



Variation in Onset of Leaf Unfolding and Wood Formation in a Central African Tropical Tree Species

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A diversity of phenological strategies has been reported for tropical tree species. Defoliation and seasonal dormancy of cambial activity inform us on how trees cope with water stress during the dry season, or maximize the use of resources during the rainy season. Here, we study the matching between leaf phenology (unfolding and shedding) and cambial activity for *Prioria balsamifera*, a key timber species in the Democratic Republic of Congo. In particular, we (i) evaluated the seasonality of cambial activity and synchrony of phenology among trees in response to climate and (ii) identified the seasonality of leaf phenology and its relation with cambial phenology. The study was conducted in the Luki Man and Biosphere Reserve, located in the Mayombe forest at the southern margin of the Congo Basin. Historic defoliation data were collected every ten days using weekly crown observations whereas recent observations involved time-lapse cameras. Cambial pinning was performed on ten trees during 20 months and radius dendrometers were installed on three trees during 13 months. Tree rings were measured on cores from 13 trees and growth synchrony was evaluated. We found that *P. balsamifera* defoliates annually with a peak observed at the end of the dry season and the beginning of the rainy season. The new leaves unfolded shortly after shedding of the old leaves. The peak defoliation dates varied across years from September 12 to November 14 and the fraction of number of trees that defoliated at a given time was found to be negatively correlated with annual rainfall and temperature; during the dry season, when precipitation and temperatures are the lowest. Wood formation (radial growth), was found to be highly seasonal, with cambial dormancy occurring during the dry season and growth starting at the beginning of the rainy season. Individual ring-width series did not cross date well. The within species variability of leaf phenology and cambial rhythms provides indication about resistance of the population against climatic changes.

Keywords: deciduousness, leaf and cambium phenology, *Prioria balsamifera*, Mayombe forest, seasonality, synchrony

INTRODUCTION

The effects of global change are already impacting forest ecosystems in terms of vegetation structure and floristic composition (Carrer, 2011). Understanding the sensitivity of tropical forests and species to climate change is becoming increasingly important (Hubau et al., 2020).

Phenology is a key variable herein, specifically to understand how trees cope with the dry season, and how they will respond to increased future droughts. The phases of leaf unfolding and defoliation of trees affect photosynthetic activity by drought response and the trade-off between the risks of carbon starvation (if there is no photosynthetic activity because of leaf shedding) and hydraulic failure (if stomata are maintained opened), which on their turn affect primary and secondary growth, survival and productivity of trees (Lisi et al., 2008). Tree mortality is an important component of forest dynamics. It is one of the vital rates of a forest community, next to regeneration and tree growth. Knowledge of the physiological mechanisms that cause tree mortality due to drought is important for documenting tree responses to environmental changes. Two different physiological mechanisms can cause tree mortality: hydraulic failure and carbon starvation. Plant death by hydraulic failure is observed when increased tension causes air bubbles in the sap flow resulting in cavitation and embolism. Carbon starvation occurs when plants close their stomata to minimize water losses, thereby also reducing carbon uptake and photosynthesis. A carbon deficit arises, maintenance of metabolism is not possible anymore, leading eventually to the death of the tree (Sevanto et al., 2014). A diversity of leaf phenology strategies has been reported for tropical tree species (Newstrom et al., 1994). Two major leaf habits are, however, generally distinguished, i.e., the evergreen habit, defined by the retention of functional leaves in the canopy throughout the year *versus* the deciduous habit for which a tree is leafless for some part of the annual cycle (Kikuzawa and Lechowicz, 2011).

Tropical trees can reduce the impact of seasonal drought by adaptive mechanisms such as defoliation or stem succulence and by using soil water reserves, which enables an evergreen canopy during periods of low rainfall (Borchert, 1998). In addition, the cambial activity decreased during the dormant period (Zang et al., 2014). Seasonal drought often leads to defoliation of trees (Lloret et al., 2004; Bréda et al., 2006; Couralet et al., 2013; Fétéké et al., 2016) and subsequent reductions in tree-ring growth (Millar et al., 2007). Depending on the impact of the drought, subsequent rains may allow canopy greenness and carbon uptake to recover, with a corresponding increase in tree-ring growth. The leaf phenology helps to enhance the resilience to drought by reducing Leaf Area Index (LAI) at the end of the wet season, thus saving soil water for the upcoming dry months (Manoli et al., 2018). Growth cessation during the dry season also demonstrates the tree's resilience to climatic variations.

