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Phenology and South American leaf blight of polyclonal seedlings population of natural rubber trees in Colombia

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A R T I C L E I N F O

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Hevea brasiliensis
Escape Zones

A B S T R A C T

The phenological development of polyclonal rubber plantations has been little explored, although they present adaptive potential to specific biotic and abiotic conditions. Between 2016 and 2021, rubber tree seedlings were evaluated for leaf ontogeny, leaf area index (LAI), and reproductive phenology (flowers and fruits). The climatic conditions were correlated with the foliar and reproductive rubber phenology and the incidence and severity of the South American leaf blight (SALB). The tree phenology showed a relationship between defoliation-refoliation with the water deficit intensity and high temperatures. The development of the trees in a polyclonal plantation was heterogeneous, and the defoliation-refoliation phases were extended over time. A higher SALB severity was associated with higher relative humidity and radiation periods, reducing the leaf area (atypical defoliation) and changing flowering and fruiting seasonality. The intensity and duration of climatic factors, particularly water deficit, are important for determining phenological processes and fungal diseases such as SALB, which serves as a tool to build management strategies both in seed production and obtaining latex in scenarios of climate change.

1. Introduction

Hevea brasiliensis is a perennial tree belonging to the Euphorbiaceae family (Priyadarshan, 2017). Its center of origin is the Amazon River basin located between 5° N and 20° S latitude and 50° and 80° E longitude (Priyadarshan, 2016). The area planted with rubber in the world is 134,409 million hectares, of which 84.9% are in a productive state, with a world production of 12.27 million tons in 2015 and a consumption of 12.15 million tons (ISGR International Rubber Study Group, 2016). Rubber cultivation occurs in regions with a rainfall of 1500 to 3000 mm year^{-1}, 25–30 °C temperature, and relative humidity of 60–80% (Sterling and Rodríguez, 2018). In Colombia, the planted area is 52,221 ha, of which the departments with the most significant area are: Meta, Vichada, Santander, Caquetá, and Antioquia, in fifth place with 3754 planted ha (Agronet, 2018).

Rubber crop is generally planted using two methods of propagation: grafted plants (clones) and plants coming directly from seeds - seedlings (Carr, 2012). Although plants from seeds are heterogeneous, their use is considered an easy, fast, and low-cost way to establish a plantation since they ensure good vigor, better anchorage, adaptability, and general resistance to diseases due to their high genetic diversity (Masson and Monteuuis, 2016). In addition, genetic variability gives the graft greater vigor and growth when the crop establishment is carried out from grafted seedlings on rootstocks from hybrid seeds of polyclonal orchards

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(Ng et al., 1982; Priyadarshan, 2017). On the other hand, because polyclonal orchards are exposed to specific environmental conditions, progeny with local adaptive potential is generated (Krishan, 2020), which originate clones with higher yield and tolerance to biotic and abiotic stresses (Krishan, 2015). In addition, plantations from seed generate the possibility of carrying out genetic breeding programs, where it is necessary to know the characteristics of the base population and its interaction with environmental conditions (Monsalve et al., 2018).

Guyot et al. (2008) indicate that rubber plants grow through an annual succession of foliar releases due to the alternation of the periods of inactivity and activity of the meristems, with a rhythmic development during the first eight years, with periods between the emergence of the bud and the maturity of the leaf of approximately one month. According to Priyadarshan (2017), this development of rubber plants is a phenological response to climatic stimuli and variations in temperature, water deficit, radiation, and nutritional content in the soil. In this sense, leaf senescence and abscission coincide with the dry season and flowering with high temperatures (Moraes, 1977; Ortolani, 1998).

Although the rubber tree growth is rhythmic, this species can produce latex throughout the year. However, yield is significantly influenced by conditions that affect its leaf area since photosynthetic rates are reduced. (Righi et al., 2001) and reserve substance accumulation (carbohydrates) is diminished (Simbo et al., 2013). Even the remobilization of nutrients and photoassimilates to new sink tissues can occur (Li et al., 2016). Rubber natural defoliation-refoliation is a phenological process that affects the leaf area and reduces tree canopy. Nonetheless, during the refoliation process, pathogens (*Pseudocercospora ulei*) and pests (*Erinnys ello*) can affect the leaf area, decreasing photosynthetic rates (Berger et al., 2007; Domiciano et al., 2009; Sterling Cuéllar et al., 2015) and generating total tree defoliation (Barrera Cubillos et al., 2014).

Thus, the occurrence of recurrent biological events, especially those related to defoliation and sprouting processes of rubber, in response to environmental factors, is fundamental for the developmental understanding of the species and its relationship with biotic factors such as foliar pathogens (Sabu and Vinod, 2009). Following those above, this study aims to identify the phenological performance of the seedlings population of natural rubber trees under premontane humid forest conditions in Colombia.

2. Materials and methods

2.1. Study area and characteristics of the plantation

The research was carried out at the El Nus research center of Agrosavia, located in the San Roque, Antioquia, Colombia (06°29’07.1" N; 74°50’32.2" W, 850 m altitude). The observations were made in a commercial seedling rubber plantation established in 1999 (23 years old). The seedlings come from a mixed clonal rubber plot (FX3864, IAN710, IAN873, RRIM703, RRIC110, PR228 RRIC102, SMR20, and SGR20) (Monsalve et al., 2018). The experimental plantation was established at a distance of 2.8 m between plants and 7 m between rows, for a density of 510 trees ha^{-1}; managed under a system of exploitation s/2 (half spiral), with typing every three days (d3), seven days a week (7d/7), nine months a year (9 m/12).

The rainfall regime is bimodal, with an annual rainfall of 2142 mm, an average maximum temperature of 30.5 °C, and a minimum of 19.6 °C. The area is generally characterized by two rainy seasons (March to May and September to November) and two dry seasons (December to February and June to August) (Poveda, 2006); this is ideal for the adequate development of the crop for this area. It presents transitional zoning from the humid tropical forest to Premontane, a hillside relief form with a slope greater than 50%, and soils of taxonomic classification Oxic Dystrudepts (IGAC Instituto Geográfico Agustín Codazzi, 2007) of low fertility, Clay-Sandy Loam textural class, characterized by presenting 3.24% organic matter, a strong-extremely acid degree (pH=4.79), a high exchangeable aluminum content (1.57 cmol$_{(+)}$ kg^{-1}), an ECEC of 6.83 cmol$_{(+)}$ kg^{-1} and low concentration of most primary and secondary macronutrients (P $<$ 3.87 mg kg^{-1}, S=4 mg kg^{-1}, Ca= 3.99 cmol$_{(+)}$ kg^{-1}, Mg= 0.67 cmol$_{(+)}$ kg^{-1}, and K= 0.15 cmol$_{(+)}$ kg^{-1}).

2.2. Climatic conditions

The meteorological variables maximum (T Max), minimum (T Min), and mean (T Mean) temperature (°C), global radiation (RAD) (MJ m^{-2} s^{-1}), rainfall (RNF) (mm), maximum (RH Max), minimum (RH Min) and mean y (RH Mean) relative humidity (%) were measured using an automated portable WatchDog® series 2000 station. This station was located 1.5 km from the evaluation plot. The water balance (WB) (mm) was quantified in weekly and monthly means using the Hargreaves equation (Allen et al., 2006). Where the evapotranspiration (ETo) (mm) was equivalent to crop evapotranspiration (ETc), given that, Crop rubber coefficient is 1 (Carr, 2012).

