

Interplay of environmental cues and wood density in the vegetative and reproductive phenology of seasonally dry tropical forest trees

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Abstract

The great phenological diversification characteristic of seasonally dry tropical forests (SDTF) suggests that these patterns result from a complex interplay between exogenous (e.g., climatic) and endogenous (e.g., morphological, physiological, anatomical) factors. Based on the well-established relationships of wood density with water-storing capacity and cavitation vulnerability in woody plants, we hypothesized differential vegetative and reproductive phenological responses to environmental cues for hardwood and softwood species. To test this hypothesis, we compared phenological patterns of pairs of conspecific populations of 10 species differing in wood density, occurring in two localities with slightly different climatic regimes, and evaluated the influence of three environmental variables (rainfall, photoperiod, and temperature) on them. Our results, based on the assessment of the overlap of the phenological curves of conspecific populations occurring in different sites and on linear modeling, showed different effects of the environmental factors on phenophase attributes, depending on wood density of the study species, thus supporting our hypothesis. Leaf out in softwood species took place in the dry season, they shed the foliage at the first signs of drought, and once leafless, they flowered and fruited shortly after. By contrast, hardwood species bore leaves and flowers in the rainy season, shed their leaves several months after the rain ceased, and produced fruits during the dry season. We conclude that the role of environmental variables in cueing growth and reproduction cycles in SDTF tree species is interrelated with their wood density, a key endogenous factor crucially linked to plant hydraulics in these water-limited ecosystems.

Abstract in Spanish is available with online material.

KEYWORDS

flowering, fruiting, functional trait, leafing, Phenological Overlap Index, tropical dry forest

1 | INTRODUCTION

The timing and duration of vegetative and reproductive cycles of plants represent fine-tuned adaptations to their biotic and abiotic habitat conditions (Fenner, 1998; van Schaik et al., 1993). These cycles are regulated by multiple drivers broadly classified as proximate (e.g., short-term variation in environmental conditions; Borchert, 1994; Borchert et al., 2004) or ultimate (e.g., phylogenetically conserved phenological traits; Davis et al., 2010). Despite long-standing research in this field, recently fueled by the urgency to understand the consequences of global change for plants' biological rhythms (Mendoza et al., 2017; Richardson et al., 2013; Siyum, 2020), assessing the extent to which each factor is responsible for tree phenology remains challenging in tropical ecology (Abernethy et al., 2018).

Seasonally dry tropical forests (SDTF) are attractive systems for studying the role of proximate causes defining phenological timing given the marked rainfall seasonality they experience (Murphy & Lugo, 1986). The timing of plant growth and reproduction in SDTF is mainly regulated by rainfall intensity and frequency (Reich & Borchert, 1984; van Schaik et al., 1993). This has led to broad generalizations regarding SDTF tree phenology. For example, deciduousness is considered the most successful foliage-related phenological pattern among SDTF plants (Singh & Kushwaha, 2005). In deciduous species, leaf shedding is often followed by flowering (Franklin, 2016), which normally occurs in the early dry season when the soil is still moist (Borchert et al., 2002; Bullock & Solís-Magallanes, 1990; Lopezaraiza-Mikel et al., 2014). Likewise, fruit maturation commonly occurs in the same dry season or the subsequent rainy season, when the strong winds (dry season) or frugivore activity (early rainy season) favor seed dispersal (Cortés-Flores et al., 2019; Justiniano & Fredericksen, 2000; Lopezaraiza-Mikel et al., 2014; McLaren & McDonald, 2005; Xu et al., 2016).

The generality of deciduousness in SDTF trees should not obscure the large intra- and inter-annual variation in water availability across this ecosystem's geographical range (Holbrook et al., 1995; Maass et al., 2018; Martínez-Ramos et al., 2018). The high spatial and temporal rainfall variability in these regions (González-M. et al., 2019; Singh & Chaturvedi, 2018) has promoted the evolution of multiple phenological strategies, allowing plants to evade, resist, or tolerate water stress through different mechanisms (Kushwaha et al., 2010; Méndez-Toribio et al., 2020; Pineda-García et al., 2013; Singh & Kushwaha, 2006). For example, in some deciduous species leaf out and flowering are not driven by rainfall but rather by photoperiod or dry season temperatures (Borchert et al., 2004; Borchert & Rivera, 2001). Other species bear leaves even in the dry season, when most deciduous species are leafless, showing a semi-evergreen (leaf-exchanging species; Singh & Kushwaha, 2005) or even an evergreen pattern (Bowman & Prior, 2005). This great diversification suggests that each species' phenological behavior results from a complex interplay between exogenous (climatic) and endogenous (genetic, anatomical, morphological, and physiological) factors (Borchert, 1994; Fallas-Cedeño et al., 2010).

