Phenological strategies of Byrsonima coccolobifolia (Malpighiaceae) and its associated galling Cecidomyiidae

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Research Article

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Abstract

Gall induction is a sophisticated adaptive strategy in ecological dynamics, which in the case of galling insects, demands the adjustment of their life cycles to the best host plant water and nutrient conditions. Such a hypothesis is herein tested in a *Byrsonima coccolobifolia*-Cecidomyiidae system, which was observed along 18 months. Ten individuals of *B. coccolobifolia* were marked and monitored in an area of Brazilian Savanna at Limeira farm in the municipality of Conceição do Pará, Minas Gerais state, Brazil. The synchronism between host plant phenophases and gall development and their responses to climatic parameters were estimated. *Byrsonima cocolobifolia* is deciduous, and the associated galling Cecidomyiidae has a univoltine life cycle, and the phase of gall induction synchronized with the first leaf flushing. Variations in plant phenology in response to environmental parameters evidenced that vegetative and reproductive phases of *B. coccolobifolia* asynchronous with gall development may be a strategy to escape the competition with the Cecidomyiidae. Nevertheless, gall development synchronized with the *B. coccolobifolia* reproductive phase may have deviated the total allocation of photoassimilates to reproductive shoots but did not impair fruit formation, besides being able to follow the delay at the beginning of leaf flushing as a function of environmental variations.

Introduction

Ecological dynamics may be interdependent and related to numerous biotic and abiotic factors (Franco et al. 2005; Doak et al. 2008; Garcia et al. 2017; García-Núñez et al. 2019). Among the fascinating diversity of ecological dynamics, gall induction is highlighted as a sophisticated adaptive strategy of many insects to obtain shelter, food, and protection from their natural enemies and environmental conditions (Mani 1992; Stone and Schonrögge 2003; Miller and Raman 2018). Galls are new plant organs developed in response to the stimuli imposed by specific gall-inducing organisms, which are mainly insects (Mani 1964). Such stimuli promote cell redifferentiation, leading to the formation of tissues with typical features and functions (Oliveira and Isaias 2009; Ferreira et al. 2019). After induction, gall development follows successive phases named growth and development, maturation, and senescence (Arduin and Kraus 1995) or dehiscence (Rohfritsch 1992), which relate to the temporal co-occurrence of the infesting forms of insects and the reactive plant tissue sites susceptible to manipulations (Oliveira and Isaias 2010, Carneiro et al. 2013). In general, the galling herbivore prefers young plant tissues, due to their ability to react to the stimuli of gall induction (Rohfritsch and Anthony 1992), and to the metabolic sinks established on host leaves and stems along their early developmental phases (Abrahamson and Weis 1987).

The time of appearance of most galling herbivores is synchronized with the time of the active growth of the host plant module in which the galls develop, evidencing ecological relationships to be explored (Mani 1964; Yukawa 2000; Carneiro et al. 2013; Oliveira et al. 2016; Guedes et al. 2018; Costa et al. 2021). For the life cycle of the galling insects, that is, for their developmental phases to be successfully completed, the synchronism with leaf flushing is fundamental for the temporal allocation of resources (Yukawa 2000; Fagundes 2014). These resources are also related to environmental variations, climatic

seasonality, and especially to the availability of water in the soil (Borchet 1994; Oliveira et al. 2013; Guedes et al. 2018; Costa et al. 2021). Moreover, the phenological synchronization of different species can be disrupted if alterations in temperature or in precipitation occur (Franco et al. 2005; Garcia et al. 2017). Such alterations peculiarly affect the phenology of different species (Weis et al. 1988; Yukawa 2000; Asch et al. 2007), with changes in the lifespan and the voltinism of the galling herbivores (Bale et al. 2002).

Species of the genus *Byrsonima* Rich. Ex. Kunth. (Malpighiaceae) has a wide occurrence in Brazilian Savanna areas, different phenological strategies (Mamede 2013), a richness of associated galls (Silva et al. 2018; Campos et al. 2021), and are elegant models for studies on phenological synchronism between host plants and galling insects. The elegance of this model lies in the combination of the wide occurrence of this genus in Brazilian savanna areas, its morphological and ecological characteristics that facilitate observation and data collection, and the complex network of interactions between host plants and galling insects.

One of its species, *Byrsonima coccolobifolia* Kunth, commonly known as “pink murici” is a tropical, deciduous species present in the “cerrado” and “campo cerrado” (Barbosa et al. 2005; CNC Flora 2023), where the individuals are superhosts of gall inducers (Gonçalves-Alvin and Wilson 2001; Araújo et al. 2015), including a Diptera, Cecidomyiidae that induces a conical leaf gall (Araújo et al. 2014). The specificity of the plant-insect interactions and the expected synchronism between *B. coccolobifolia* and this galling Cecidomyiidae were addressed through the investigation along 18 months. Our hypotheses are that (1) the host plant may have subtle phenological strategies toward windows of opportunity to escape gall induction, and (2) the galling Cecidomyiidae life cycle may adjust to the best water and nutritional conditions during the phenology of *B. coccolobifolia* with a negative impact on flowering and fruiting.

