers	Unripe fruits	Ripe fruits	Mature galls	Emergent inflorescences	Flowers	Unripe fruits	Ripe fruits	Mature galls
Gcc										
N of observations	82	104	211	84	51	68	50	133	90	72
Mean vector (μ)	127.62	201.70	263.57	312.92	333.39	161.92	205.37	277.29	297.55	302.73
Mean date	May	July	Sept	Nov	Dec	June	July	Oct	Oct	Nov
Standard error of mean angle	3.21	3.1	2.49	2.92	7.37	3.81	4.49	2.57	2.57	4.21
Lenght of mean vector (r)	0.828	0.752	0.692	0.81	0.53	0.753	0.745	0.78	0.849	0.707
Rayleigh test (Z)	92.04	106.99	187.44	104.44	25.80	71.40	52.18	146.48	116.66	63.94
Rayleigh test (p)	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Gcp										
N of observations	24	22	29	14	11	24	30	34	13	10
Mean vector (μ)	56.75	204.62	272.23	306.78	348.62	127.85	173.67	267.54	296.65	261.93
Mean date	February	July	October	Nov	Dec	May	June	Sept	Oct	Sept
Standard error of mean angle	7.07	7.46	5.91	4.95	9.90	11.02	9.05	4.01	4.10	14.96
Lenght of mean vector (r)	0.479	0.432	0.407	0.563	0.45	0.35	0.38	0.7	0.866	0.405
Rayleigh test (Z)	28.87	26.65	43.01	55.16	15.01	12.66	18.55	71.49	41.97	6.71
Rayleigh test (p)	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	0.001
	Period									
	Sep 16–Aug 17					Sep 17–Aug 18				
	Emergent inflorescences	Flowers	Unripe fruits	Ripe fruits	Mature galls	Emergent inflorescences	Flowers	Unripe fruits	Ripe fruits	Mature galls
Gcc										
N of observations	76	83	113	37	84	75	85	153	51	135
Mean vector (μ)	163.20	219.59	273.65	336.06	4.13	137.17	224.06	268.54	327.03	355.65
Mean date	June	August	Oct	Dec	Jan	May	August	Sept	Nov	Dec
Standard error of mean angle	4.8	5.15	4.12	5.54	12.56	3.85	5.80	2.90	4.07	4.84
Lenght of mean vector (r)	0.611	0.59	0.60	0.712	0.25	0.714	0.585	0.68	0.768	0.478
Rayleigh test (Z)	55.99	51.1	77.16	36.51	10.07	75.41	39.41	140.16	60.22	61.74
Rayleigh test (p)	< 0.001	< 0.001	<0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001	< 0.001
Gcp										
N of observations	27	29	45	15	9	27	34	30	13	26
Mean vector (μ)	64.57	179.57	284.79	347.44	3.65	114.11	219.48	288.06	314.31	50.63
Mean date	March	July	Oct	Dec	Jan	April	August	Oct	Nov	Feb
Standard error of mean angle	14.70	12	5.83	5.68	11.52	12.72	4.45	3.62	5.90	18.51
Lenght of mean vector (r)	0.249	0.29	0.467	0.723	0.521	0.279	0.724	0.756	0.724	0.198
Rayleigh test (Z)	7.35	10.9	42.75	34.02	10.59	9.74	55.49	78.30	31.48	4.70
Rayleigh test (p)	< 0.001	< 0.001	<0.001	< 0.001	<0.001	< 0.001	< 0.001	< 0.001	< 0.001	0.009