Wood density is a functional trait involved in the integrated vegetative and reproductive tree phenology due to its complex relation with plant hydraulics (Castellanos-Castro & Newton, 2015; Chave et al., 2009; Lima et al., 2012; Mendivelso et al., 2013; Scholz et al., 2014). The wide vessels typical of low-density wood (softwood or SW) species are related to efficient water transport and large water storage, allowing them to flush before the rains start; however, this xylem trait also increases cavitation risk (Markestijn et al., 2010; Zanne et al., 2010) and endorses a less conservative water use (Reyes-García et al., 2012), inducing leaf shedding at the first signs of drought (early deciduous species; Méndez-Alonzo et al., 2012). By contrast, species with high-density wood (hardwood or HW species) tend to have narrow vessels and less efficient xylem water transport and storage (Chave et al., 2009); yet they are more resistant to cavitation and retain their leaves longer once the rain ceases (late deciduous species; Méndez-Alonzo et al., 2012). Hence, the denser the wood of SDTF species, the stronger the relationship between leaf out and the onset of the rainy season, while the relationship between leaf fall and the end of the rainy season dwindles (Borchert, 1994; Kushwaha et al., 2010; Lima & Rodal, 2010).

Although less studied, the link between wood density and reproductive phenology of SDTF trees is also complex, as suggested by observations relating flowering and fruiting with the leafy or leafless state of the trees (Borchert et al., 2004; Kushwaha et al., 2011; Rivera et al., 2002; Singh & Kushwaha, 2006). Thus, reproductive events in SDTF trees are not necessarily independent of the plant's vegetative condition, calling for a comprehensive examination of vegetative and reproductive phenology of SDTF trees and its drivers.

A promising way to examine the interplay of environmental cues and wood density in defining the integrated vegetative and reproductive SDTF tree phenology is the simultaneous evaluation of phenological events in conspecific populations occurring in distant sites, exposed to slightly different climatic conditions. This "natural experiment" approach may potentially reveal phenological responses to gradual changes in water stress in species with different wood densities (Borchert et al., 2002; Goulart et al., 2005; Kushwaha et al., 2010; Lobo et al., 2003; Morellato et al., 2000). Therefore, we hypothesized differential vegetative and reproductive phenological responses to environmental cues for HW and SW species, with higher homogeneity for some phenophase attributes (i.e., start, peak, and end) across conspecific populations than for others. Specifically, based on the tendency of leaf out in SW species to be decoupled from the onset of the rainy season and the tendency of leaf fall to be decoupled from the end of the rains in HW species, we predicted a larger overlap in leafing between sites in the early rainy season for SW species, while HW species should show larger overlaps in the late rainy season. Also, we predicted that vegetative and reproductive phenology should be more independent in SW than in HW species. Admittedly, the recognition of these two extreme functional designs (SW vs. HW species) oversimplifies the large and continuous variation existing between them (Méndez-Alonzo et al., 2012). We expected

stronger support for our hypotheses for vegetative phenology, since flowering and fruiting are additionally affected by many other factors (e.g., pollination type, seed development strategy; Elzinga et al., 2007).