Material and Methods

Study area

The phenological events of *B. coccolobifolia* (voucher deposited in herbarium IBIUEMG 167) were analyzed in a forest fragment of Brazilian Savanna on the Limeira farm in the municipality of Conceição do Pará (19°.45’ 25.3” S, 44° 50’ 01.2” W), state of Minas Gerais, Southeast Brazil (Fig. 1) between September 2018 and March 2020. The area has 704 m of altitude with typical Savanna vegetation and the individuals of *B. coccolobifolia* are arranged at the edge of the forest fragment, a region with sparse vegetation and rocky soil. According to the Köppen system, the climate of the region is classified as Cwa (Humid subtropical with dry winter, and hot summer) (Alvares et al. 2013), with marked seasonality. Meteorological data were collected at the Instituto Nacional de Meteorologia (INMET) in Estação Meteorológica Automática de Divinópolis, Minas Gerais, Brazil, and defined the dry and rainy seasons. The rainy season began in September 2018 and extends to April 2019, with the highest accumulated rainfall (380 mm) in February 2019. The dry season began in May 2019, with no rainfall between July and

August 2019. The highest values of maximum temperature were recorded in January 2019 (24.2°C) and the lowest values of minimum temperature were recorded in July 2019 (16.9°C) (Fig. 2).

Data sampling of host plant phenology

The phenological observations were conducted at a 15-day interval from September 2018 to February 2020 at the individuals (n = 10) of *B. coccolobifloia* with a minimum circumference at breast height greater than 10 cm and good canopy visibility. Ten individuals of *B. coccolobifolia* were marked and monitored in a population of 42 individuals, located in an area of Brazilian Savanna at Limeira farm in the municipality of Conceição do Pará, Minas Gerais state, Brazil. The vegetative phenophases were characterized by the presence of leaf flushing (leaf up to 2 cm long and reddish with green veins (Fig. 3A), young leaves (green leaf with pinkish veins) (Fig. 3B), mature leaves (green leaf with light green veins) (Fig. 3C), senescence (yellowish leaf with the presence of necrotic areas stained in brown) (Fig. 3D), and leaf abscission (Fig. 3E). For the reproductive phenophases, the inflorescence bud (terminal raceme-type inflorescence with pinkish flowers) (Fig. 3F) and inflorescence anthesis (pale pink hermaphrodite flowers) (Fig. 3G), immature fruits (globose, green) (Fig. 3H) and mature fruits (yellow) (Fig. 3I).

The percentage of phenophase intensity, i.e., the Fournier index (Fournier 1974), was evaluated using a five-category scale from 0–4 with 25% intervals (0 = absence of the phenophase; 1 = 1–25%; 2 = 26–50%; 3 = 51–75%; and 4 = 76–100% intensity of the phenophases) in each *B. coccolobifolia* individual. The presence and absence of vegetative and reproductive phenological phases, as well as phenological synchrony, were evaluated for each plant by applying the activity index (Bencke and Morellato 2002). This method estimates the percentage of individuals in the population that present a particular phenological event and indicates the synchrony of this phenological event throughout the year.

Data sampling of the gall developmental phases

The gall developmental phases, induction, growth and development, maturation and senescent phases were rated on five marked branches in each of ten individuals (n = 50 branches). The canopy was radially divided into five parts for branch marking. On each branch, the presence of each gall development phase was counted every 15-day interval from September 2018 to February 2020. The induction phase (hard to be visualized) was defined by the presence of distinct light green spots on the adaxial surface of the young leaf (Fig. 4A), and the growth and development phase was indicated by the gall pinkish color on the adaxial surface and green on the abaxial surface (Fig. 4B); the maturation phase was indicated by the gall brownish color in the tapered apex on the adaxial surface (Fig. 4C); and the senescent phase was indicated by the change in gall to pallid green color (Fig. 4D).

Data analysis

The synchrony between the plant phenophases, between individuals in the same phenophase, and of the phenophases with gall development, and the climatic parameters were estimated by the non-parametric Kendall correlation considering the measurements of all the 18 months.

To evaluate the relationship between two quantitative variables (rainfall and temperature), the non-parametric Kendall's correlation was calculated for each pair. Illustrative graphs were constructed for significant relationships. A Principal Components Analysis was performed with the correlation matrix, and prior to the analysis, the data were previously transformed into ranks. This methodology corresponds to evaluation relationships among the vegetative and reproductive phenology, gall development, and climatic variables from a non-parametric perspective (Conover 2012). All statistical analyzes were performed using R software version 3.6.1 (R Core Team 2019).

Results

The phenological behavior of the host plant

Byrsonima coccolobifolia is a deciduous species, which lost all its leaves in the dry season, i.e., between May and September 2019 (Fig. 5A-B). Leaf flushing occurred at two periods of the year, with an intensity peak in September 2018. In 2019, there was a peak in February and another one with a higher intensity in October. In 2020, the leaf flushing peak occurred in February. Young leaves occurred from September to November of 2018, but in 2019, this phenophase was less intense and extended until January 2020. Mature leaves had maximum intensity from December to February in both years, with a decrease in April 2019, when the precipitation index decreased. The occurrence of senescent leaves began in April 2019, with a peak of intensity in June 2019. Leaf falling began in June 2019, at the beginning of the dry season. The tree was totally leafless between July and August 2019, when the lowest precipitation was registered along the dry season (Fig. 5A). The floral buds appeared soon after leaf flushing between September and October in both years (2018 e 2019), and full inflorescence anthesis occurred in November; immature fruits had maximum intensity in January 2019 e 2020 and fruit ripening occurred in February 2019 e 2020. A leaf flushing occurred in February (2019 e 2020), and a new reproductive cycle occurred from March to June 2019, concomitant with the end of the rainy season and the beginning of the dry season, and the occurrence of senescent leaves (Fig. 5B). Most of the individuals sampled showed synchrony in the vegetative and reproductive phenophases (Figure S1).