Radial growth is often monitored through repeated measurements in permanent sample plots (Lewis et al., 2019; Angoboy Ilondea et al., 2020; Hubau et al., 2020) but dendrochronological analysis can complement successive growth measurements in permanent sample plots with added precision

(Swetnam et al., 1999; Angoboy Ilondea et al., 2020). A sound interpretation of growth patterns of tropical trees depends on understanding phenological rhythms (Enquist and Leffler, 2001) at the primary (apex growth, leaf unfolding) and secondary meristem level (cambium, wood formation) (De Mil et al., 2019).

Most research on seasonality of cambial activity in the tropics has been performed in South America and in South-East Asia. In the tropical rainforest of French Guiana, the cambial activity of two dominant tree species was significantly reduced during the leafless period, irrespective of rainfall (Morel et al., 2015). In contrast, in Colombia, Herrera-Ramirez et al. (2017) observed a successfully crossdated tree-ring series in *Prioria copaifera* Griseb. However, the ring series did not show a signal for mean annual rainfall and temperature. In Thailand, cambial activity varied significantly between species, ranging from being active right on the transition from the dry season to the wet season, to peak activity in the midst of the wet season (Pumijumnong and Buajan, 2013).

Studies on seasonality of cambial activity in species from the Congo Basin are, however, limited (Beeckman, 2016). In addition to the response to seasonal drought, radial growth has been found to vary according to light requirements (Couralet et al., 2013; Hubau et al., 2019). A detailed study on three commercial species showed that growth rings were anatomically distinct, annual and closely modeled by cambial seasonality in Cameroon (Fétéké et al., 2016). Couralet et al. (2010) and De Mil et al. (2017) used cambial pinnings for monitoring cambial activity of understory species in the Luki Man and Biosphere Reserve, in the Democratic Republic of Congo (DRC). Both studies showed that growth is related to variations in the environment and mainly to variations in precipitation.

The existence of annual growth rings that are associated to climate seasonality, primarily to rainfall (Worbes, 1999) is mostly limited to deciduous species growing in the canopy with their crowns fully exposed to external environmental factors (Pumijumnong and Park, 1999; Worbes, 1999). Successful crossdating of ring-width series denotes consistent and synchronous patterns of variation and indicates that a common external factor controls ring formation in different trees (Singh and Venugopal, 2011). In most tropical regions (and especially DRC) exactly dated reference chronologies are not available, so crossdating consists of comparing growth curves of different trees visually and statistically to synchronize ring-width series. A lack of growth synchrony of trees from the same species is an important aspect of diversity and adds to the resilience capacity of a population (Worbes, 1999). The lack of crossdating indicates that individuals of the same species in the same environment would react differently to a disturbance. In extreme cases where many individuals are killed by stressful growth conditions, the population can potentially recover thanks to individuals that survived because they are less susceptible to the environmental stressors. Camarero et al. (2015) considered increases in synchronicity among trees as an early warning signal for increased sensitivity to drought and augmented vulnerability of populations of Scots pine (*Pinus sylvestris*) and Aleppo pine (*Pinus halepensis*). Tree-to-tree growth synchronicity indeed often increases with drought stress (Fritts, 2001) or other

unfavorable conditions. Hence, a population with diverse growth patterns can be assumed to be more resilient.

In this work, we contribute to understand the resilience of *Prioria balsamifera* (Vermoesen) Breteler (Fabaceae-Caesalpinioideae) in the Mayombe forest based on an analysis of synchrony of defoliation and cambial activity by: (i) evaluating the seasonality of cambial activity and synchronicity in response to climate and (ii) identifying the seasonality of leaf phenology. To do so, we used series of growth rings from cambial marks from 1947 to 2014, intra-annual cambial marks from the season of 2006–2007, and dendrometer data from 2017 to 2018, observations of inter-annual defoliation from 1947 to 1957, time-lapse camera observations of defoliation from 2015 to 2016, and measured tree-ring width series (1811–2014). We studied *P. balsamifera*, a commercial tree species under strong pressure from logging to supply local artisanal markets. *P. balsamifera* is one of the main species of the timber industry in the DRC. It is a brevi-deciduous species, reaching 55 m in height and 1.5 m in diameter, with a spherical crown and open foliage (Arno, 2001; Meunier et al., 2015).