As stated, to test this hypothesis (Figure 1c) one should ideally use data from multiple sites with low and high, as well as early and late, rainfall regimes within the SDTF range. Since this option is

highly impractical, it may suffice to find pairs of sites in the same biome in which the rainy season in one site is delayed with respect to the other one. This study takes advantage of a pair of distant sites within the SDTF biome in southern and western Mexico that meet this criterion. For these two localities we compared the vegetative and reproductive phenology in a group of species representing the wood density range reported for SDTF (Poorter et al., 2019; Romero

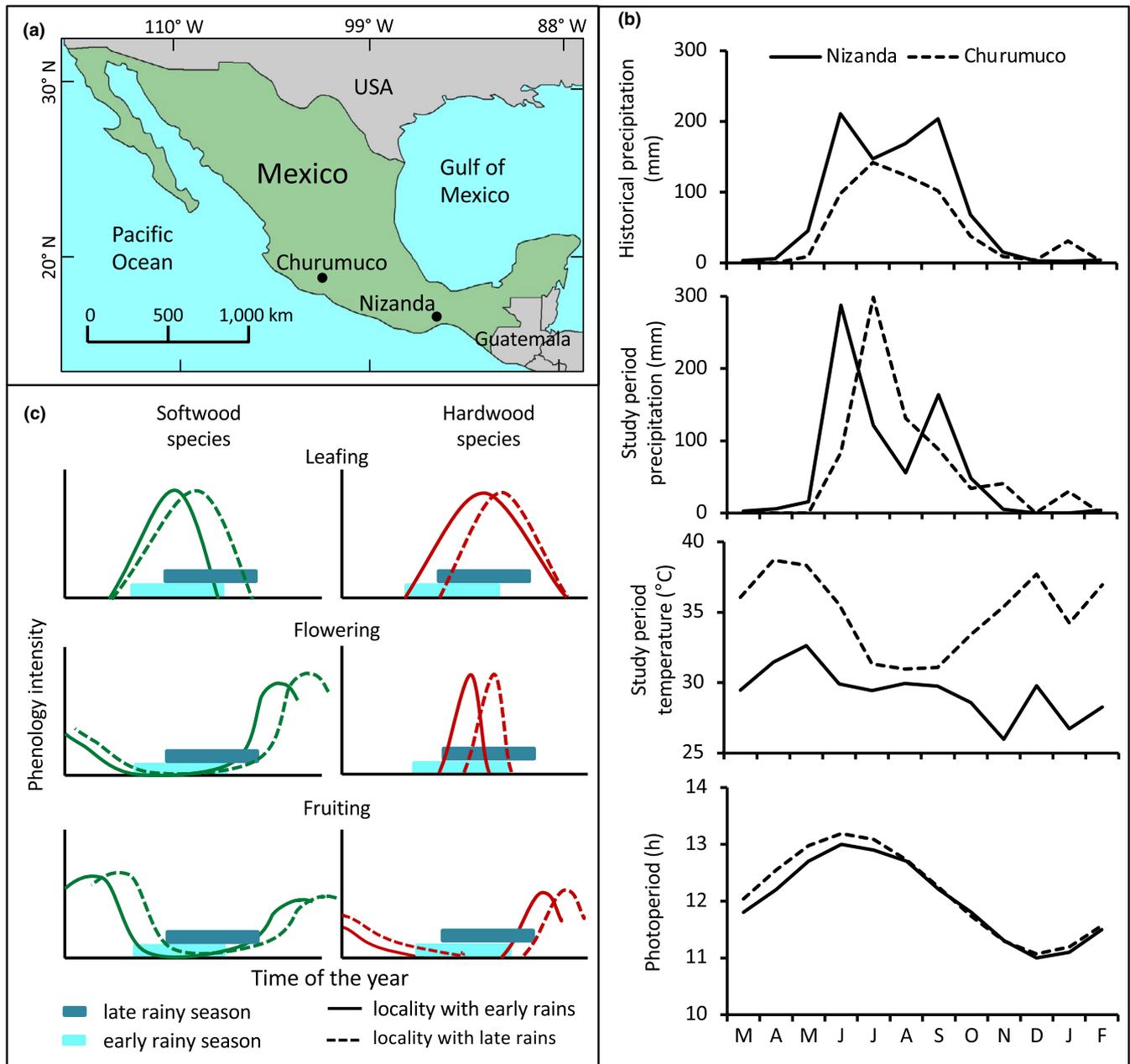


FIGURE 1 Location, climate, hypothesis, and predictions of the study. (a) Location of Churumuco (Michoacán) and Nizanda (Oaxaca) in the seasonally dry tropical forest region of the Pacific watershed of Mexico. (b) Climatic conditions in the two localities; historical precipitation data are for the 1951–2010 period, whereas current information for precipitation and temperature is for the study year (2012–2013). Note that photoperiod is invariable among years. (c) Graphic representation of the hypothesis tested in this study (differential vegetative and reproductive phenological responses to environmental cues for hardwood and softwood species), showing the predicted phenological patterns for softwood (left, green lines) and hardwood (right, red lines) species, and for the leafing (top), flowering (middle), and fruiting (bottom) phenophases in two localities differing in the timing of the rainy season (light blue and dark blue bars). Continuous lines represent predicted phenological curves for the locality with early rains, and broken lines represent the corresponding curves for the locality with late rains