2.3. Experimental unit

Using the proposed methodology by Guerra-Hincapié et al. (2020) and Gutiérrez-Vanegas et al. (2020), a total of 15 observational-type permanent monitoring plots (PMP) were implemented for the phenological and phytosanitary measurements. Each PMP was randomly distributed and composed of four adjacent trees, two in each row. Evaluations of foliar, floral, and fruiting phenology were conducted from November 2016 to March 2021; the frequency of evaluations was monthly between April and November and biweekly between December and March for each year.

2.4. Leaf ontogeny

In each tree of the PMP, the leaf density was determined with a scale of 0–10, where 10 corresponds to all the leaves present (100%), and 0 is the total absence of leaves (Gutiérrez-Vanegas et al., 2020; Rivano et al., 2016). Leaf ontogeny was determined by quantifying the percentage of leaves in states A (meristem development), B (copper-colored leaves), C (color change), and D (mature leaves) (Hallé et al., 2012; Lieberei, 2007). D1 corresponds to the mature leaves of the first cycle, and D2, D3, D4, D5, and D6 to those formed after each leaf renewal cycle of subsequent years.

2.5. Leaf area index

The rubber canopy light environment was characterized through hemispherical images at 1.5 m and directed to the canopy using a Canon Powershot Sx530 digital camera (Chazdon and Field, 1987). These images were analyzed with the Gap Light Analyzer software (Frazer et al., 1999) to estimate the variation of the leaf area index (LAI - m^2 m^{-2}), according to Guerra-Hincapié et al. (2020).

2.6. Reproductive phenology

Floral density was evaluated from a 0–10 scale, where ten corresponds to 100% flowering branches and 0% to the absence of flowers. Additionally, the proportion of floral stages was determined: without flowers (WF), expanding flowers (ExpF), open flowers (OF), and overblown flowers (OvbF) in each tree (Gutiérrez-Vanegas et al., 2020). The fruit set was estimated by quantifying the number of fruits and classifying them into the following categories: Fruits in formation (FrIF), formed fruits (FFr), fruits with color change from green to brown (BFr), dry fruits (DryFr) and dead fruits (DFr). The phenological calendars of the rubber in the study area were constructed from foliar, floral, and fruiting density measurements.

2.7. South American leaf blight (SALB)

The SALB incidence and severity caused by *P. ulei* (Henn.) were determined on the canopy in each tree of the PMP between January 2018 and March 2021 using binoculars (Nikon Aculon A211) to evaluate the leaves in the upper third of the tree. The incidence was determined by quantifying the number of affected plants about the number of plants sampled, and severity was estimated using the scale proposed by Chee and Holliday (1986) and adapted by (Rivano et al., 2010). This scale presents four stages of affectation (0–4), where 0 = null (<1% of the leaf area with lesions), 1 = low (1–5% of the leaf area with lesions), 2 = medium (6–15% of the leaf area with lesions), 3 = high (16–30% of the leaf area with lesions), 4 = very high (>30% of the leaf area with lesions). Based on these results, the canopy affectation degree was constructed, making a weighted average of the states of affectation in each evaluation.

2.8. Statistical analysis

The phenological calendars, SALB severity, and incidence were analyzed through graphic representations of the trend of the variables that best described these events. For this, the foliar and floral density variables were analyzed, transforming the density values into percentages using the methodology described by Gutiérrez-Vanegas et al. (2020); fruiting was analyzed by converting each state to an absolute percentage of the canopy of each individual as follows: $\%X = ((x \times 100))/n$. Where %X corresponds to the portion of each stage of fruit development, x is the number of fruits of each stage, and n is the total number of fruits by a tree.

Statistical analyses, including multivariate statistical methods as principal component analysis (PCA) were performed using R version 4.2.0 and R studio ver. 03.0 statistical software, and the *ade4* and *car* procedures. PCA was performed to identify the relationship between the climatic characteristics of the study area and summarized every 7, 14, and 30 days both with the foliar, floral and fruit phenological component as well as with its relationship with the affectation by SALB disease.

3. Results

3.1. Local climatic characterization

The radiation increased towards the middle of each year and decreased at the end of this (Fig. 1). The months with the highest radiation were July and August, and the lowest was November for all years. It should be noted that this considerable variable increase (~ 600 MJ m^{-2} s^{-1}) was obtained in May 2019. The average T max was between 29 and 32 °C, with increases of 1–2 °C in the periods of highest radiation; the T Mean was 24 °C and had no considerable fluctuations, and the T min was 18–20 °C.

When rainfall (RNF) was lower than evapotranspiration (ETo), the deficit between water supply and demand generated a negative balance (WB) (Fig. 2). This condition generally led to two dry seasons between December - March and, in some years, June - August (2017 and 2019); therefore, a bimodal rainfall regime is considered in the study area. The water balance was negative between December and March, with a monthly deficit from 26 to 108 mm month^{-1}. The RH max and RH Mean decreased from August 2017 to April 2019, with an increase of around 25% until it generally remained at 100% and 80% RH max and RH min, respectively. The RH min was more variable and had a development similar to precipitation.

3.2. Phenological calendars - leaf ontogeny

Five defoliation-refoliation periods were recorded during the evaluation period (2016–2021). These processes generally occur every year simultaneously, with slight variations in intensity and duration. Defoliation began from weeks 40–50 of the year, intensified until the trees had the lowest percentage of leaves (15–35%) in the fourth week of the year, and extended until weeks 6 and 7. After leaf loss, the leaf flushing begins, characterized by buds or immature stages of leaf development (stages A, B, and C). this phase, on average, presented a duration per tree of 2–4 weeks. However, since not all trees defoliate and foliate synchronously, this phenological process showed a greater amplitude at the plantation level from 8 (2020) to 11 (2018 and 2019) weeks (Fig. 3).

3.3. Leaf area index (LAI)

The leaf area index (IAF) fluctuated between 2 and 2.5 m^2 m^{-2} during the periods in which the rubber trees were foliated with leaves in stage D (March to December) in the years 2017–2020 (Fig. 3). The minimum LAI was found around week 7 (February) when a peak of defoliation was reached, leaf flushing was starting, and only a few trees were showing leaves in stages A and C. During 2019 the lowest LAI was observed with an average of 1.7 m^2 m^{-2}. In 2020, a mean LAI of 2.1 m^2 m^{-2} was obtained, with a progressive reduction from 2.7 to 1.9 m^2 m^{-2} starting in March. It should be noted that atypical defoliation events occurred in 2017, 2019, and 2020, in which the leaf area index reached 1.5 m^2 m^{-2}, reducing by 26%, 33%, and 41%, respectively.