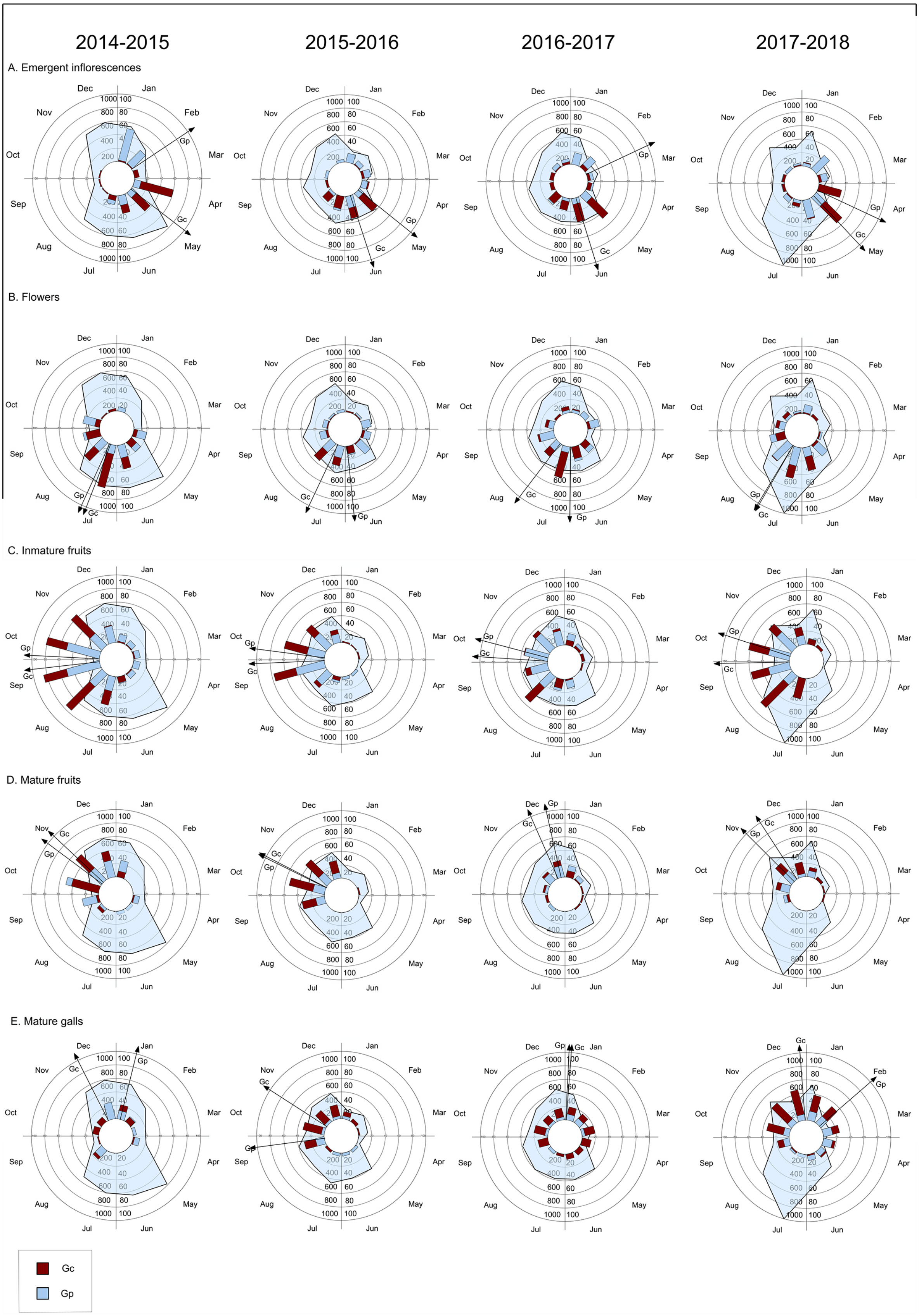

Fig. 2. Reproductive phenology of *Geonoma cuneata* subsp. *cuneata* (*Gcc*, red) and *G. cuneata* subsp. *procumbens* (*Gcp*, light blue) from September 2014 to August 2018 at Tirimbina Biological Reserve, Sarapiqui, Costa Rica. Values to the right indicate the percentage of individuals in each phenophase. Values to the left represent the total rainfall in each month. The bold arrow represents the mean angle

occurred between October and December (Table 1, Fig. 2). Moreover, ripe fruit was the only phenophase in which we did not find a statistically significant difference between the two subspecies during the four study years (Table 2). In contrast, mature galls were present most of the year, but differed between subspecies, and had the lowest r values (Tables 1 and 2, Fig. 2). The year of observation did not exhibit any influence on the studied phenophases. In both subspecies the emergent inflorescences were influenced by average temperature. Also, in both subspecies flowering was influenced by rainfall and average temperature. However, the r values were relatively low ranging between 0.26 and 0.54 (Table 3). Nonetheless, the emergence peak of new inflorescences mostly occurred at the end of the dry season and beginning of the rainy season. Also, in all years flowering coincided with the beginning of the rainy season. In addition, for both subspecies, the ripe fruit peaked in the middle of the rainy season and ended slightly prior the driest period of the year (Fig. 2).