et al., 2020) and evaluated the influence of three environmental variables (precipitation, temperature, and photoperiod) and one functional trait (wood density) on them. For these species, we asked: (1) Do phenological curves for leafing, flowering, and fruiting of softwood species show the same between-population overlap as the curves of hardwood species? (2) How does wood density interact with precipitation, temperature, and photoperiod to determine phenological attributes in the leafing, flowering, and fruiting patterns in these populations?

2 | METHODS

2.1 | Study sites

The study was conducted in two distant Mexican SDTF sites (735-km separation) experiencing slightly different climatic regimes: Churumuco (Michoacán), located in the lower Balsas River Basin (18° 41' 55" N, 101° 39' 12" W), and Nizanda (Oaxaca), located in the Isthmus of Tehuantepec (16° 39' 30" N, 95° 00' 40" W; Figure 1a). In both regions, climate is markedly seasonal, but there are important differences. In Churumuco, the dry season is harsher due to a lower mean annual precipitation (620 mm), concentrated between June and September, and a higher mean monthly maximum temperature (39.2 °C in May); by contrast, in Nizanda mean annual precipitation is higher (900 mm), mostly falling between May and October, and mean monthly maximum temperature is lower (33.0 °C). The prevalent soil type in Churumuco is Eutric Regosol (Conanp, 2014), whereas in Nizanda there is a mosaic of Eutric Leptosol, Eutric Regosol, and Calcaric Phaeozem (C. Miguel, unpublished data).

2.2 | Climatic data

We obtained daily precipitation and temperature data for the study period from the closest meteorological station to each study site: Las Cruces de Turicato (19° 03' 15.3" N - 101° 25' 11.3" W; 742 m) for Churumuco, and Santiago Chivela (16° 42' 47.8" N - 94° 59' 47.1" W; 221 m) for Nizanda. Photoperiod was obtained from the Astronomical Applications Department of the U.S. Naval Observatory (<http://www.usno.navy.mil>).

In the study period, the rainy season in Nizanda spanned from May to October, whereas in Churumuco it started one month later (June) and lasted until November; thus, in both localities it rained for six months but there was a 1-mo lag in Churumuco. Total annual precipitation was nearly identical in both localities (ca. 740 mm), but the rainiest month differed between Churumuco and Nizanda (July and June, respectively). Mean monthly maximum temperature was higher in Churumuco than in Nizanda throughout the year (5 to 10 °C higher). Finally, due to their similar latitudes (2° difference), photoperiod in both sites is nearly identical; the largest disparity occurs in April, when the day lasts on average 24 min more in Churumuco (Figure 1b).

2.3 | Phenological data

To conduct comparative phenological observations, we selected ten typical SDTF tree species with sufficiently large populations in both localities and with different wood densities (range, 0.1–0.94 g/cm³, values extracted from the literature; Table 1). We classified five species as soft-wooded (<0.55 g/cm³) and five species as hard-wooded (>0.55 g/cm³), following the criteria proposed by Barajas-Morales (1987), Borchert and Pockman (2005), and Chave et al. (2006).

At each site, we marked ten reproductive individuals by species (200 individuals in total). Trees with diameter at breast height (DBH) ≥ 8 cm were chosen by order of appearance, as this size defines reproductive adults (Luna-Nieves et al., 2017). The selected trees were separated by distances > 50 m to minimize genetic relatedness and data spatial dependency. Monthly phenological observations were conducted in the last week of the month from March 2012 to February 2013. We quantified the presence of leaves, flowers, and fruits using a semi-quantitative scale of five categories (0–4), each representing a 25% interval of total crown volume where the target structure was present (Fournier, 1974). Leafing included all stages of leaf development from leaf flush through full blade expansion to leaf fall (Reich et al., 1992). Similarly, flowering included all phases of floral development from floral bud formation to anthesis, while fruiting included all phases from the appearance of visible fruits to their maturation.