MATERIALS AND METHODS

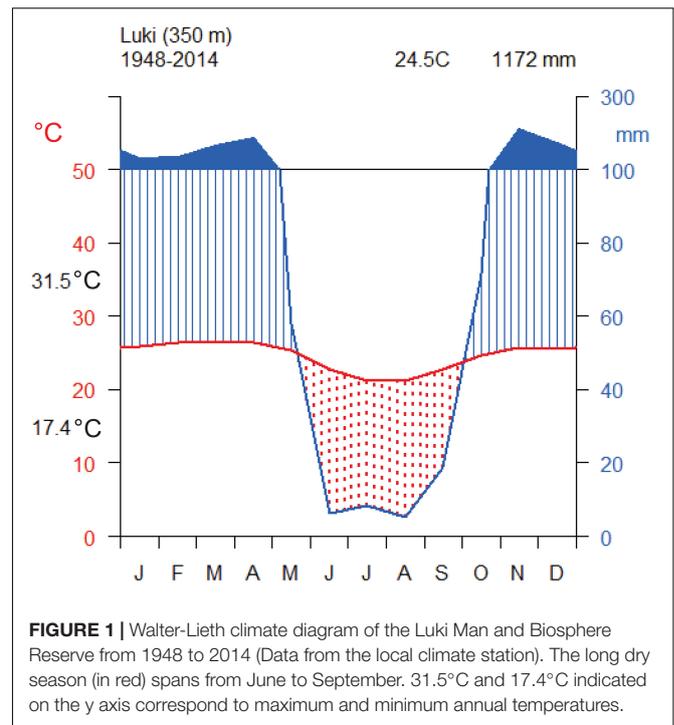
Study Site

The Luki Man and Biosphere Reserve is located in the southwest of the DRC (latitude between 05° 35' and 05° 43' S, longitude between 13° 10' and 13° 15' E), in the Kongo Central province at 120 km from the Atlantic coast. It belongs to the Mayombe forest which constitutes the southern margin of the Guineo-Congolese forests (Lubini, 1997). It is considered representative of the Mayombe flora (Lubini, 1997) and classified as “Central African moist forest” (Fayolle et al., 2014). Soils are ferrallitic, acidic with a low cation content (Sénéchal et al., 1989).

The climate is moist tropical and corresponds to type Aw₄ of the Köppen classification (Peel et al., 2007). It is influenced by the cold oceanic current of Benguela and the southeast winds, also due to its proximity to the Atlantic coast (Lubini, 1997; Couralet et al., 2010). In the Luki Man and Biosphere Reserve, rainfall and temperature are being recorded since 1948 (Couralet et al., 2013; Angoboy Ilondea et al., 2019). The daily data collected onsite show a strong inter-annual variation of rainfall with an average of 1,201 mm·year⁻¹ and a standard deviation of 323 mm from 1947 to 1958. This is very low for dense forest sites, so cloud cover in the morning during the dry season is probably a key factor to maintain forest cover there. The seasonality of rainfall is bimodal, with two rainy seasons interspersed with a large and very marked dry season (June–September), and to a much lesser extent during December–January (Figure 1), where rainfall is less pronounced in amplitude and intensity (Angoboy Ilondea et al., 2019).

Tree-Ring Measurements and Wood Formation

A total of 194 trees of *P. balsamifera* nail tagged with metal plates by the Institut National pour l'Étude Agronomique du Congo Belge (INEAC), later renamed Institut National pour



l'Étude et la Recherche Agronomiques en R.D. Congo (INERA) at the end of 1947 were monitored for phenology between 1947 and 1958 (Couralet et al., 2013; Angoboy Ilondea et al., 2019). Wood samples were collected from the nail area in 2014 for 13 trees that showed a clear nail trace. A selection of increment cores or stem fragments was made, based on whether clear wood markings were visible after sanding (Hubau et al., 2019). For every core, growth-ring series were visualized using imaging methods as previously described in De Mil et al. (2016). Core surfaces were smoothed with a core microtome (Gärtner and Nievergelt, 2010) and scanned using a flatbed scanner at 2400 dpi (EPSON Perfection 4990 PHOTO). Rings formed between 1948 and 2014 were measured on the stem fragments and cores using a LINTAB measuring stage in combination with TSAP-WinTM software (Rinntech, Germany), as well as with the DHXCT graphical user interface (De Mil et al., 2016), available on www.dendrochronomics.ugent.be.

Every first week of the month between April 2006 and August 2007, cambial pinning was performed on the stem, each new mark was made 5 cm to the right in a spiral arrangement to avoid interference of nearby wound tissue. When a circumference was fully occupied, the next pinnings were made on a new circumference 20 cm higher. The diameter of these trees varied between 15.4 and 40.8 cm. After 20 months, we obtained the proper authorization to cut the trees that were monitored. Stem sections were sawn at the level of the markings visible on the bark and all pinning positions were indicated with paint. Samples were air-dried and then cut into small pieces, each containing one wound. The surface was sanded with gradually increasing grid from 50 to 600 or 1200 and the different wood tissues were observed macro- and microscopically (Couralet et al., 2013).

Finally, from 2016 to 2017, electronic radius dendrometers (EcoMatik) were mounted on three trees of *P. balsamifera* to account for daily variations in stem diameter, and as an additional verification for cambial growth. The dendrometers were installed at 1.30 m height and stem diameter variations (SDVs) were logged every 30 min using ONSETComp HOBologgers (Onset; De Mil et al., 2019).