Comparisons between subspecies: We counted 434 inflorescences: 325 from *Gcc* and 109 from *Gcp*. The average annual inflorescences per individual varied between 0.25–4, with an average of 1.60 in *Gcc* and 1.50 in *Gcp*. The average number of inflorescences that produced ripe fruit ranged between 0–2.5, with an average of 0.96 in *Gcc* and 0.63 in *Gcp*. No significant differences were observed between the

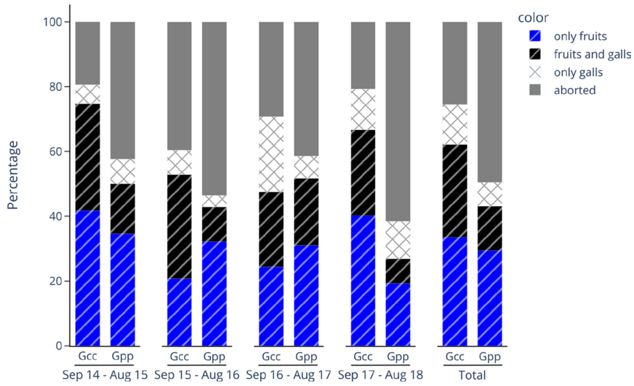

Fig. 3. Yearly inflorescence outcome of *Geonoma cuneata* subsp. *cuneata* (*Gcc*) and *G. cuneata* subsp. *procumbens* (*Gcp*) from September 2014 to August 2018 at Tirimbina Biological Reserve, Heredia, Costa Rica

Table 2. Watson-Williams test results comparing the mean angles of the different phenophases of *Geonoma cuneata* subsp. *cuneata* and *G. cuneata* subsp. *procumbens* during the period between September 2014–August 2018 in Sarapiqui, Heredia, Costa Rica

	Period			
	Sep 14–Aug 15	Sep 15–Aug 16	Sep 16–Aug 17	Sep 17–Aug 18
Emergent inflorescences	F = 161.42; p < 0.001	F = 9.24; p = 0.002	F = 36.43; p < 0.001	F = 3.12; p = 0.077
Flowers	F = 0.247; p = 0.62	F = 10.51; p = 0.001	F = 8.39; p = 0.004	F = 0.685; p = 0.408
Unripe fruits	F = 3.15; p < 0.076	F = 3.319; p = 0.068	F = 2.01; p = 0.16	F = 12.423; p < 0.001
Ripe fruits	F = 1.301; p = 0.25	F = 0.084; p = 0.771	F = 0.746; p = 0.058	F = 3.237; p = 0.072
Mature galls	F = 0.448; p < 0.001	F = 4.367; p = 0.037	F = 0.961; p = 0.002	F = 6.801; p = 0.01

Table 3. ANOVA table of the influence of climate variables (sum of monthly precipitation and average monthly temperature) on the phenophases of *Geonoma cuneata* subsp. *cuneata* (*Gcc*) and *G. cuneata* subsp. *procumbens* during the period between September 2014–August 2018 in Sarapiqui, Heredia, Costa Rica

Variable	Inflorescence			Flower			Mature Fruit		
	Chi square	Df	*P* value	Chi square	Df	*P* value	Chi square	Df	*P* value
Geonoma cuneata subsp. *cuneata*									
Rain	0.99	1	0.32	27.3	1	0.000	0.19	1	0.67
Temp. average	23.42	1	0.000	17.4	1	0.000	1.36	1	0.24
Year	4.64	3	0.20	0.97	3	0.81	3.57	3	0.31
Rain × Temp.	0.001	1	0.98	0.001	1	0.94	4.91	1	0.03
Rain × Year	1.7	3	0.64	2.74	3	0.43	8.66	3	0.03
Temp. × Year	0.94	3	0.81	4.8	3	0.19	4.31	3	0.23
Rain × Temp. × Year	2.04	3	0.56	3.87	3	0.28	2.65	3	0.45
R^2			0.37			0.54			0.31
G. cuneata subsp. *procumbens*									
Rain	0.07	1	0.8	17.89	1	0.000	0.4	1	0.52
Temp. average	4.54	1	0.03	22.12	1	0.000	2.77	1	0.09
Year	0.63	3	0.88	0.5	3	0.92	0.91	3	0.82
Rain × Temp.	7.2	1	0.007	0.01	1	0.93	6.63	1	0.01
Rain × Year	4.87	3	0.18	1.68	3	0.64	10.32	3	0.02
Temp. × Year	8.61	3	0.035	4.63	3	0.2	10.41	3	0.02
Rain × Temp. × Year	4.41	3	0.22	7.29	3	0.06	1.19	3	0.75
R^2			0.26			0.53			0.34