2.4 | Data analysis

We used a two-pronged approach to analyze our research questions. First, for each phenophase we assessed the overlap of the phenological curves of the two populations of each species and compared it between the broad wood density species groups (SW or HW). Next, we used linear modeling to analyze the effects of environmental variables and wood density on the key moments that define the phenological curve (phenological attributes).

2.4.1 | Between-population comparison of phenological curves

To assess the between-population intraspecific variation of leafing, flowering, and fruiting, we developed a new application of the Morisita-Horn Index (Horn, 1966; Morisita, 1959) to be used in phenological studies, and we named it the Phenological Overlap Index (POI). POI offers a comprehensive way to quantitatively assess whether all attributes defining the phenological curves of two sets (either two populations of the same species, two species, or two communities) differ from each other. The first step in calculating POI was the computation of Fournier's (1974) intensity index, which evaluates the proportion of leafing, flowering, and fruiting in each population, by month (the relative intensity of each phenophase can vary from 0 to 1). Fournier's intensity index was calculated through the following formula:

TABLE 1 Study species from the seasonally dry tropical forest of Churumuco, Michoacán State, and Nizanda, Oaxaca State, southern Mexico, and their grouping according to their wood density. Wood density groups: HW, hardwood; SW, softwood. Superscript numbers indicate the sources of wood density information for each species: 1, Barajas-Morales (1987); 2, Méndez-Toribio et al. (2017); 3, Romero et al. (2020)

Family	Species	Wood density (g/cm ³)	Wood density group
Fabaceae	<i>Apoplanesia paniculata</i> C. Presl	0.94 ¹	HW
Fabaceae	<i>Vachellia campechiana</i> (Mill.) Seigler & Ebinger	0.94 ¹	HW
Fabaceae	<i>Lysiloma divaricatum</i> (Jacq.) J.F. Macbr.	0.88 ^{2,3}	HW
Resedaceae	<i>Forchhammeria pallida</i> Liebm.	0.84 ¹	HW
Bignoniaceae	<i>Handroanthus impetiginosus</i> (Mart. ex DC.) Mattos	0.68 ²	HW
Apocynaceae	<i>Plumeria rubra</i> L.	0.50 ²	SW
Malvaceae	<i>Ceiba aesculifolia</i> (Kunth) Britten & Baker f.	0.48 ¹	SW
Anacardiaceae	<i>Amphipterygium simplicifolium</i> (Standl.) Cuevas-Figueroa	0.40 ¹	SW
Bixaceae	<i>Cochlospermum vitifolium</i> (Willd.) Spreng.	0.27 ¹	SW
Caricaceae	<i>Jacaratia mexicana</i> A.DC.	0.10 ^{2,3}	SW

$$I_j = 100(mn)^{-1} \sum_{i=1}^n I_{ij}$$

where I_{ij} = intensity assessed at time j to the i -th individual; m = number of intensity categories; and n = number of studied individuals per population in a given time (in our case, the 10 individuals by species).

We then calculated POI with the following formula:

$$POI(A, B) = 2 \sum_{j=1}^{12} I_{A_j} I_{B_j} / \left[\sum_{j=1}^{12} I_{A_j}^2 + \sum_{j=1}^{12} I_{B_j}^2 \right]$$

where I_{A_j} = Fournier's intensity index for a given species in site A at time j (in our case, month, i.e., 1 to 12), and I_{B_j} = Fournier's intensity index for the same species in site B at time j . POI ranges from 0 to 1, with 1 denoting the maximum possible overlap between phenological curves for a given phenophase in the two populations, and 0 denoting total lack of overlap. To further develop intuition on this index, we include in Appendix S1 (in Supporting Information) scenarios of change in different attributes of the phenological curve and the impact of these changes on the degree of overlap between two curves as measured by POI.