A synopsis of canopy changes during the weeks before defoliation (week 3), the maximum stage of defoliation (week 7), and leaf renewal

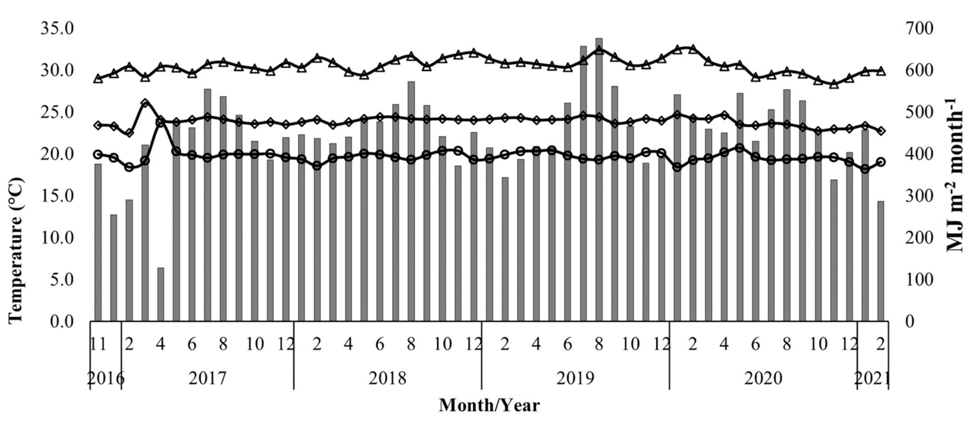

Fig. 1. Monthly accumulated global radiation (RAD) (MJ m^{-2} month^{-1}), minimum temperature (T Min) (°C), mean temperature (T Mean) (°C) and maximum temperature (T Max) (°C), San Roque (Antioquia)—Average monthly data from November 2016 to March 2021.

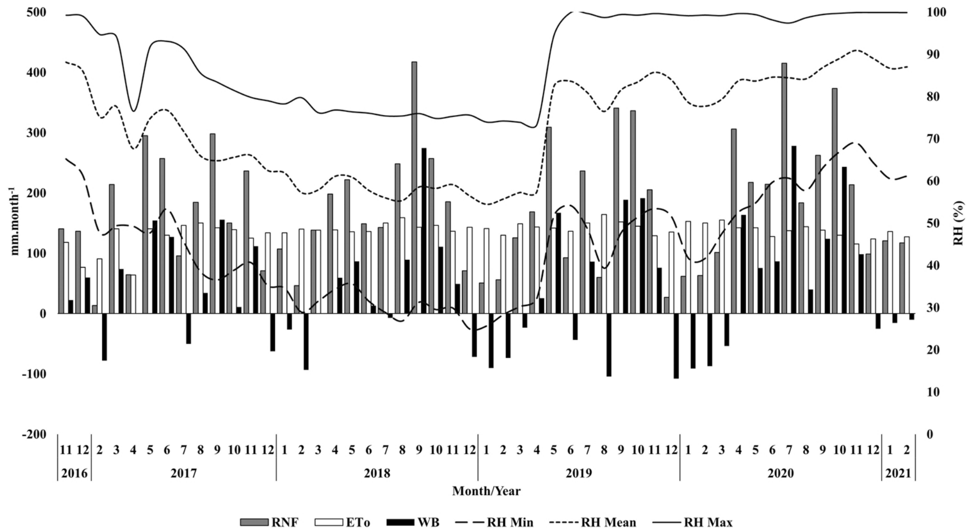

Fig. 2. Rainfall (mm month^{-1}), evapotranspiration (ETo) (mm month^{-1}), water balance (WB) (mm month^{-1}), minimum relative humidity (RH Min) (%), mean relative humidity (RH Mean) (%) and maximum relative humidity (RH Max) (%), San Roque (Antioquia). Monthly average data from November 2016 to March 2021.

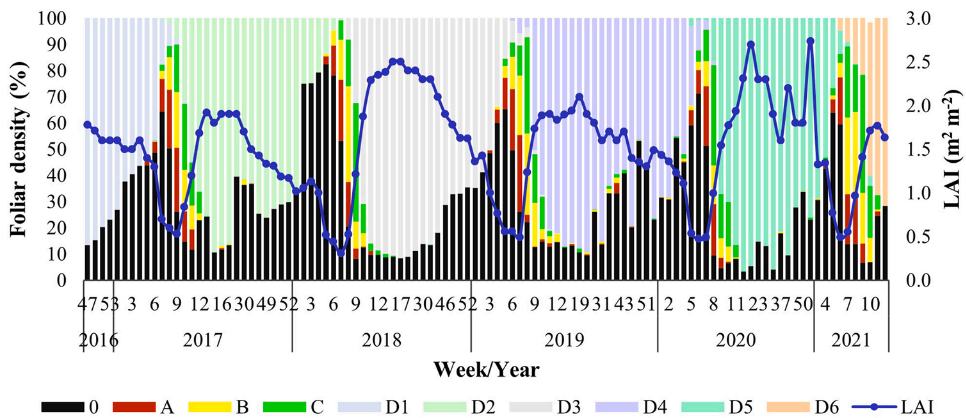

Fig. 3. Leaf area index (LAI) and leaf density as a percentage of leaves by states (0, A, B, C, D) in seedlings rubber trees. San Roque (Antioquia). November 2016 – March 2021.

(week 9) for each year are presented in Fig. 4. This figure shows how in 2018 and 2019, there are still foliated trees, which represents the extension in the duration of the defoliation processes and subsequent foliar renewal in week 9. In addition, the foliar density observation is related to the canopy with the LAI, where it is observed how only in two weeks (weeks 7–9) the LAI increases from 0.3 to 0–6, up to > 1.2.

3.4. *Flowering phenological calendars*

The inflorescence expansion coincides with the leaf flushing process, concentrating between weeks 5 and 17 of the year, with a maximum of open flowers in March (weeks 11–13) (Fig. 5). The presence of open flowers lasted from 1 to 4 weeks per tree and from 5 to 9 weeks at the plantation level. It should be noted that 2020 presented the shortest flowering and therefore presented a higher concentration (46%) of open flowers in week 12, unlike 2018 and 2019, which had a greater extension in their flowering and, therefore, a higher proportion of withered flowers.

3.5. *Fructification phenological calendars*

Regarding fruiting, this phenological stage was generally concentrated between weeks 13 and 40, after flower pollination; in particular, the greatest fruiting period occurred on average in weeks 31–34 (beginning of August), with 50% of the plantation with fruits formed. On average, fruit formation stages were four weeks, six weeks until fully developed, and two weeks in senescence (color change, dehiscence, and death) (Fig. 6). For the years 2018 and 2020, a more homogeneous fruiting was found, represented by the distribution of the development stages of the fruit sequentially more uniform and with a shorter duration. However, atypical and uneven fruiting occurred in the first quarter of 2020. Less than 20% of trees with fruits were related to the last flowering (less than 1% in weeks 35–43 of 2019).

3.6. *Incidence and severity of South American leaf blight (SALB)*

SALB disease was still prevalent throughout the study period, with changes in its severity corresponding to specific phenological stages and years (Fig. 7). The behavior of the disease lies in increasing incidence as the leaves mature after leaf flushing. Therefore, the incidence after week 10 increases from 10% to 15% to 60–70%. In 2018 the severity was lower, with a percentage of affectation of a maximum canopy of 21%. However, 2019 was the year with the highest disease severity, where greater than 20% affectation was found since week 19, with two peaks of 32% and 33% canopy damage. For 2020, although the affectation was less than in 2019, levels above 20% were found, with a maximum of 26% in week 49.