The gall phenological behavior

We monitored two gall life cycles, one recorded from September 2018 to May 2019, and another one recorded from October 2019 to February 2020. The maximum peak of induction activity was recorded in October 2018 and November 2019 in synchrony with the occurrence of young leaves, the appearance of floral buds, and the onset of the rainy season. Galls entered the growth and development phase in October 2018 and 2019, with a peak in November of both years. The peaks of the maturation phase

occurred on December 2018 and January 2019, coinciding with the peak of mature leaves and the development of immature fruits. The galls entered the senescent phase from February to May 2019 at the onset of the dry season and low temperatures. The second event of gall senescence occurred from January to February 2020 in the middle of the rainy season (Fig. 5C). The synchronism between gall phases was observed in most host plants (Figure Sa), and the species of Cecidomyiidae associated with *B. coccolobifolia* has a univoltine life cycle.

Correlations between the phenological phases of the host plant and the gall

Leaf flushing and young leaves were strongly correlated and happened concomitantly ($R = 0.77$; $p < 0.001$) (Figure S2 e Figure S3). Leaf flushing ($R = 0,53$, $p = 0,008$), floral buds ($R = 0,47$, $p = 0,017$), and galls in the growth and development phase ($R = 0,59$, $p = 0,006$) were moderately correlated and occurred at the same time of the years when the highest water availability occurred ($R = 0,44$; $p = 0,012$). The temperature was positive and moderately correlated with the mature leaf ($R = 0,45$, $p = 0,013$ and immature fruit ($R = 0,39$; $p = 0,045$) phenophases. Precipitation was positive and moderately correlated with the young leaf ($R = 0,38$, $p = 0,38$), mature leaf ($R = 0,51$, $p = 0,005$), and mature fruit ($R = 0,38$, $p = 0,045$) phenophases. Temperature ($R = 0,38$, $p = 0,04$) and precipitation ($R = 0,51$, $p = 0,005$) were negatively correlated with the leaf abscission phenophase and occurred when water availability was minimal, and the temperature was falling.

Principal Component Analysis (PCA)

The first two axes of the PCA explained 46.5% of the total variability of the matrix. Evaluating by axis 1, we observed the formation of a group of variables positively associated with each other (left quadrants), encompassing the variables: temperature, precipitation, mature leaf, ripe fruit, maturation, and senescence of the galls. This group is negatively associated with the variable leaf abscission, located in the lower right quadrant. A second group is formed by variables that are positively associated with each other, which are leaf flushing, young leaves, inflorescence floral buds, inflorescences, induction, and growth and development, and was negatively associated with senescent leaves.

Two groupings of variables, one being the vegetative period associated with the beginning of flowering and the other the reproductive/dispersive period with the presence of fruits. This last period is associated with the hottest and most humid period of the year (rainy summer). Internal or physiological factors and external or edaphoclimatic factors are positively or negatively associated with the vegetative and reproductive phenophases of the host plant and with the life cycle of the galling insect. The vegetative and reproductive phenophases overlapped with the growth and development phase of the gall and were positively correlated with temperature and precipitation (Table 1) (Fig. 6).

Table 1
Principal components 1 (PC 1) and 2 (PC 2) obtained from the correlation matrix of the phenological phases of the *Byrsonima coccolobifolia* Kunth (Malpighiaceae) and life cycle phases of the galls.

Variables	Axes	
	PC1	PC2
Flushing	-0.05	0.35
Young Leaf	-0.15	0.25
Mature Leaf	-0.40	-0.29
Senescent Leaf	0.13	-0.34
Leaf abscission	0.41	-0.13
Inflorescence buds	-0.01	0.30
Inflorescence anthesis	-0.21	0.32
Immature Fruit	-0.09	-0.01
Ripe Fruit	-0.25	-0.33
Induction	-0.05	0.37
Growth/Develp.	-0.14	0.26
Maturation	-0.28	-0.10
Senescence	-0.25	-0.28
Precipitation	-0.45	-0.01
Temperature	-0.39	0.05
Explained variance (%)	26.7	19.8

Discussion

From the host plant perspective

The individuals of *B. coccolobifolia* exhibited a deciduous habit characterized by a total leaf falling for three months (June to August) in the dry season. This seasonal behavior has been similarly reported for *B. coccolobifolia* in some Brazilian Savanna areas (Morais et al. 1995), but the semi-deciduous (Barbosa et al. 2005; Pereira 2018) or evergreen habit (Figueiredo 2008) have also been observed. The variation in the leaf dynamics of *B. coccolobifolia* can be related to phenological adjustments at the individual level and may explain the species success in different phytogeographic domains (Barbosa et al 2005).

Variations in water availability and temperature in different habitats can influence the intensity and duration of the vegetative phases of plant populations (Boas et al. 2013; Silveira et al. 2013). In species of the Brazilian Savanna and other seasonal environments, leaf falling synchronizes with lower water availability, as a mechanism to reduce water loss and maximize the acquisition of nutrients (Pedroni et al. 2002; Silvério and Lenza, 2010). In this perspective, the variation in rainfall volume at the beginning of the rainy season (about 1 month later in 2019 than in 2018) interfered with the phenophases of *B. coccolobifolia*. Hence, it is plausible to admit a phenological adjustment of *B. coccolobifolia* individuals to the condition of low water availability of the Brazilian Savanna.

Regarding temperature and rainfall, the ranges between 23–25°C and 80-1020 mm were not directly correlated to leaf flushing, which occurred before the onset of rainfall, and is a strategy reported for other Neotropical savanna species (Borchert 1994; Rivera et al 2002; Franco et al 2005; Lenza 2005). The occurrence of leaf flushing just before the rains can optimize the photosynthetic rate in deciduous species, as it allows the complete regeneration of the canopy at the onset of the rainy season (Franco et al. 2005) and prevents the prolonged exposure of young leaves to water stress, mitigating the damage imposed by herbivorous insects (Rivera et al 2002), including the gall inducers. In the tropics, herbivorous insect populations decrease in the dry season, and new life cycles start at the beginning of the rainy season (Coley and Barone 1996; Bale et al. 2002). Accordingly, the new leaves produced during the rainy season will suffer less insect damage than leaves produced during the dry season, the time of highest leaf production (Marquis et al 2001).