For each pair of conspecific populations, we compared their POI with the Wilcoxon-Mann-Whitney rank test. These comparisons were done not only for the entire phenological curves but also for sections of the curves corresponding to the first or the second half of the study year, given our hypothesis that the overlap could be smaller either in the early rain or late rain period, depending on wood density. Additionally, we calculated the Spearman rank correlations between wood density of the ten study species and their POI, again for the entire phenological curves, and the respective sections of the first and second halves of the year.

2.4.2 | Evaluation of environmental and wood density effects on phenological responses

Although each phenophase of a species is a continuous process over time, the influence of exogenous and endogenous factors

differs between key moments of this process. Therefore, in assessing the influence of the environmental variables and wood density on the vegetative and reproductive phenology, each phenophase was discretized by defining three phenological attributes. The first attribute, phenophase start, was defined as the first month in which the observed individual presented the phenophase. Although for most individuals the start was identified without ambiguity, there were some instances in which the trees bore leaves, flowers or fruits all year round; in these cases, the start was recorded as the month in which a noticeable increase in the production of new structures was observed. The second attribute, phenophase peak, was defined as the month in which the maximum activity (i.e., largest number of structures) was observed in the individual tree; when the maximum activity took the form of a high plateau lasting for two or three months, phenophase peak was recorded as the first month of such high activity period. Last, we defined phenophase end as the last month in which the observed individual bore leaves, flowers or fruits; as this phenological attribute is less relevant for reproductive phenophases, we only evaluated it for the leaves.

We constructed a set of Bayesian generalized linear and non-linear (additive) mixed models (GLMMs and GAMMs, respectively) that considered wood density and the environmental cues as explanatory variables, and the phenological attributes of each phenophase as response variables (start, peak, and end). The set of environmental variables analyzed included maximum monthly temperature, photoperiod, and total monthly precipitation. Because the effect of precipitation may not be immediate (for example, if plant tissues take some time to rehydrate to functional levels), we also assessed the effect of precipitation in the previous month on phenological activity (Cortés-Flores et al., 2017). The models were constructed with individual identity nested within species and site as random effects. Phenological attributes were restricted to the (0, 1) interval to assume a beta distribution. All possible combinations of explanatory variables were considered, both with main and interaction effects. In these models, *Forchhammeria pallida* was excluded because this species displays an inverse vegetative phenology (i.e., leafing occurs in the dry season)

that acted as an outlier in our data, strongly distorting parameter estimates (results not shown here). A model was selected for each phenophase attribute using the Widely Applicable Information Criterion (WAIC; Gelman et al., 2014; Watanabe, 2010). The best-supported model was the one having the smallest WAIC value. Modeling was performed using the `brms` package (Bürkner, 2017, 2018) in R (R Core Team, 2018). Table S1 shows all evaluated models along with their WAIC values. Best-supported models were plotted in a circular fashion to reflect the cyclic nature of phenophases; plots were constructed using the `plotly` package (Sievert, 2020) in R.

3 | RESULTS

3.1 | Phenological overlap between sites

Regarding leafing phenology, the overlap for the entire leafing curves between all conspecific populations was considerably high, regardless of wood density (mean POI for HW leafing = 0.928, mean POI for SW leafing = 0.939; Table 2). Yet, when comparing the overlap for separate portions of the phenological curve important differences between HW and SW species emerged (Table 2): in the first half of the study period (late dry season-early rains) the POIs of conspecific populations of SW species revealed a significantly larger overlap than for HW species (HW mean POI = 0.917; SW mean POI = 0.979; $p = .032$). By contrast, in the second half

of the study period (late rains-early dry season), POIs were significantly larger for HW than for SW species (HW mean POI = 0.944; SW mean POI = 0.683; $p = .032$).

Unlike the case of leafing phenology, the entire phenological curves of all species for the reproductive phenophases showed smaller overlaps between localities (Table 2). This result was mostly accounted for by the very limited or null reproductive activity of some species in the study period (e.g., *Apoplanesia paniculata* and *Handroanthus impetiginosus*). Interestingly, although neither for flowering nor for fruiting were there significant differences between the POIs of HW and SW species (Table 2), the comparison of the overlap in separate sections of the phenological curves was revealing; whereas in the second part of the year SW species showed a high interpopulation overlap, this was null for those HW species that flowered in the study period (HW mean POI = 0; SW mean POI = 0.463; $p = .064$). The Spearman rank correlations between POI and wood density were only significant for the relationships of leafing and flowering with the POI for the second half of the year (Table S4).