Table 4. Outcome of the inflorescences flowering during the peak period (June–September) and outside the peak period (October−May) for *Geonoma cuneata* subsp. *cuneata* (*Gcc*) and *G. cuneata* subsp. *procumbens* during the period between September 2014–August 2018 at Tirimbina Biological Reserve, Heredia, Costa Rica. Different letters in a column for the same subspecies indicates a statistical significant difference ($p < 0.05$) following a chi square test

	N inflorescences	Aborted	Not aborted	Galled	Fruited
Gcc					
Peak period	279	62 (22.22%)^a	217	109 (50.2%)^a	197 (90.7%)^a
Outside peak period	46	21 (45.65%)^b	25	24 (96%)^b	6 (24%)^b
Gcp					
Peak period	66	23 (34.84%)^a	43	17 (39.53%)^a	40 (93%)^a
Outside peak period	43	31 (72.09%)^b	12	6 (50%)^a	7 (58.3%)^b

subspecies in the average number of inflorescences produced per individual ($z = 0.97$, $p = 0.33$). However, *Gcc* had a significantly higher average number of inflorescences that successfully produced fruit per individual ($z = 2.43$, $p = 0.014$). The latter was explained by a higher proportion of *Gcp* individuals that failed to yield fruit during the study period. For *Gcc*, 109 (33.5%) inflorescences produced fruits only, 93 (28.6%) produced fruits and galls, 40 (12.3%) produced galls only, and 83 (25.5%) aborted. For *Gcp*, results were 32 (29.4%), 15 (13.8%), 8 (7.3%), and 54 (49.5%), respectively (Fig. 3). Among the subspecies, *Gcc* showed a higher proportion of inflorescences that produced fruit during 14–15 ($\chi^2 = 4.92$, $p < 0.026$, df = 1) and 17–18 ($\chi^2 = 11.37$, $p < 0.001$, df = 1). Additionally, *Gcc* infructescences were more likely to harbor galls during the year 15–16 ($\chi^2 = 4.39$, $p < 0.036$, df = 1). In contrast, *Gcp* showed higher abortion rates in 14–15 ($\chi^2 = 4.77$, $p < 0.029$, df = 1) and 17–18 ($\chi^2 = 14$, $p < 0.001$, df = 1). However, there were no differences in the total fruit load ($z = 0.91$, $p = 0.363$) or total gall load ($z = -0.86$, $p = 0.390$) between the subspecies. Individuals flowering outside the peak period had higher abortion rates in both subspecies (*Gcc* $\chi^2 = 11.40$, $p < 0.001$, df = 2; *Gcp* $\chi^2 = 14.45$, $p < 0.001$, df = 2; Table 4). Similarly, inflorescences that were not aborted had a higher chance of developing fruits when flowering during the peak period in both subspecies (*Gcc* $\chi^2 = 73.96$, $p < 0.001$, df = 2; *Gcp* $\chi^2 = 9.08$, $p = 0.003$, df = 2; Table 4) while *Gcc* had a smaller chance of developing galls ($\chi^2 = 18.97$, $p < 0.001$, df = 2; Table 4). Moreover, the inflorescences that flowered outside of the peak period showed higher gall loads than those that flowered during the peak period ($z = -3.71$, $p < 0.001$). We did not find any association between the percentages of galls and fruits.

Discussion

General phenology and seasonality

Tropical areas are characterized by a wide array of phenological behaviors (Sakai, 2001; Stevenson et al., 2008). Among them, several tropical forest phenological studies at the community level had shown that flowering and fruiting during the same rainy season are common in arboreal (Lobo et al., 2008) and epiphytic species (Cascante-Marín et al., 2017) even in tropical forests without clear seasonality (Liuth et al., 2013; Morellato et al., 2013). At our study site, both subspecies of *G. cuneata* showed annual, primarily seasonal, and overlapping behavior, which began during the dry period with the appearance of inflorescences and continued until the end of the rainy season with the peak of fruiting. Our results agree with other tropical palm species that have been studied (De Steven et al., 1987; Henderson et al., 2000; Ávila et al., 2022) but contrasts with the flowering behavior in four subspecies of *G. cuneata* in Ecuador where minimal flowering overlap was found (Borchsenius, 2002).