The low correlation between leaf flushing, floral bud emergence, and gall induction in *B. coccolobifolia*-Cecidomyiidae system with the abiotic parameters suggests that the host plant accumulated nutrient resources that allowed leaf flushing even before the onset of rains as proposed for other phenological studies (Garcia et al. 2017; García-Nuñez et al. 2019). The vegetative and reproductive cycles observed at two different times of the year, at the end of the rainy season, in the individuals of *B. coccolobifolia* may constitute a strategy to escape the attacks by the galling herbivores. This strategy was also evidenced in the early leaf flushing of *Copaifera langsdorffii* before the rainy season and resulted in a higher event of herbivory on plants that emerged later (Fagundes et al. 2016). As the galling Cecidomyiidae associated with *B. coccolobifolia* has a univoltine life cycle, during the second cycle of the year, there are no adult individuals to oviposit, despite the availability of host plant-responsive tissues.

The positive and moderate correlation of young leaf emergence with precipitation and temperature increasing, which coincided with the phases of gall induction and growth and development, indicated an allocation of resources shared by the vegetative, the reproductive phenophases, and the gall development. However, the presence of the galls, as a third sink of photoassimilates, does not seem to negatively influence the phenological events of *B. coccolobifolia* since fruiting occurred abundantly in both reproductive cycles.

Senescent leaves and leaf abscission had a significant positive correlation with precipitation and temperature. As well, the production of immature and ripe fruit correlated to the lowest precipitation and the highest temperature variations.

From the galling insect perspective

Gall establishment and development require plant-responsive tissues (Carneiro et al. 2013), which are the main components of young leaves, the preferred oviposition sites of the galling Cecidomyiidae associated with *B. coccolobifolia*. The young leaves as preferred sites of oviposition have also been reported for *Piptadenia gonoacantha* (Arduin and Kraus 1995), *Ficus microcarpa* (Souza et al. 2000), *Baccharis concina* and *B. dracunculifolia* (Arduin and Kraus 2001) and *Mimosa gemmulata* (Costa et al. 2021) in different areas of the Brazilian Savanna, as well as in other biomes, as reported for *M. tenuiflora* in Caatinga (Nogueira et al. 2022) and *Schinus polygama* in the Mediterranean climate of southern Chile (Guedes et al. 2018). This preference for young leaves can be interpreted as a strategy from the structural and nutritional points of view, which favor the development of the gall and, consequently, the life cycle of the gall inducer (Miller and Raman 2018). From the structural point of view, young leaves are composed of tissues that are more reactive to gall induction stimuli and respond by hyperplasia and cell hypertrophy, common plant responses observed in galls (Rohfritsch and Anthony 1992). From the nutritional point of view, young leaves are richer in water and nitrogen than mature leaves (Coyle et al. 2010; Liu et al. 2010) due to metabolic sinks, which young leaves establish in their early phases of development (Abrahamson and Weiss 1987).

The peak of gall induction on *B. coccolobifolia* varied about one month from the first to the second year of sampling, indicating that the associated galling Cecidomyiidae has strategies to exploit the host plant species even with changes in its phenology in response to climatic events. This refined synchronism of the gall inducer was demonstrated in the *Lopesia mimosae* galls on *Mimosa tenuiflora* (Nogueira et al. 2022), as well as, for other groups of gall-inducing insects (Castro et al. 2012; Magalhães et al. 2014).

In the gall growth and development phase, the feeding activity of Cecidomyiidae larvae in plant tissues is intense and alters photoassimilate allocation by acting as an additional sink (Mothes et al. 1961; Stone et al. 2002; Schultz et al. 2013; Ekholm et al. 2019). The gall maturation phase corresponds to the main trophic phase of the gal inducer, and, consequently, the sink of photoassimilates toward the gall is even stronger than in gall induction (Rohfritsch 1992). This new sink can disturb the homeostasis of plant tissues, reducing the availability of plant resources for growth and reproduction (Isaias et al., 2015; Oliveira et al., 2017), which in the case of *B. coccolobifolia*, did not negatively influence the fruiting phase, and suggest the occurrence of a redistribution of photoassimilates.

The synchronism with the host plant phenophases is fundamental to the success of the life cycle of the galling insects (Weis et al., 1988; Yukawa 2000; Oliveira et al., 2016). In *B. coccolobifolia*, the associated Cecidomyiidae has a univoltine life cycle in which gall induction was synchronized with the first event of leaf flushing observed in 2018. The second leaf flushing observed in the population of *B. coccolobifolia* in 2019 occurred when there were no adults of Cecidomyiidae able to oviposit. This asynchrony with the

life cycle of the Cecidomyiidae configures a window of opportunity for the host plant escape gall induction, which corroborates our first hypothesis. The galling Cecidomyiidae life cycle adjusts to the environmental variations, but does not have a negative impact on the flowering and fruiting of *B. coccolobifolia*, which does not corroborate our second hypothesis.

Declarations

Competing Interest

The author(s) declare no potential conflicts of interest with respect to the research, authorship, and/or publication of this article.