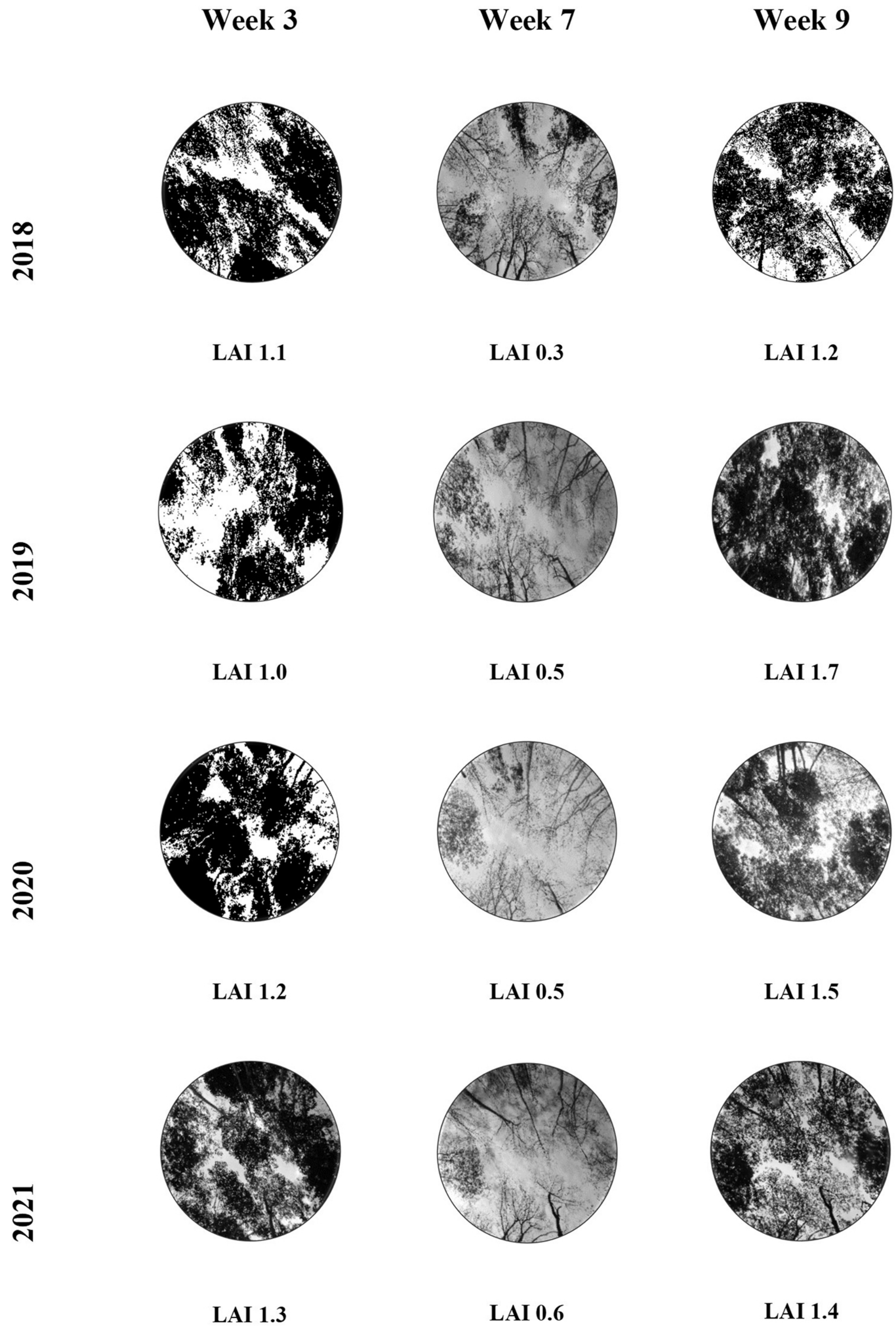

Fig. 4. Hemispherical images and LAI (m^2 m^{-2}) of the rubber canopy for weeks 3, 7, and 9 in seedlings rubber trees.

3.7. Principal component analysis

Analytical data were taken to principal component analysis to determine correlations between leaf phenology processes and stages of affectation of the South American leaf blight (SALB) (Table 1) concerning climatic conditions. For leaf phenology from 52 principal components, two principal components (PC1, PC2) explain 42.18% of the total variance (Fig. 8). PC1 presents 26.29% of the total variance of the data, and PC2 exhibits 15.89% of the total variance of the data. For SALB affectation from 40 principal components, two principal components (PC1, PC2) explain 53.70% of the total variance (Fig. 8). PC1 presents 35.81% of the total variance of the data, and PC2 exhibits 17.89% of the total variance of the data.

The biplot representation (Fig. 8) shows the relationship between the foliar and reproductive phenology processes and climatic components. The phenological processes at the beginning of the year (January - March), such as defoliation (DF), immature leaf stages (A, B, C), and the beginning of floral budding (ExpF), were related to climatic conditions of lower water balance and conditions that represent greater water drought (ETo and Tmax). While the mature leaves stages (D), LAI, fruits in formation (FrIF), and dead fruits (DFr) were associated with a higher water balance and lower temperature. Open flowers (OF) and wilted

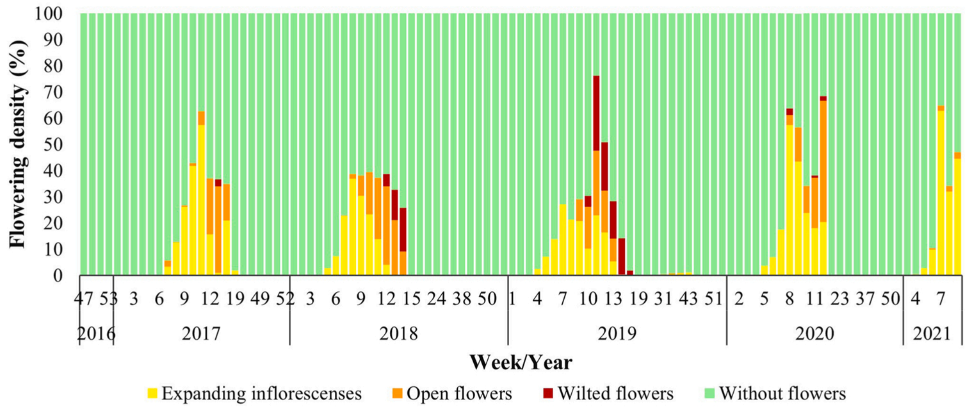

Fig. 5. Flower density and percentage of inflorescences by stages (expansion, open flowers, withered and without flowers) in seedlings rubber trees. San Roque (Antioquia). November 2016 – March 2021.