Defoliation Data

A total of 194 trees of *P. balsamifera* were monitored for phenology every 10 days from 1947 to 1958, and phenological observations, i.e., the presence of flowers, fruits, dissemination and defoliation in the crown, were reported in notebooks. These historical phenology data have been previously analyzed (Couralet et al., 2013; Angoboy Ilondea et al., 2019). More recently, leaf unfolding was daily monitored for two trees using Wingscapes time-lapse cameras (Alberton et al., 2017), the pictures were taken from 6 a.m. to 6 p.m. at an interval of 1 h. The time-lapse cameras were operational from December the 14th, 2015 to September the 16th, 2016, thus covering one entire dry season. The images were visually analyzed and four defined leaf unfolding stages were identified: buds swelling, buds break, buds open and leaf unfolding adapted from Malaisse (1964). The occurrence of each leaf unfolding stages is compared with the corresponding season.

Data Analysis

All analyses were performed in R Studio (R Core Team, 2016). Tree rings series were analyzed with the R package “dplR” (Bunn, 2008, 2010), defoliation with the R package “Circular” (Morellato et al., 2000) and the cambial pinning data by fitting a Gompertz function.

Relative growth rate (RGR) (%) within the growing season was calculated to obtain growth curves of seasonal wood formation, given that variability of absolute growth along the circumference can be too high to construct a growth curve that is typical of the individual (Seo et al., 2007; De Mil et al., 2017). The Gompertz equation defined as follows was fitted to the data for each tree separately ($n = 10$ for cambial pinning and $n = 3$ for radius dendrometers).

$$RGR = ae^{-e^{\beta-kt}}$$

RGR is the relative growth rate (in %), a is the upper asymptote, β is the x-axis placement for the location of the origin, k stands for the rate of change parameter and t is the time, expressed in number of days since the first cambial pinning.

Tree-Ring Analysis

We attempted to crossdate 13 cores from 13 trees, but of these, only 3 had 66 rings between 1948 and 2014, so all the others could not have been crossdated since there are too many missing rings. The function “interseries.cor” of the R package “dplR” has been used (Bunn, 2008, 2010). The three trees were located at the same slope and altitude. The signal strength and confidence of these series is assessed by calculating inter-series correlation (Rbar; Wigley et al., 1984). Successful crossdating of ring-width series denotes consistent and synchronous patterns of variation (Cook

and Kairiukstis, 1990). Crossdating was performed visually in combination with a correlation analysis using Cofecha software (Holmes, 1983).

Seasonality of Defoliation

Using the crown observation data from 1947 to 1957, circular statistics allowed to detect and to test the synchrony of defoliation at the population level (all trees) and separately for individual trees between years. This also allowed quantifying the degree of temporal aggregation of defoliation (Davies and Ashton, 1999). The length of the vector ρ (ranging from 0 to 1) indicates the duration and the concentration of phenological events. This vector was calculated for the species. In both cases, a lower ρ value indicates a phenological activity occurring several times per year. A ρ value close to 1 indicates a phenological event occurring once a year. Rayleigh uniformity test was performed to test the significant aggregation of defoliation events (Davies and Ashton, 1999).