Ethics approval

Not applicable

Consent to participate

Not applicable

Consent for publication

Not applicable

Authors' contributions

RSMM: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Data curation, Writing – original draft, review & editing. JNM: Conceptualization, Validation, Formal analysis, Writing – original draft. ECC: Writing – review & editing. GPPB: Writing – review & editing. RMSI: Conceptualization, Resources, Writing – original draft, review & editing, Supervision, Project administration.

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Author Contribution

RSMM: Conceptualization, Methodology, Validation, Formal analysis, Investigation, Data curation, Writing – original draft, review & editing. JNM: Conceptualization, Validation, Formal analysis, Writing – original draft. ECC: Writing – review & editing. GPPB: Writing – review & editing. RMSI: Conceptualization, Resources, Writing – original draft, review & editing, Supervision, Project administration.

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Data Availability

Data will be made available on request.

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Figures

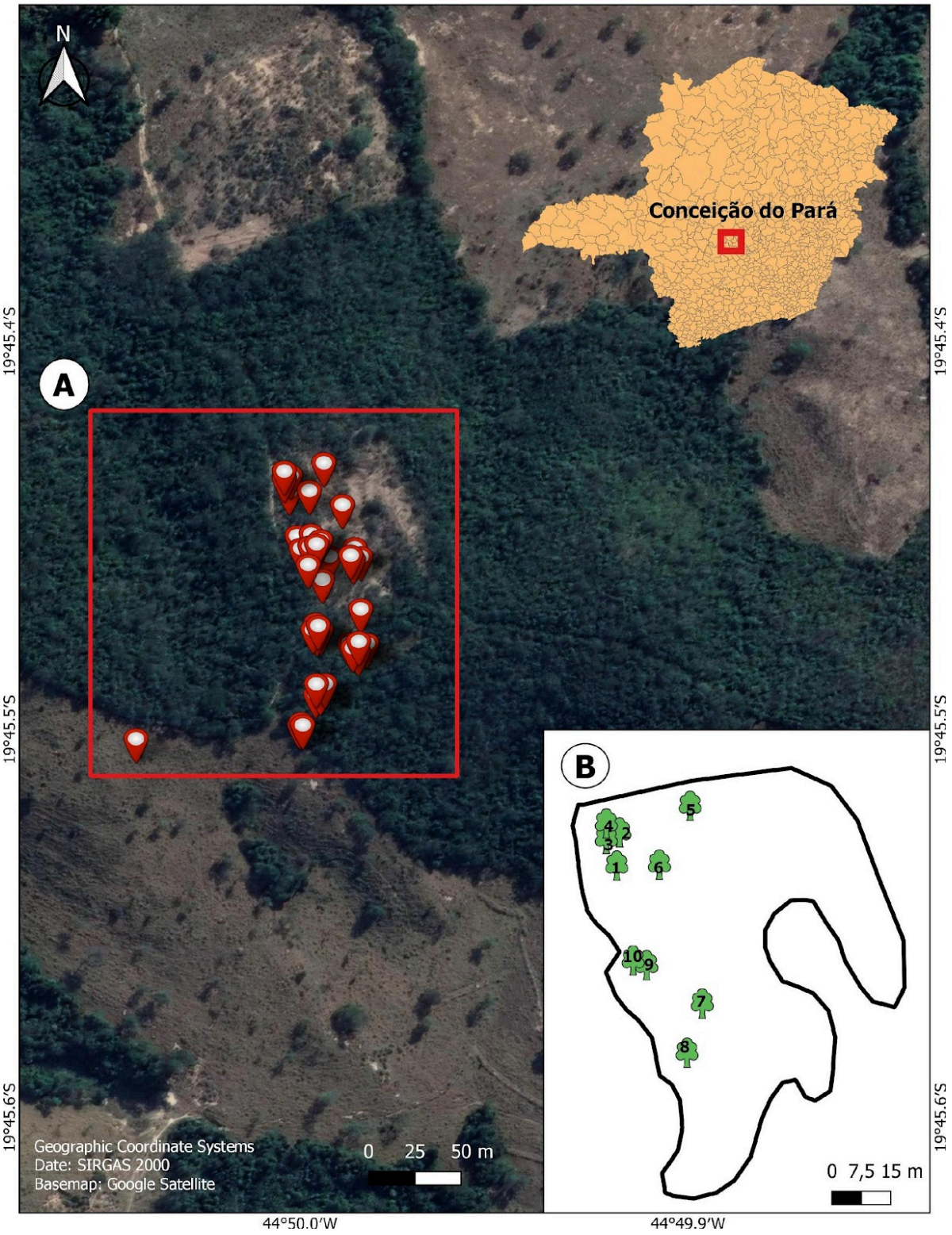

Figure 1

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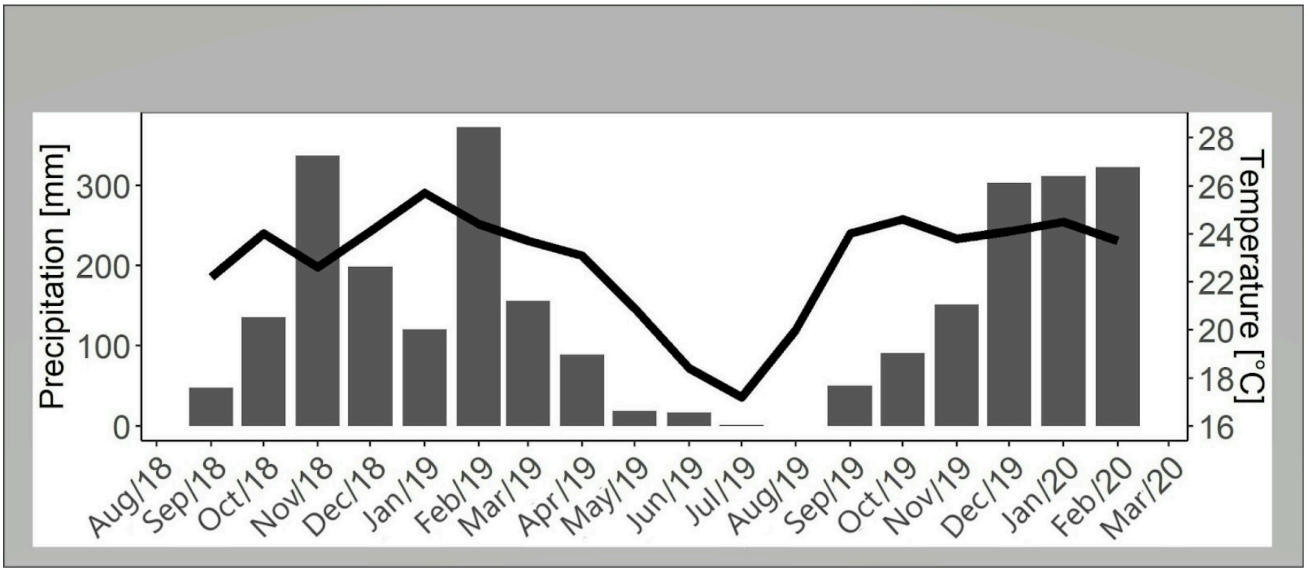

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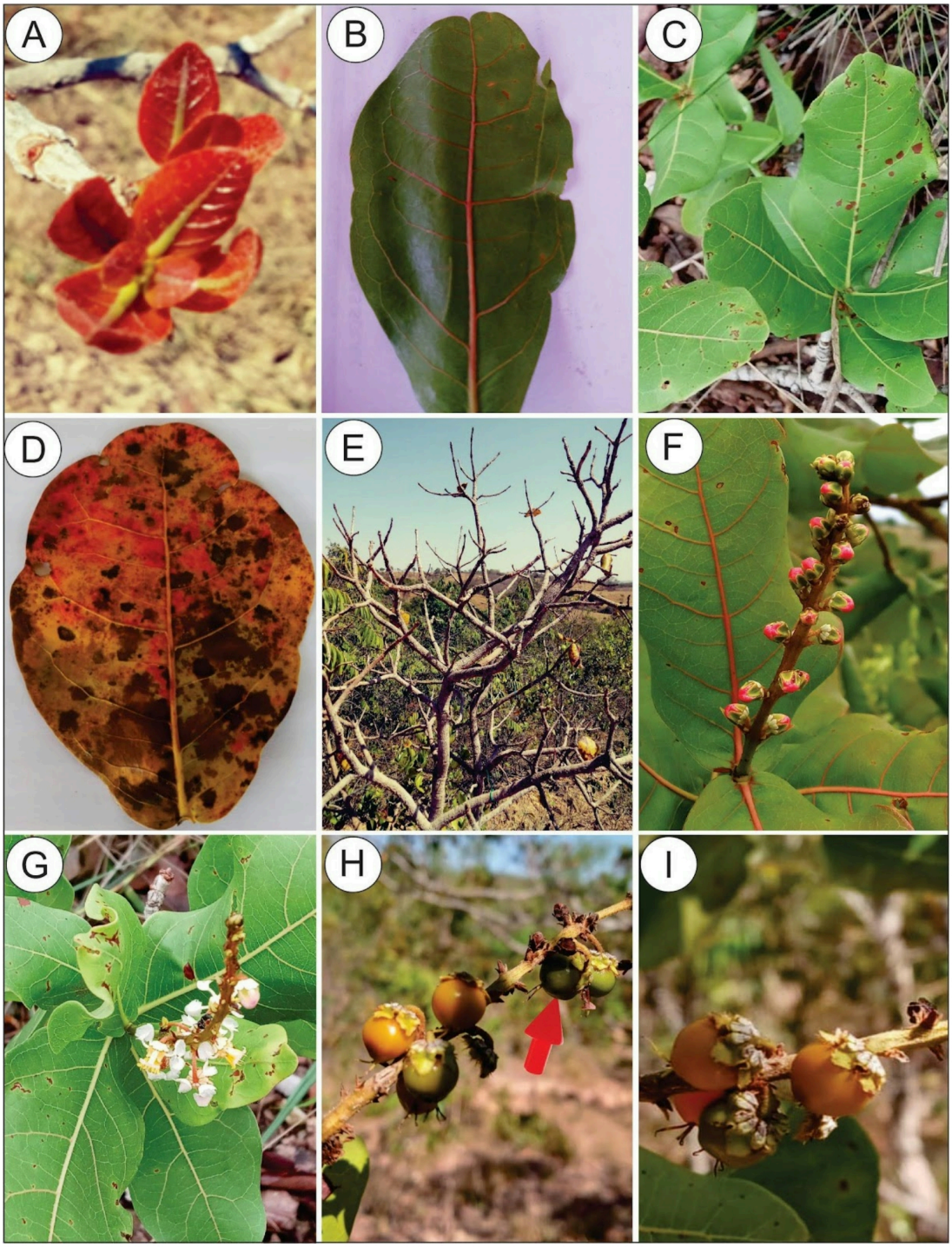