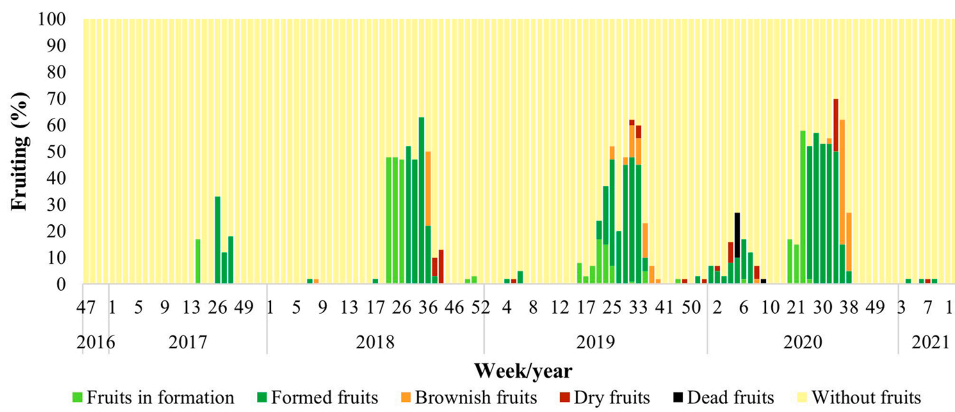

Fig. 6. Fruiting phenological calendars from November 2016 to March 2021 in seedlings rubber trees. San Roque (Antioquia). November 2016 – March 2021.

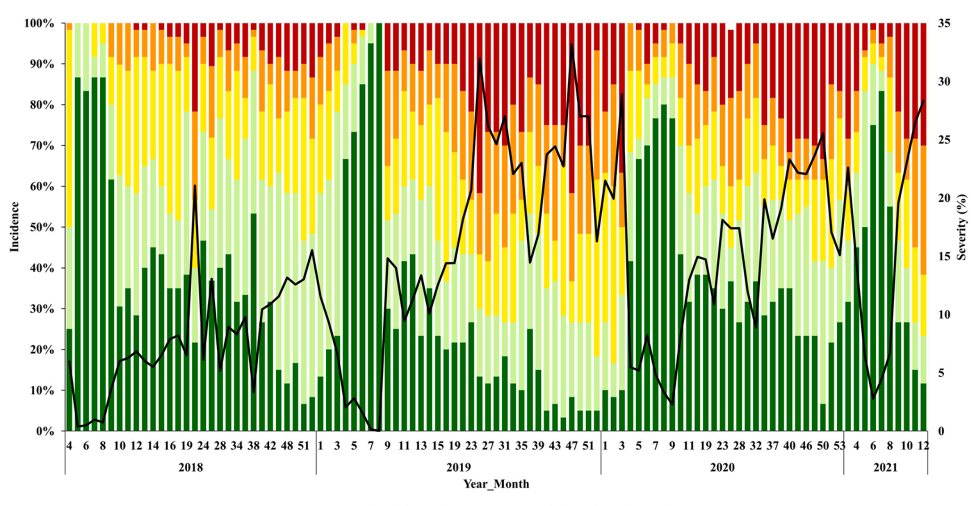

Fig. 7. SALB incidence (%) and severity (%) in seedlings rubber trees according to Chee and Holliday (1986). The affectation states from 0 to 4: 0= null (30% of the leaf area with lesions). San Roque (Antioquia). January 2018 – March 2021.
Adapted by Rivano et al. (2010).

flowers (WiltF) had a closer relationship with higher evapotranspiration and temperature. The fruiting variables were generally more related to a higher water balance. This was related regardless of the year of evaluation and for the climatic variables summarized for 7, 14, or 30 days. Therefore, leaf ontogeny and floral differentiation occur under water deficit conditions, while leaf ripening and fruit development require conditions with a water supply.

Fig. 9 shows the biplot representation for the climatic characteristics and South American leaf blight relation. It is observed that the severity and the greatest canopy affectation intensity by SALB (Leaf stages 3 and

Table 1
Discrimination table for ten principal components (PC) constructed with leaf phenology and South American leaf blight affectation concerning climatic conditions.

Leaf phenology			
Principal component	**Standard deviation**	**Proportion of Variance**	**Cumulative Proportion**
PC1	3.6617	0.2629	0.2629
PC2	2.8463	0.1589	0.4218
PC3	2.5852	0.1310	0.5528
PC4	1.86254	0.06802	0.62082
PC5	1.76043	0.06077	0.68159
PC6	1.54724	0.04694	0.72853
PC7	1.29379	0.03282	0.76135
PC8	1.16865	0.02678	0.78813
PC9	1.08271	0.02299	0.81111
PC10	1.0641	0.0222	0.8333
South American leaf blight affectation			
Principal component	**Standard deviation**	**Proportion of Variance**	**Cumulative Proportion**
PC1	3.7848	0.3581	0.3581
PC2	2.6748	0.1789	0.5370
PC3	2.4121	0.1454	0.6824
PC4	1.76816	0.07816	0.76060
PC5	1.62578	0.06608	0.82668
PC6	1.14027	0.03251	0.85918
PC7	1.07736	0.02902	0.88820
PC8	0.88958	0.01978	0.90798
PC9	0.8247	0.0170	0.9250
PC10	0.78208	0.01529	0.94028

4) are associated with all the variables of higher relative humidity and radiation. On the contrary, stages 1 and 2 (low and medium affectation) are related to minimum temperatures. The non-infected stage (Stage 0) is linked with higher evapotranspiration and maximum temperature. The water balance and rainfall were not associated with a specific phytosanitary event; therefore, although water availability and rainy conditions are present, RH is the definitive factor for the evolution of the disease to more severe states.

4. Discussion

4.1. Phenological calendars

In our study, the beginning of leaf senescence was generated between October and December. Similar results were reported by Liyanage et al. (2019) for Asian clones at 21°N. Where defoliation began between December and January, and leaf renewal (refoliation) ended in February with a duration of 5 weeks. Nevertheless, this study considers that the non-uniformity, both for the initiation of defoliation and leaf renewal, was due to the heterogeneity of the genetic material (Monsalve et al., 2018). However, the duration of leaf renewal at the individual level was minor. Zhai et al. (2019) mention that in Asian plantations, the immature leaf stages are observed between mid-February and early March, and the leaf density reaches 100% in the mature leaf stage at the end of March. Therefore, the immature period lasts 2–3 weeks, and maturity completes a month (Guyot et al., 2008). This could be visualized in this work through the gradual increase of the IAF and the achievement of a leaf density of 100% in April.

Silva et al. (2012) mentioned that defoliation occurs regardless of climatic variations and that the deciduous habit is intrinsic to the