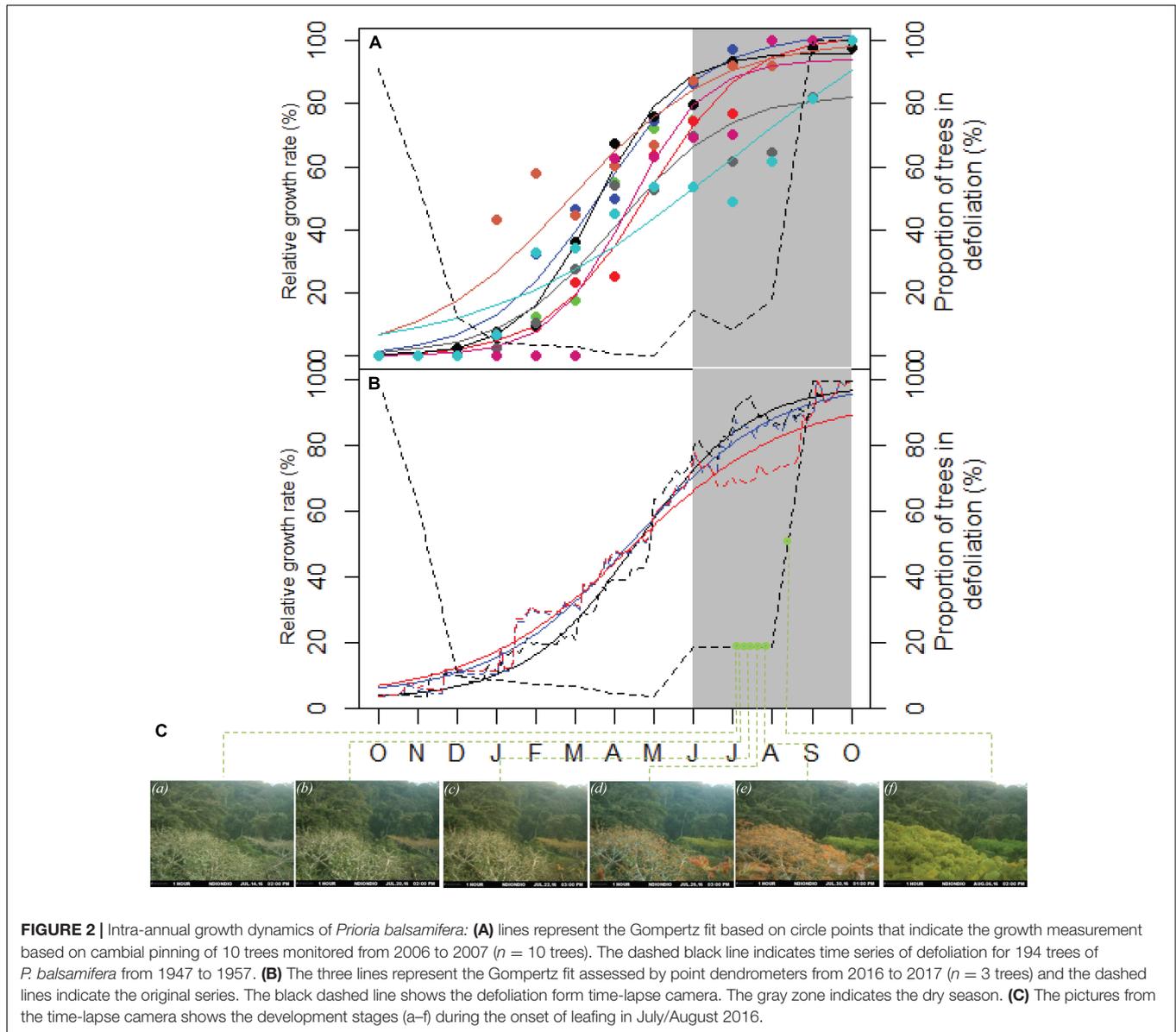
We then tested the correlation between the percentage of trees showing defoliation (1947–1957) with the rainfall and temperature of the same period using the Pearson’s correlation coefficient. This makes it possible to define the potential influence of the variation in precipitation and temperature on the defoliation.

RESULTS

Wood Formation and Timing of Leafing Recorded by Time-Lapse Cameras

The cambium of *P. balsamifera* is dormant from the end of the dry season and growth starts at the beginning of the rainy season in October (Figure 2). This was also detected by the cambial pinning and by the dendrometer measurements that follow the tree growth with higher resolution and accuracy. Growth rings are not always annual and are generally formed during the rainy season as illustrated by the Gompertz fit to show relative growth for all trees (Figure 2).

The maximum time between the development stages of leaf buds (Figure 2C) is about 7 days. Time-lapse camera photos, taken between December 14, 2015 to September 16, 2016, have indicated that the leaf unfolding is often short and all phenological stages of the leaves of one tree occur in only 1 week and confirmed the short defoliation episodes detected by circular statistics using the data of 1947–1957 (Figure 4). Analysis of camera’s pictures has shown that the leaf unfolding follows shortly after the defoliation. Analysis of the camera’s pictures has shown the leaf unfolding starts before the rainy season (July, August, and September) and continues until October. Leaf unfolding and defoliation are overlapping (Figure 2). The gray zone indicates the dry season (Figure 2C). The pictures from the time-lapse camera during the onset of leafing in July/August 2016 showed the development stages adapted to the characterization of Malaisse (1964): (a) old leaves, (b) stage 0: dormant buds, (c) stage I: buds swelling, (d) stage II: bud break, (e) stage III: buds open, (f) stage IV: leaf development.



Tree-Ring Crossdating

Core images and ring-width data for *P. balsamifera* were extracted from Hubau et al. (2019). Cambial marks due to tree tagging indicated the year 1948 and thus serve as an absolute dating point. From these 13 trees (showing on average 111 rings from the pith onward), only the 3 trees for which we counted 66 rings between 1948 and 2014 (**Figure 3**) were retained. For these three trees (**Figure 3B**), the peak of defoliation was observed on October 10 (Tw77843), September 7 (Tw77847) and October 20 (Tw77877).