3.2 | Environmental cues and wood density effects on phenology

Figure S1 illustrates the temporal behavior of the phenological attributes (aggregated across all species classified as softwood or hardwood) recorded in the two localities for the vegetative and

TABLE 2 Phenological Overlap Index (POI) values calculated to compare phenological curves of two conspecific populations of SDTF species of two groups defined by wood density (HW, hardwood; SW, softwood). The comparisons were performed for the entire phenological curves and for sections of these curves corresponding to the first half (late dry season and early rainy season; March to August) and the second half (late rainy season and early dry season, September to February) of the study year. Bold typeface indicates significant between-group differences according to a Wilcoxon-rank test. Lf, leafing; Fl, flowering; Fr, fruiting

Species	POI of entire study year			POI of 1st half of study year			POI of 2nd half of study year		
	Lf	Fl	Fr	Lf	Fl	Fr	Lf	Fl	Fr
Hardwood species									
<i>Apoplanesia paniculata</i>	0.913	0	0	0.911	NA	NA	0.915	0	0.249
<i>Forchhammeria pallida</i>	0.925	0	0.348	0.943	0	0.857	0.902	0	0.303
<i>Handroanthus impetiginosus</i>	0.913	NA	NA	0.858	NA	NA	0.989	NA	NA
<i>Lysiloma divaricatum</i>	0.951	0.871	0.680	0.970	0.871	0.885	0.941	NA	0.670
<i>Vachellia cochliacantha</i>	0.940	0.688	0.903	0.904	0.696	0.359	0.975	0	0.952
Mean for HW species	0.928	0.390	0.483	0.917	0.522	0.700	0.944	0	0.544
Softwood species									
<i>Amphipterygium simplicifolium</i>	0.915	0.099	0.197	0.995	0.099	0.117	0	NA	0.249
<i>Ceiba aesculifolia</i>	0.961	0.223	0.494	0.976	0.800	0.683	0.923	0.160	0.287
<i>Cochlospermum vitifolium</i>	0.928	0.687	0.265	0.968	0	0	0.819	0.702	0.464
<i>Jacaratia mexicana</i>	0.952	0.525	0.915	0.969	0	0.871	0.895	0.526	0.955
<i>Plumeria rubra</i>	0.941	0.898	0.807	0.985	0.898	0.753	0.777	NA	0.811
Mean for SW species	0.939	0.486	0.536	0.979	0.359	0.485	0.683	0.463	0.553
Wilcoxon-Mann-Whitney test p-value	0.841	0.539	0.905	0.032	1.000	0.393	0.032	0.064	0.905

reproductive phenophases, and the annual march of climatic variables. This figure depicts a 3D environmental (climatic) space through which phenological behavior proceeded in the study year in a circular fashion, but this space may differ substantially even between contiguous years.

Most species were leafless for some time during the dry season in both localities except for *Forchhammeria pallida*, a species that displayed inverted leaf phenology, producing leaves in the dry season and becoming semi-deciduous in the rains (Figure 2). Thus, this species was excluded from Figure S1. For the remaining species, the timing of leafing start, peak, and end differed between SW and HW species, with each phenological attribute being affected differently by the climatic variables (Table S3). According to the best-supported models, variation in leafing start was best explained by precipitation in the previous month, and to a lesser extent by photoperiod (Table S3). In both localities, leaf out in SW species concentrated in months preceded by a month of little or null precipitation, when photoperiod begins to increase (on average, in April; Figure 3a-d). In turn, leaf out in HW species occurred mostly in June and July, showing more variable water and photoperiod requirements; while in some individuals leaf out started when precipitation of the previous month was null, in others it occurred when the highest precipitation of the year was recorded in the previous month. A similar variation was observed for photoperiod, with leaf out taking place in days with 11 to 13 daylight hours (Figure 3a, b). Intriguingly, in Churumuco HW species required a much lower precipitation to produce new leaves (85 mm: Figure 3a) than in Nizanda, where leaf out in HW species required a precipitation of nearly 300 mm in the previous month to take place (Figure 3b).