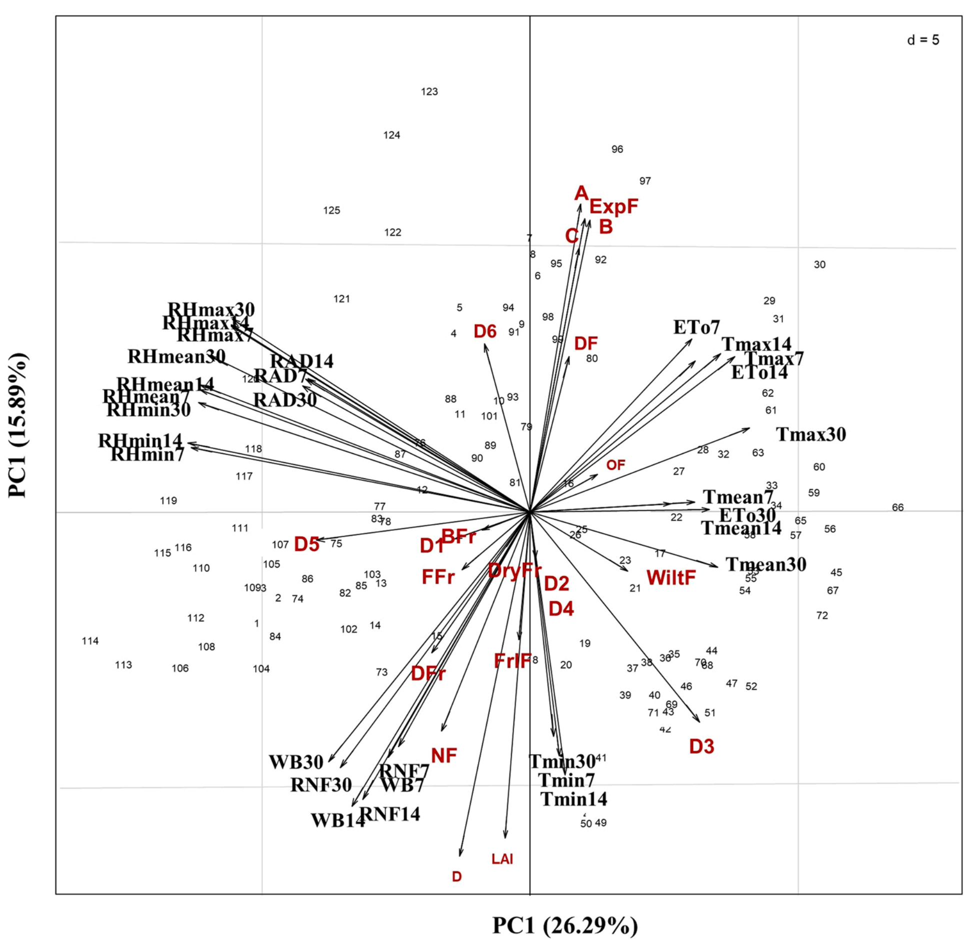

Fig. 8. Biplot representation of leaf phenology processes: Defoliation intensity (DF), immature leaves (A, B, C), mature leaves (D), floral phenology (no flowers (WF), expanding flowers (ExpF), open flowers (OF), and withered flowers (WiltF)), and fruit phenology (fruits forming (FrIF), fruits formed (FFr), fruits changing color (BFr), senescent fruits (DryFr) and dead fruits (DFr)) concerning climatic conditions: maximum (T max), minimum (T min) and average (T mea) temperatures, global radiation (RAD), precipitation (RNF) and maximum (RH max), minimum (RH min) and average (RH mea) relative humidity; evapotranspiration (ETo) and water balance (HB) consolidated every 7, 14, and 30 days.

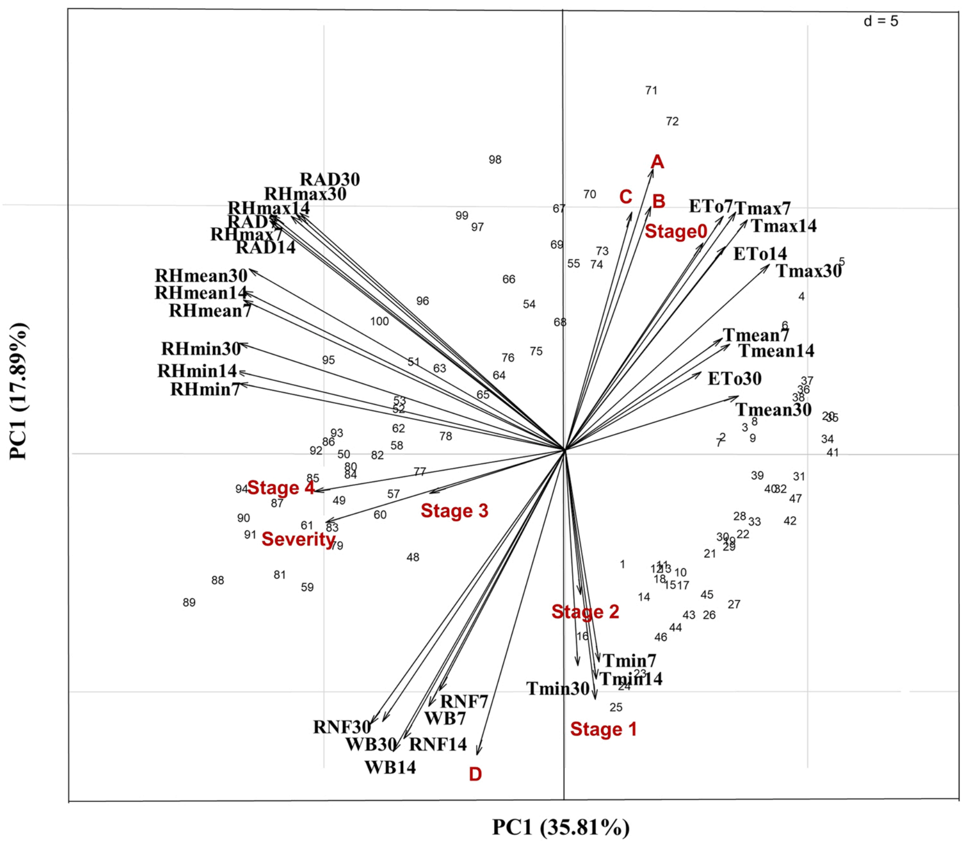

Fig. 9. Biplot representation of the stages of affectation of the South American leaf blight (SALB): null (Stage 0), low (Stage 1), medium (Stage 2), high (Stage 3), very high (Stage 4), and percentage of severity(Severity) related to localities climatic conditions: maximum (T max), minimum (T min) and mean (T mea) temperature; global radiation (RAD), rainfall (RNF) and maximum (RH max), minimum (RH min) and mean (RH mea) relative humidity; evapotranspiration (ETo) and water balance (HB) consolidated every 7, 14 and 30 days.

genotype (Sambugaro, 2007). In contrast, Rattanawong (2012) indicates that climatic variables are intrinsically related to defoliation and play a more important role than genetic material. Rivano et al. (2016) mention that there may be phenological differences between clones that are reflected in early defoliation and relatively rapid leaf flushing, and they can have complete and constant defoliation progress (Suryakumar et al., 2002). Therefore, there are annual variations for defoliation-refoliation (occurrence and duration). Considering the latitudinal position where the rubber crop is grown, these phases generally occur at the same time of the year, in our case, between January and March.

The climatic events do not have immediate effects on tree phenology; a climatic period preceding the onset of a plant phenological event regulates its occurrence (preseason) (Azizan et al., 2022). We estimate a preseason of 7, 14, and 30 days, and according to our results, water balance had an inverse association with defoliation regardless of the preseason period. Although other studies (Azizan et al., 2022; Liu et al., 2012) found correlations between precipitation and defoliation with a preseason of 90 days, Fu et al. (2015), in a phenology of deciduous trees study, found that the optimal preseason ranged from 15 to 120 days.

There has yet to be a consensus regarding the climatic variable most related to defoliation processes in rubber cultivation. Authors like Elliott et al. (2006), Guardiola-Claramonte et al. (2008), Liyanage et al. (2019), and Williams et al. (2008) indicate that the increase in day length (photoperiod) is the variable that triggers defoliation. The above is because there is synchrony between its occurrence and phenological patterns. In addition, it has been identified that this process often induces bud dormancy or delayed vegetative growth rate, so the phenophases advance as day length increases (Filho et al., 1997). Therefore, this process occurs differentially depending on the latitude in which the plantation is established, with defoliation periods being in January - March in the northern hemisphere and August - October in the southern hemisphere (Gutiérrez-Vanegas et al., 2020).