Seasonality and Asynchrony in Leaf Phenology

In addition to the 1 year leaf phenology monitoring campaign with time-lapse cameras, we used historical phenological

observation data and we found that, every year a peak of defoliation was observed at the end of the dry season and the beginning of the rainy season. The peak dates varied across years from September 12 to November 14. Over the 11 years of phenology observations, peaks of defoliation were obtained in November for 5 years (1952–1955) and 1957, in September for 4 years (1947, 1949–1951) and in October for 2 years (1947 and 1956). The defoliation of *P. balsamifera* at the population level can thus be characterized as annual and irregular and of short duration (ρ generally close to 1, **Figure 4**). Globally, the ρ values of defoliation ($\rho > 0.5$) indicate the high degree of synchronization for the studied *P. balsamifera* population each year. The trees begin to lose their leaves mainly in the dry season and achieve a complete loss at the beginning of the rainy season. However, in 1955, the defoliation was not synchronous and was relatively spread out ($\rho = 0.47$) in contrast to the year 1952

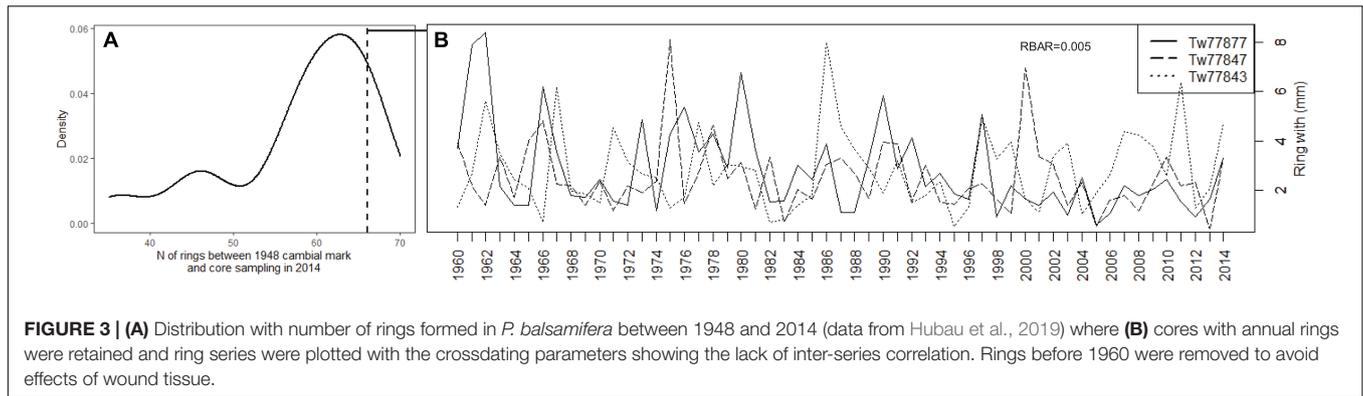


FIGURE 3 | (A) Distribution with number of rings formed in *P. balsamifera* between 1948 and 2014 (data from Hubau et al., 2019) where **(B)** cores with annual rings were retained and ring series were plotted with the crossdating parameters showing the lack of inter-series correlation. Rings before 1960 were removed to avoid effects of wound tissue.

which corresponds to a synchronous and very brief defoliation ($\rho = 0.94$). The lower number of defoliated trees is observed between 1952 and 1954.

Negative correlation were observed between the maximum number of defoliated trees and both annual rainfall and mean temperature ($P > 0.05$).

DISCUSSION

Cambial Phenology and Lack of Crossdating

Our results show that cambial phenology of *P. balsamifera* is dormant during the dry season and growth starts at the beginning of the rainy season (Figure 2). The first rains often trigger radial growth as already shown for other species using cambial pinning in the Mayombe forest: *Aidia ochroleuca* (K.Schum.) (Couralet et al., 2010), *Terminalia superba* Engl. & Diels (De Ridder et al., 2013), *Greenwayodendron suaveolens* (Engl. & Diels) Verdc. (De Mil et al., 2017). De Mil et al. (2019) detected that *Terminalia superba* Engl. & Diels begins unfolding its leaves well before the rainy season, whereas dendrometer data complemented with cambial pinning showed that the wood is being formed after the first rains. Likewise, pre-rain green-up has been found to be ubiquitous across (sub) tropical savannas and woodlands of southern Africa (Trouet et al., 2012; Ryan et al., 2017).

The lack of crossdating (Figure 3, $RBAR = 0.005$) indicates that climate response of *P. balsamifera* is not obvious. Nevertheless, the sensitivity values of individual series are above 0.2, which is generally accepted as a series that might be sensitive enough for climate reconstruction (Tang et al., 2018).