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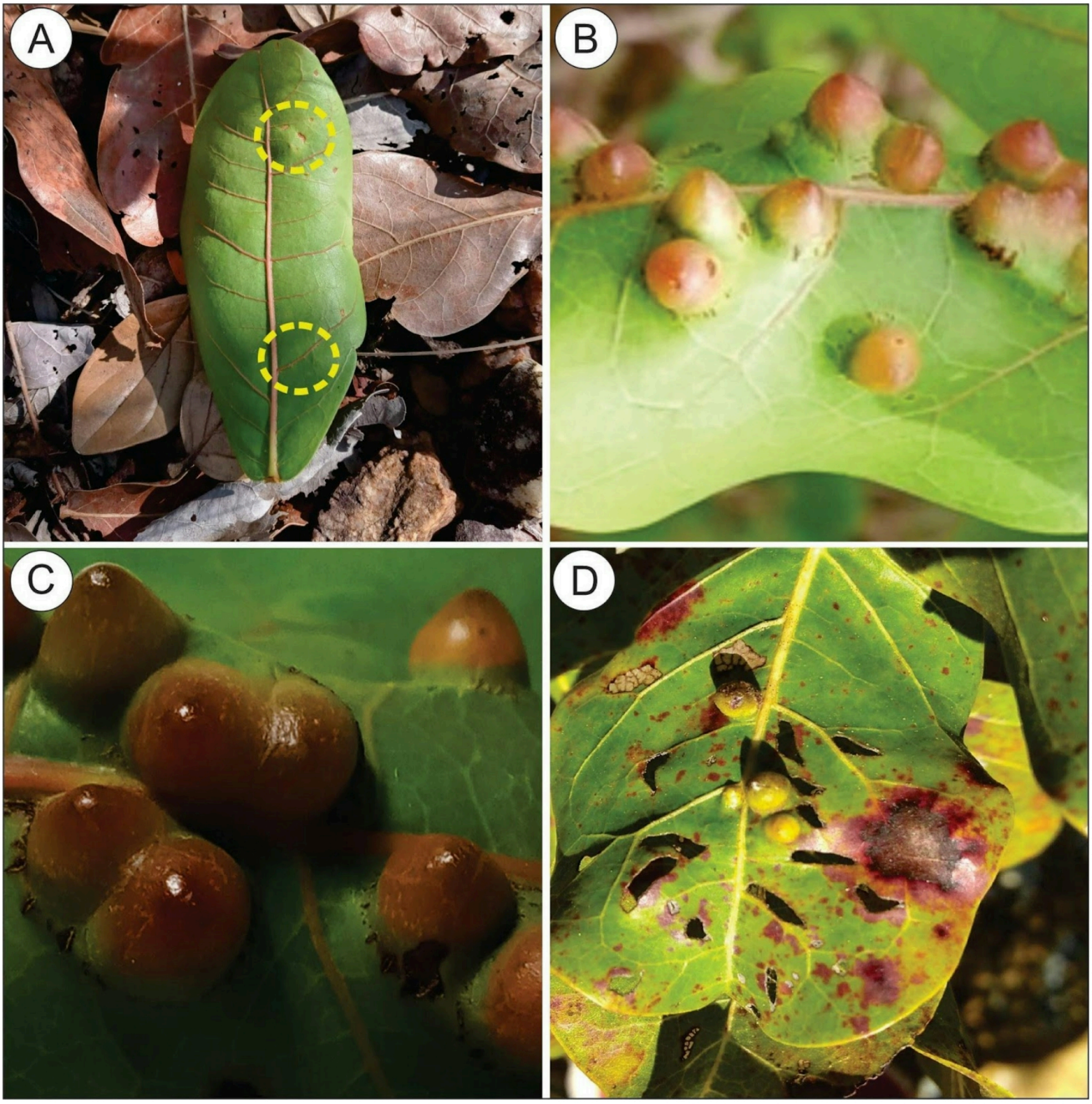

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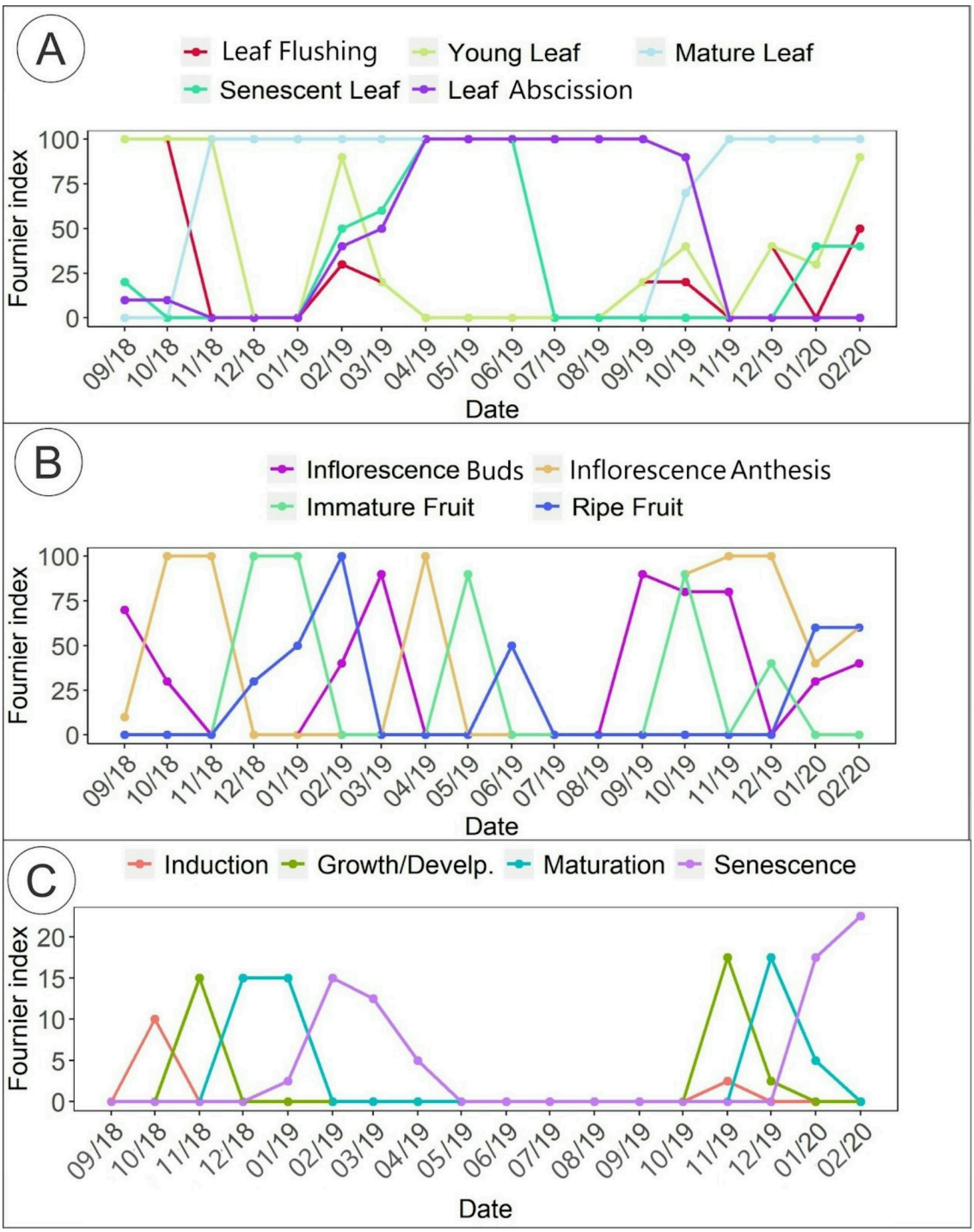