Phenological studies have found that seasonal palms tend to adjust their phenophases to environmental conditions (Rojas-Robles & Stiles, 2009; Rosa et al., 2013; Peñuela et al., 2019; Pedroso et al., 2021) or pollinator behavior (Carreño-Barrera et al., 2020). In our study, emergent inflorescences were influenced by average temperature while flowering was influenced both by average temperature and monthly rainfall. Despite correlations were relatively low, peak of flowering and fruiting in both subspecies always occurred during the rainy season. There are several complex factors that trigger flowering in tropical plants (Günter et al., 2008). In aseasonal tropical rainforest, decreased rainfall, increased solar radiation, and low soil humidity are the main proximate factors triggering flowering and shaping the phenological patterns (Günter et al., 2008; Wright & Calderón, 2017). Solar radiation, photoperiod and soil moisture were not considered in our study. However, they are important factors that influence phenophases in several tropical palms (Sampaio & Scariot, 2008; Vogado et al., 2020). Also, at our study site, precipitation patterns were irregular with a slight annual variation in temperature throughout the year. Moreover, our studied species was also characterized for showing relatively long phenophases. Several palm species show extended phenophases or irregular behavior among years, sites and individuals (Rojas-Robles & Stiles, 2009; Bruno et al., 2019; Martínez et al., 2021). Therefore, a lack of correlation or low correlations between abiotic variables and phenology are a common finding (Henderson et al., 2000). For instance, in a three year study on three populations of *Euterpe edulis* a positive correlation between flowering and day length was found every year in one population, only two years in the second population, and only one year in the third population (Castro et al., 2007). In three *Syagrus* species in Brazil precipitation had an irregular effect on fruiting and flowering over three years (Bruno et al., 2019). Similarly, no correlation was found between flowering and rainfall or temperature in two of the three *Johannesteijsmannia* species, despite all flowering occurring during the wet season (Chan & Chua, 2019).

Our results indicate a pressure to flower synchronously during the rainy season. In areas with high precipitation, pollination can be affected by decreased pollinator visitation (Antiqueira et al., 2020). Moreover, heavy rain could dilute nectar and degrade pollen therefore reducing pollination chances (Lawson & Rands, 2019). Increasing flowering synchrony can maximize the chances of pollination and individual reproductive success (Rocha et al., 2018). The flowering biology of *G. cuneata* has characteristics that make it susceptible to low pollination success and, therefore, to pressure for higher synchrony. Firstly, as a protandrous plant, it depends heavily on the availability of flowering congeners for pollination. Second, pollination is carried out by Drosophilidae and Sphaeroceridae flies, which are inefficient pollinators (Borchsenius, 1997, 2002). Third, the anthesis period lasts only a few hours and heavy rains can easily reduce pollination success. The high number of inflorescence abortions, substantial variation, and low percentage of fruit production may also indicate inadequate pollination. Similarly, flowering synchrony was lower in *Gcp*, but this subspecies also showed high abortion rates, supporting the importance of flowering synchrony.

Flowering patterns partly explain fruiting seasonality because most individuals that flower outside the peak period fail to produce fruit (De Steven, 1987). Therefore, fruit maturity showed the highest levels of synchrony and was the only phenophase that did not differ between the subspecies. Such behavior suggests intense pressure for synchronous fruiting or, alternatively, pressure to flower synchronously at the cost of lower fruiting success. Although the fundamental factors shaping fruiting patterns in palms may be associated with flowering, they may also be independent and associated with seed dispersal or germination (Adler & Lambert, 2008). In fact, several palm species bear fruit throughout the year despite short and synchronous flowering (Ibarra-Manríquez, 1992; Genini et al., 2009). In the study area, the fruiting peak of *G. cuneata* occurred during the fruiting peak of the palm community (Ley-López & Avalos, 2017), suggesting strong competition for dispersers. In addition, in several tropical plants, fruit maturity and rainfall are coupled to allow germination during the rainy season and increase seedling survival (Mendes et al., 2017; Satake et al., 2021). A previous study showed that the mean length of germination for *G. cuneata* is close to four months (Ley-López & Avalos, 2017), which coincides with the lag time between mature fruits and the beginning of the next rainy season. Such a pattern could be advantageous as a lack of water availability during the dry season is the main cause of seedling mortality in *G. cuneata* (Collins et al., 2022).