Leaf Phenology Related to Environmental Factors

The defoliation of *P. balsamifera* is annual, but quite irregular from year to year (Figure 4), which has also been shown for other populations of trees (Newstrom et al., 1994).

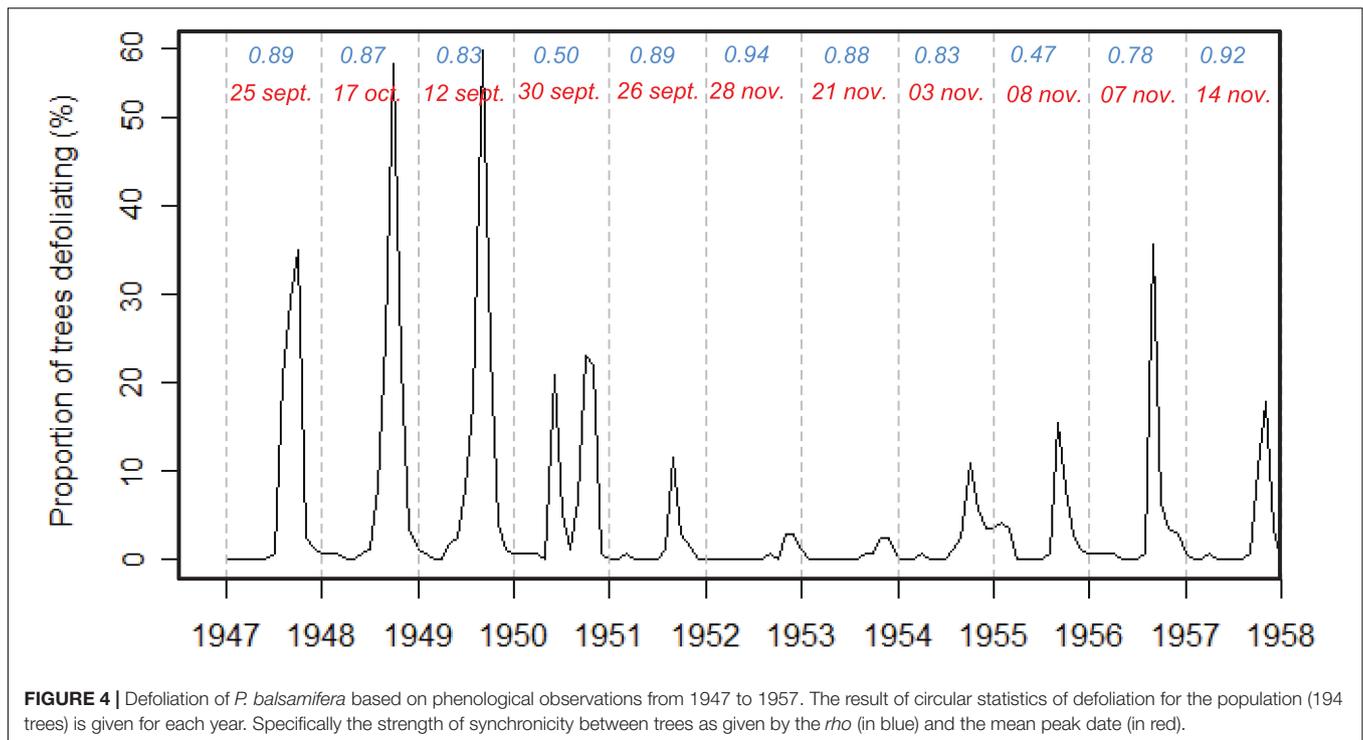
Defoliation occurs during the dry season (July and August) but the new leaves appear rapidly after defoliation. The impact of the dry season on the seasonal functioning of tropical trees has already been studied for *Terminalia superba* Engl. & Diels, in DRC (De Mil et al., 2019) and across the tropics

(Wagner et al., 2014). During seasonal drought, many trees renew their leaves and suspend their radial growth. In our study area, this phenomenon does not seem to be as important because the air humidity always remains high, even during the dry season because of the Benguela current (Lubini, 1997; Couralet et al., 2013; Angoboy Ilondea et al., 2019; Aleman et al., 2020). Therefore, the cambial dormancy period might be less strict than in other tropical regions with a more seasonal climate. In the Luki Man and Biosphere Reserve there are at least 3 months with less than 50 mm of rainfall each year, but the dense cloud cover as a result from the proximity of the ocean and the hilly landscape provides a constant high level of air humidity (Lubini, 1997).