On the contrary, Li et al. (2016) and Priyadarshan (2017) state that the most influential factors are high temperatures or a significant reduction in rainfall. In contrast, other authors (Chen et al., 2022) indicate that cold stress was the critical driving factor in rubber defoliation rather than drought stresses. The effect of temperature was related to water balance since it is a variable associated with evapotranspiration. Therefore, this research identified a direct relationship between defoliation and water deficit. Consequently, we suggested water availability in the soil as the triggering factor of this phenological process rather than only water input by precipitation.

Since defoliation and leaf flushing occur in dry seasons with a water deficit greater than 26 mm month^{-1}, the rubber tree must have sufficient water reserves for the subsequent unfolding and foliar expansion (Elliott et al., 2006; Guardiola-Claramonte et al., 2010; Williams et al., 2008). Accumulation of high temperature (thermal time) is often required for breaking de dormancy of leaf budburst (Basler, 2016). And after foliar induction, the temperature decreases at the beginning of the rainy season, which indirectly reduces the rate of leaf development by reducing enzymatic activity (Zhai et al., 2019).

Defoliation, stomatal closure, and leaf fall are plant strategies to reduce transpiration and water consumption during dry seasons. Therefore, the tree must absorb water through roots in deep soil horizons to increase the necessary water potential in the foliar renewal stage (Guardiola-Claramonte et al., 2010). Stomatal conductance dominates in controlling high temperatures and water vapor pressure deficit (Lin et al., 2018). At this time, tree growth is significantly reduced and only associated with water storage in tissues such as stems, branches, and leaves (Lin et al., 2018) because the water demand for leaf flushing is considerably high (Elliott et al., 2006). Water availability and defoliation affect photosynthetic efficiency and latex biosynthesis, generating a yield reduction of up to 60% (Azizan et al., 2021). Hence, when the rubber tree achieves the maximum leaf area and full photosynthetic capacity, it is possible to reach the highest yield due to no restrictive factors such as water stress or phytosanitary limitations (Moreno et al., 2005).

The differences in the intensity of defoliation depend on the degree of water stress generated during the dry season (Elliott et al., 2006; Yoshifuji et al., 2006) since it has been observed that the more pronounced the reduction in rainfall, the faster and more uniform the leaf abscission is (Gasparotto et al., 2012). Sambugaro (2007) highlights that these characteristics are adaptive and genetically determined. Except for 2016, a cumulative water deficit (183 and 265 mm) was observed between December and March during the defoliation and leaf flushing phases. The water deficit was lower than that reported in plantations in southwestern Colombia (419 mm for three months and 570 mm in 4 months), where defoliation occurred with subsequent recovery of the foliage with a high density (Gutiérrez-Vanegas et al., 2020). This indicates that having a water deficit for four months is enough to generate defoliation and that the intensity of the dry season is not a factor that necessarily causes uniformity in polyclonal plantations.

Similarly, Li et al. (2016) demonstrated that, in the face of water stress, in the defoliation stage, the translocation of approximately 50% of the nitrogen, phosphorus, and potassium occurs from the senescent leaves. The leaves begin the process of senescence and abscission due to an imbalance between the ratio of the growth-promoting hormone (indole acetic acid) and the growth inhibitor abscisic acid (ABA) (Seneviratne et al., 2020). The plant response to water stress is the expression of genes, which, dependent on ABA, act by modulating the synthesis of proline, the transport of $Na+$ and $K+$. In addition to ABA, ethylene has a critical role in regulating leaf senescence and the biosynthesis of secondary stress response metabolites (Z. Li et al., 2012; Vishwakarma et al., 2017; Wang et al., 2013), such as reactive oxygen species (ROS) (Kang et al., 2021).

In this study, Leaf flushing and the beginning of flowering were associated with water deficit conditions and elevated temperatures. However, leaf expansion generally requires cell elongation, highly susceptible to water stress (Borchert, 1994). So, just as available water is needed for foliar sprouting, floral induction must guarantee optimal water status and carbon reserves in the stem (Elliott et al., 2006; Williams et al., 2008). Water absorption in deeper horizons increases the necessary water potential in this stage (Guardiola-Claramonte et al., 2010). After foliar induction, net mobilization of carbohydrates to the foliar and floral meristems occurs (Lacointe et al., 1993; Silpi et al., 2007), and with the beginning of the rainy season, the temperature decreases, generating a reduction in the rate of leaf development indirectly by reducing enzymatic activity (Zhai et al., 2019).

Regarding the LAI, the values vary according to tree age, management, and climate (Kumagai et al., 2015). The leaf area index describes the potential area for transpiration and is an essential factor in canopy dynamics for water loss (Cotter et al., 2017). Pradeep et al. (2014) indicate that the LAI ranges for mature rubber plantations with their developed foliage vary between 3.5 and 4 and can drop to 1 in the greatest defoliation or disease involvement stage. Other studies mention that the LAI was minimal (almost zero) during defoliation season and a maximum between 2.1 and 2.9 after leaf flushing (Zhou et al., 2019). Nonetheless, under similar conditions in Antioquia (Colombia), with rubber clonal genetic material, the minimum IAF value was 0.5–1 between weeks 5 and 7 of the year. In refoliation, it reaches a 2.5–3 (Guerra-Hincapié et al., 2020). This study reached similar values (0.3–0.6 LAI) in the weeks of greatest defoliation. Nevertheless, in the years with atypical defoliation, the LAI after leaf flushing was not higher than 2, which indicates a 24% reduction in the leaf area.

4.2. Flowering and fruiting

The genotype, clone age, and climatic characteristics determine flowering patterns in rubber plantations (Liyanage et al., 2019). Although the floral differentiation process lasts four weeks, from the budding of the inflorescence to its wilting (Sabu and Vinod, 2009), in this research, the genetic heterogeneity (Monsalve et al., 2018) generated a duration of up to 10 weeks at the population.

Parallel to leaf renewal, floral meristem development occurs, which is influenced by water availability and the reduction in temperature (Webster CC, 1989; Yeang, 2007). In tropical plantations, including rubber, this phenomenon generally occurs around the vernal equinox, although in some areas, additional flowering may occur close to the autumnal equinox (Gutiérrez-Vanegas et al., 2020; Yeang, 2007). Floral induction occurs in the dry season, before leaf flushing and with a shorter photoperiod (winter solstice) (Gutiérrez-Vanegas et al., 2020; Yeang, 2007). However, dormancy occurs in the emerging flowers in mid-March until favorable environmental conditions occur (Priyadarshan, 2017) since the hormonal activity that regulates the beginning of flowering may be affected by high temperatures (Veriankaitė et al., 2010). However, the high intensity of solar radiation induces rubber bloom synchronously (Liyanage et al., 2019).