Comparisons between subspecies and gall phenology

In palms, differences in phenological behavior have been suggested to maintain the reproductive isolation of highly related taxa. For *G. cuneata*, this idea is supported in Ecuador, where there is a high degree of temporal variation in flowering in four subspecies (Borchsenius, 2002). In contrast, our subspecies showed a clear overlap in all phenophases over the four years of the study. The contrasting results of these studies suggests a climatic mechanism that drives species phenology (Günter et al., 2008). *Geonoma cuneata* has a wide distribution. Borchsenius (2002) hypothesized that if precipitation regimes were an important factor influencing flowering, such patterns would vary within different populations. This was the case in the present study. However, despite flowering convergence, both subspecies often exhibit different phenological peaks and are morphologically differentiated, indicating that other factors are involved in delimiting coexistence (Park et al., 2022). Competition among plants that share the same pollinators can be reduced if they have different habitat requirements (Pauw, 2013). At our study site, *Gcp* was uncommon and was often found near water bodies, whereas *Gcc* was common throughout the reserve. Studies have shown that several closely-related understory palms have highly specialized soil types and moisture contents (Peres, 1994; Souza & Martins, 2004; Poulsen et al., 2006). Indeed, an edaphic specialization was found in nine sympatric *Geonoma* species in Ecuador (Svenning, 1999). Other studies have shown that niche soil preferences and differences in flowering biology may prevent gene flow and contribute to reproductive isolation in sympatric *Geonoma* species (Listabarth, 1993; Borchsenius, 1997; Borchsenius et al., 2016).

Both subspecies showed other differences in their phenological and reproductive behaviors, with implications for gall induction. Synchrony and seasonality were pronounced in *Gcc,* showing lower abortion rates and a higher probability of developing infructescences with galls. In comparison, *Gcp* is characterized by more extended and less concentrated phenophases. Such differences benefit the gall inductor, which requires a high degree of synchrony with the host plant to complete its life cycle. First, flowering dissimilarities provide the gall inductor with an extended oviposition period, which could be crucial because oviposition is probably limited to a short anthesis period in the palm (Gagné et al., 2018). The above conditions are favored by two flowering peaks during the year and sporadic individual flowering throughout the year. In concordance with flowering, oviposition peaks should occur between June and early September. However, flowers in anthesis that later developed galls, were also recorded year-round (except in February and April), considerably extending the oviposition period. Moreover, inflorescences with lower synchrony and at the end of the flowering season usually develop higher gall loads. Mature galls showed the lowest synchrony values and were the only phenophases that were consistently asynchronous among the subspecies in all four years. The adults must remain alive between hatching and the subsequent anthesis period. Therefore, extended gall occurrence and emergence could increase the chances of survival in gall-inductor adults (Ferraz & Monteiro, 2003). Although the development of pupae in the soil or old infructescences can occur, adult emergence can be observed directly in mature galls (Gagné et al., 2018). In this scenario, most adult emergence occurs between September and February and adults will have to survive until June, when the flowering peak occurs. Finally, although it was difficult to quantify the extent of the adverse effects of the galls on the host, two preliminary observations were made. Almost 10% of the infructescences developed galls without fruit, suggesting a mechanism to avoid plant defense. Galling without fruit production was particularly important outside the flowering peak between November and March, when all 16 non-aborting inflorescences developed galls, whereas only two produced fruits. Second, galls are more likely to develop in inflorescences with lower synchrony at the end of the flowering period. The impact of gall behavior on host reproductive success and flowering patterns requires further investigation.

Conclusions

Our study is one of the first to compare the phenology of tropical sympatric palm subspecies and analyze its implications for a closely interacting species. Both *Geonoma cuneata* subspecies showed mostly seasonal behavior that overlapped in all their phenophases and was particularly strong for fruit synchrony. *Geonoma cuneata* subsp. *cuneata* showed higher synchrony values and a higher probability of inflorescences with galls. In contrast, the *Gcp* group exhibited lower synchrony values and higher abortion rates. Such differences are partly explained by the lower fruiting and higher gall incidence in individuals flowering outside the peak period. However, flowering convergence does not support the idea that phenology is a mechanism of reproductive isolation. Differences in phenological behavior and reproductive success indicate some degree of divergence among the subspecies. Similarly, the extended combination of flowering and fruiting in both subspecies benefits the gall inducer by providing an extended period of oviposition and adult emergence.

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