It has been reported earlier that the tropical rainforests characterized by a strong annual dry season show an adjustment in leaf production and defoliation (Reich, 1995). Our results show a consistent yearly defoliation: trees leafing early in 1 year also do so in other years (Figure 4). However, the results indicate that there is a considerable variation between trees in a single year. The use of time-lapse cameras allowed a detailed monitoring of the leafing process (from the first buds to the complete new leaves) that occurs on a relatively short period of time, one single week, possible due to the high humidity. Such quick processes are not detected using crown observations, classically used for phenology monitoring, and done every 10 days (Angoboy Ilondea et al., 2019) but more generally only once a month (Bush et al., 2017). The lower number of defoliated trees between 1952 and 1954 was observed by Couralet et al. (2013) in the Luki Biosphere Reserve for flowering, fruiting and dissemination. This would be due to the very low rainfall in 1953 and 1954 caused by an El Niño event. They indicated that annual rainfall sums were slightly above average in 1948 and 1949 (1268 and 1260 mm, respectively) and extremely high in 1950 (1845 mm).

Asynchrony in Buffering Climate Change and Population Resilience

Asynchronous leaf and cambial phenology has been earlier observed for the same site for *Terminalia superba* (De Mil et al., 2019), which confirms what is shown here for *P. balsamifera*. The dendrometers showed that the wood growth of *T. superba* starts after budburst between November and January (De Mil et al., 2019). Cambial pinnings confirmed that *P. balsamifera* growth starts at the beginning of the rainy season in October



(Figure 2) and the leaf unfolding occurs before the start of the rainy season (July, August, and September) and continues until October. Causes for asynchrony have not been thoroughly explored but differences in genetics, life history traits and habitat conditions encountered by individual trees may influence the way that populations as a whole experience environmental conditions, potentially leading to a diversity of responses among trees to the same environmental conditions (Thorson et al., 2014). Consistent lags in phenology are known to be genetic (te Beest et al., 2012). Indeed, given the diverse and consistent growing period, the environmental responses of *P. balsamifera* trees are variable and create diversity within the species. This lack of synchrony adds to the resilience of *P. balsamifera* populations. This way, as suggested by Fritts (2001) and Camarero et al. (2015), the concept of resilience is being addressed, not at the individual level of the organism, but rather at the population level and is similar to the general biological strategy of “bet hedging” (Cohen, 1966). The data we analyzed suggest that the *P. balsamifera* population is resilient (Figure 3). The lack of crossdating indicates that individuals of the same species in the same environment would react differently to a disturbance (Fritts, 2001). This will increase the resilience of the stand against unfavorable environmental fluctuations.

Many of the trees have less than 66 rings between 1948 and 2014, which shows that missing rings are common for the species. For the three trees that formed 66 rings between 1948 and 2014 (Figure 3), there was hardly any synchrony. This means that shifts (thus not synchronous) in leaf unfolding and defoliation and certainly different periods of cambial activity do have far-reaching consequences. This would be an advantage for the species in the face of the various changes that could occur

in its environment, because the trees would react differently. Whether this is due to local site conditions, or genetics, is unclear.

Although at the individual level, tree rings provide a useful tool to analyze the resilience, this approach has seldom been used to evaluate resilience at the population level (DeClerck et al., 2006). Crossdating of ring-width series allows for the detection of synchrony between trees. The successful crossdating of ring-width series denotes consistent and synchronous patterns of variation (Cook and Kairiukstis, 1990; Couralet et al., 2010) and indicates that the radial growth of different trees is controlled by a common external factor, e.g., rainfall and temperature (Couralet et al., 2010).

CONCLUSION

The studied population of *P. balsamifera* showed a synchronous phenology with a distinct defoliation period. Defoliation starts during the dry season in June–July with peaks during the rainy season in October–November, but the defoliation date varied across years and is consistent (annual ranks of trees according to leaf development and start of cambial activity do not change). Chronological series were built from wood samples collected from trees that were phenologically monitored. Xylem formation is seasonal, with cambial dormancy occurring during the dry season. The absence of crossdating between the chronological series of different trees suggests a varying response of *P. balsamifera* trees to environment. Based on the analyses carried out and the results obtained, *P. balsamifera* populations are likely resilient.

DATA AVAILABILITY STATEMENT

The raw data supporting the conclusions of this article will be made available by the authors, without undue reservation.

AUTHOR CONTRIBUTIONS

BAI: literature review (lead), conceptualization (equal), formal analysis (lead), project administration (supporting), investigation (lead), methodology (lead), and writing-original draft (lead). JvDB, CC, AF, WH, NB, VD, CE, and TDM: conceptualization (equal), investigation (equal), supervision (equal), and writing – review and editing (equal). HB: conceptualization (equal), funding acquisition (lead), investigation (equal), project administration (equal), supervision (equal), and writing – original draft (equal). CK, MR, and EKY: conceptualization

(equal), investigation (equal), and writing – review and editing (equal). All authors contributed to the article and approved the submitted version.

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