Rubber clones vary widely in flowering, pollination, and fruit set, from almost sterile to prolific (Priyadarshan, 2017), which can generate a low percentage of fruit set, less than 5% (Nair, 2021). Although having different genotypes in a plantation does not substantially increase the fruiting setting (Hamzah et al., 2002), the heterogeneity of polyclonal plantations ensures maximum cross-pollination that will generate seeds for the development of better-performing seedlings (Sobha et al., 2019). The duration of the entire fruit cycle is close to 140 days (20 weeks) (Priyadarshan, 2017), where up to week four after the fruit set, abscission of non-viable fruits occurs (Wongvarodom et al., 2019). This may be due to genetic, hormonal, or abiotic factors, including greater evaporation, high temperature, and humidity (Priyadarshan, 2017).

In the same way, intense rainfall during the expansion and opening of the inflorescences negatively affects fruit sets since the rains generate greater humidity and increase the incidence of diseases (Wongvarodom et al., 2019). In this study, the SALB severity caused atypical defoliation and refoliation and a modification in flowering behavior in 2019. Consequently, fruit setting since different fruiting stages were identified in December and January 2020. These atypical fruits become a significant source when the plant accumulates reserves for leaf flushing.

So, determining the phenological development in polyclonal plantations is essential to identify the time and duration of seed production and the biotic and abiotic events that can affect this process. Therefore, the present study becomes relevant for the technical planning in producing rootstocks from seeds and plant material for establishing new plantations for the local environmental supply.

4.3. Foliar phenology and SALB

The South American leaf blight (SALB) affects the canopy. When its severity is very high, it can cause defoliation in the plantation and even the death of the plant (Lieberei, 2007). The immature leaves have a condition of greater receptivity to the disease (Rivano et al., 2016), which decreases as it matures (Guyot et al., 2010).

The incidence of diseases depends on the clones' susceptibility and their phenological pattern development (Suryakumar et al., 2002). Therefore, heterogenicity in the genetic material generates disparity in the degree of SALB infection (Guyot et al., 2008). Since the leaf flushing (susceptible stage) phase will extend to the population level, the inoculum will remain in the environment within the plantation for a longer time, thus renewing the disease cycle. Therefore, rapid refoliation is considered a characteristic of interest for selection programs of genetic materials (Rivano et al., 2016). Introgressive hybridization in the genus *Hevea* can be of such a dimension that the original populations from crosses within the same species can lose their identity, originating ecotypes or hybrids (Araújo et al., 2001). The above may explain that rubber trees from seed exchange leave an irregular manner and different reaction to SALB.

During ontogeny, immature leaves (A and B) have less chlorophyll, flavonoids, and anthocyanins (de Oliveira Pita et al., 1990). This condition, added to the presence of cyanuric acid (Lieberei, 2007), generates a hypersensitive defense response (Suarez et al., 2015), causing the death of leaf tissue and increasing SALB development. In mature leaves, lignin production during leaf ontogeny acts in the hardening of the cell wall, generating a physical barrier for the entry of the fungal hyphae into the intercellular space (Lieberei, 2007). Therefore, an essential characteristic of a rubber plantation is to use genotype with short leaf ontogeny, mainly stage A to C, which are the most susceptible, and source tissues for photoassimilates.

Environmental factors promote the development and spread of the pathogen that causes SALB since correlations have been found with temperature, rainfall, and relative humidity with this disease (Guyot et al., 2014). However, the parameter with the greatest influence is the relative humidity, as we found in this study, being that the severity of the disease had a direct association with all temporary relative humidity evaluated. According to Guyot et al. (2014), although leaf flushing occurs without rain, having a relative humidity greater than 90% directly correlates with a high SALB infection. In addition, temperatures above 20 °C generate favorable conditions for the development of the pathogen (Gasparotto et al., 1989). According to the population's susceptibility, favorable conditions for SALB development can lead to fungal epidemics that generate severe leaf fall (atypical defoliation) and canopy depletion (Liyanage et al., 2019). In this sense, among the Hevea species, some completely lose their leaves during the dry season, which precedes the formation of new shoots and flowering (*Hevea brasiliensis* and *Hevea benthatniana*), and those that retain their leaves two previous years during the dry season (*H. paucijiora*) (de Carvalho, 1980).

The SALB inoculum (*Pseudocerscopora ulei*) remains in the environment and can be infective throughout the year if conditions are favorable (Guyot et al., 2008). Therefore, it has been found that the rainy season and relative humidity greater than 90% generate repetitive epidemics during the year with affectations of up to 80% in leaf density in the rubber plantation (Rivano et al., 2016).

Among the disease-managing strategies, the planting of rubber in the so-called escape zones (regions with environmental conditions such as annual potential evapotranspiration >900 mm, relative humidity-drier month <65%, yearly water deficit >200 mm, and mean minimum temperature < 20 °C) are considered a SALB disease-managing (Ortolani, 1998), due these climatic conditions, favored a lower pressure of the disease (Rivano et al., 2010). During the investigation, there was a degree of disease involvement in the plantation greater than 20%, where the heterogeneity of the plant material caused a significant reduction in leaf density, especially in 2019 and 2020, related to increased precipitation and humidity. Furthermore, according to the results obtained by Correa-Pinilla et al. (2022), the study area (premontane humid forest) does not have the conditions above. It is defined as a no-escape zone to SALB.

In this study, water availability was the most influential factor in the occurrence of phenological processes. Both due to its absence (defoliation - leaf renewal) and presence (fruiting and seed production), environmental conditions such as relative humidity triggered a higher SALB infection. The heterogeneity of the genetic material in the plantation favors an increased incidence of diseases. In sensitive rubber materials, a more significant infection occurs, which generates atypical defoliation and refoliation with stages of development of the susceptible leaf, generating a higher prevalence of the disease. Therefore, seedlings plantations cause a significant unevenness, both in phenological behavior and in response to infections, which increases the complexity of developing disease strategies and crop management. For this reason, identifying environmental conditions and their relationship with the intensity and occurrence of phenological calendars allows for establishing management strategies, which is essential in climate change scenarios.

5. Conclusions

This study found that different climatic variables participate in rubber phenological processes, making water deficit the predominant factor for the defoliation-refoliation phases. The relative humidity has the greatest influence on the severity of SALB. The phenological rubber tree development in a seedling plantation is heterogeneous, mainly because they present long defoliation-refoliation phases and high susceptibility to disease. These conditions generate an increased risk of infection of SALB in non-escape zones. Knowledge of the rubber seedling plantation leaf ontogeny occurrence and duration and their non-uniformity flowering is important to develop sexual and vegetative propagation strategies. Rootstock and grafting processes for stump production as new planting material and obtaining seed for new seedling rubber plants could be possible throughout the year since the seeds can be obtained in a broad time.

CRediT authorship contribution statement

Juan José Guerra Hincapié: Conceptualization, Methodology, Investigation, Data curation, Writing – review & editing, Visualization, **Juan Pablo Gil Restrepo:** Methodology, Formal análisis, Data curation, Investigation, Writing – review & editing. **Ruddy Lizette Huertas Beltrán:** Investigation, Data Curation, Writing – review & editing, Visualization. **Albert Julesmar Gutiérrez Vanegas:** Methodology, Funding acquisition, Project administration, Supervision, Writing – review & editing. **Diana Elisa Correa Pinilla:** Conceptualization, Methodology, Writing – review & editing. **Oscar de Jesús Córdoba Gaona:** Funding acquisition, Project administration, Supervision, Conceptualization, Formal analysis, Data curation, Writing – review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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