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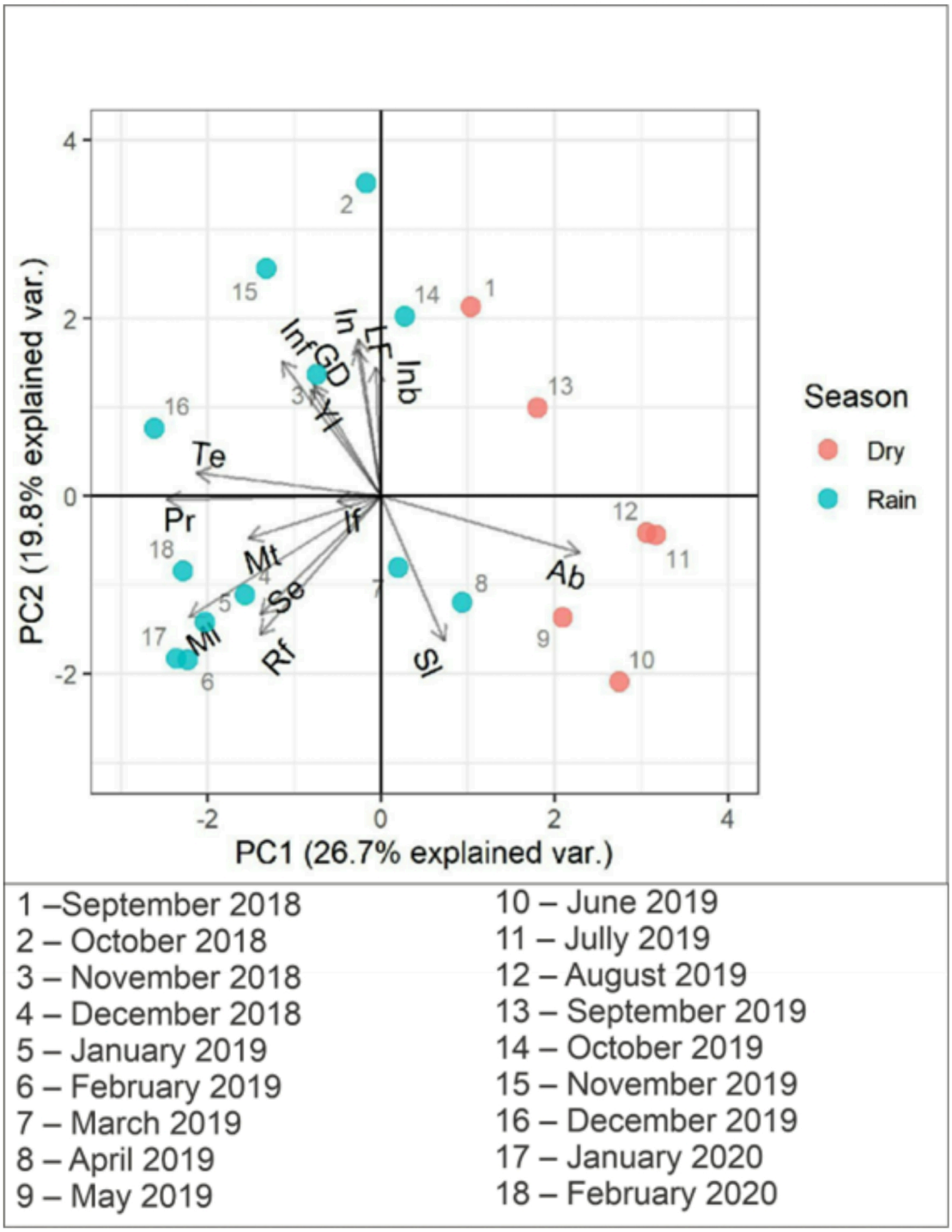

Figure 6

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