In both localities, leafing peak was negatively affected by maximum monthly temperature, and to a lesser extent, positively by photoperiod (Table S3). In some individuals, leafing peak coincided with the hottest month (May), although most trees displayed maximum leafing in months having the longest photoperiod (13 h) and when maximum temperature was not highest (June and July, Figure 3e-h). Notably, individuals of HW species had their leafing peaks one month later than those of SW species (Figure S1c,d). This pattern was clearer in Nizanda, where leafing peak concentrated in May and June for SW species but in June and July for HW species (Figure 3f); conversely, in Churumuco leafing peak for both SW and HW species coincided between May and July (Figure 3e).

Variation in the timing of leafing end was mainly explained by wood density, with additional albeit weaker effects of precipitation in the previous month, and of photoperiod (Table S3; Figure 3i-l). Individuals of SW species shed their foliage earlier than those of HW species, with a 1-mo difference between populations (Figure S1e,f): October-November in Churumuco (early deciduous species; Figure 3i,k) and November-December in Nizanda (Figure 3j,l). Contrastingly, individuals of HW species did not shed their leaves until the very end of the dry season (late deciduous species), also with a 1-mo difference between populations: January-February in Churumuco (Figure 3i), but mid-December to April in some cases in Nizanda (Figure 3j). Individuals of both SW and HW species shed

their foliage in the shortest days of the year, with photoperiods between 11 and 12 h (Figure 3k,l).

Regarding reproductive phenophases, the relationships between their start and peak, the climatic variables examined, and wood density were less clear than those observed for the leafing phenophase (Figure 4). However, it became apparent that the timing of the reproductive activity is far more variable than for leafing, both among species and conspecific individuals (Figure S1, g-n). Although we recorded flowering and fruiting individuals for most species, there were two exceptions: *Handroanthus impetiginosus*, with no reproductive activity recorded in any locality, and *Aoplanesia paniculata*, with flowering only recorded in Churumuco and fruiting only recorded in Nizanda, but with very low intensity (Table S2).

These peculiarities aside, we were able to classify the species into three functional phenological strategies based on the timing of phenophase start. These strategies were always coincident between populations from the two localities: (1) flowering in the rainy season and fruiting at the end of this season or in the early dry season, just after the end of the rains (*Amphipterygium simplicifolium*, *Aoplanesia paniculata*, *Lysiloma divaricatum*, and *Vachellia campechiana*), (2) flowering in the early dry season, and fruiting two or three months later in the same season (*Ceiba aesculifolia*, *Cochlospermum vitifolium*, *Forchhammeria pallida*, and *Jacaratia mexicana*), and (3) flowering in the late dry season, and fruiting in the late rains (*Plumeria rubra*). Overall, in species displaying the first and third functional strategies, vegetative and reproductive phases overlapped (i.e., flowering was recorded on leafy branches). Conversely, species of the second group showed lags in their reproductive phenology relative to the previous vegetative phenophase (i.e., flowering was recorded on leafless branches). The first strategy was the most common among HW species, except for *Amphipterygium simplicifolium*, whereas the second strategy was most frequent among SW species.

As for flowering, no best-supported model included wood density as explanatory variable, indicating that neither flowering start nor its peak differed between the two species groups (Figure S2). Variation in the timing of flowering was clearly related to low precipitation in the previous month and high photoperiod values (Table S3, Figure S2a-d,g-j). In Churumuco, such environmental combination defined the end of the dry season and the early rainy season (May-July), which is the part of the year when flowering peaked, indicating that it is a short-lasting event (Figure S2g,i,k). In Nizanda, both flowering start and peak took place in the driest part of the year (November-March; Figure S2b,j), with a noticeable increase in response to increasing photoperiod (May-June; Figure S2d,h).

In the case of fruiting start and peak, variation was mainly explained by low precipitation and temperatures (Table S3; Figure S3). Fruiting start differed between SW and HW species regarding temperature and rainfall. In Churumuco, SW species began fruit production from June to March, whereas this attribute lagged a couple of months in HW species (August to January; Figure S3a). In Nizanda, fruiting start in individuals of HW species concentrated in the rainy season (July and August; Figure S3b). Conversely, individuals of SW species began fruit production in the dry season exclusively

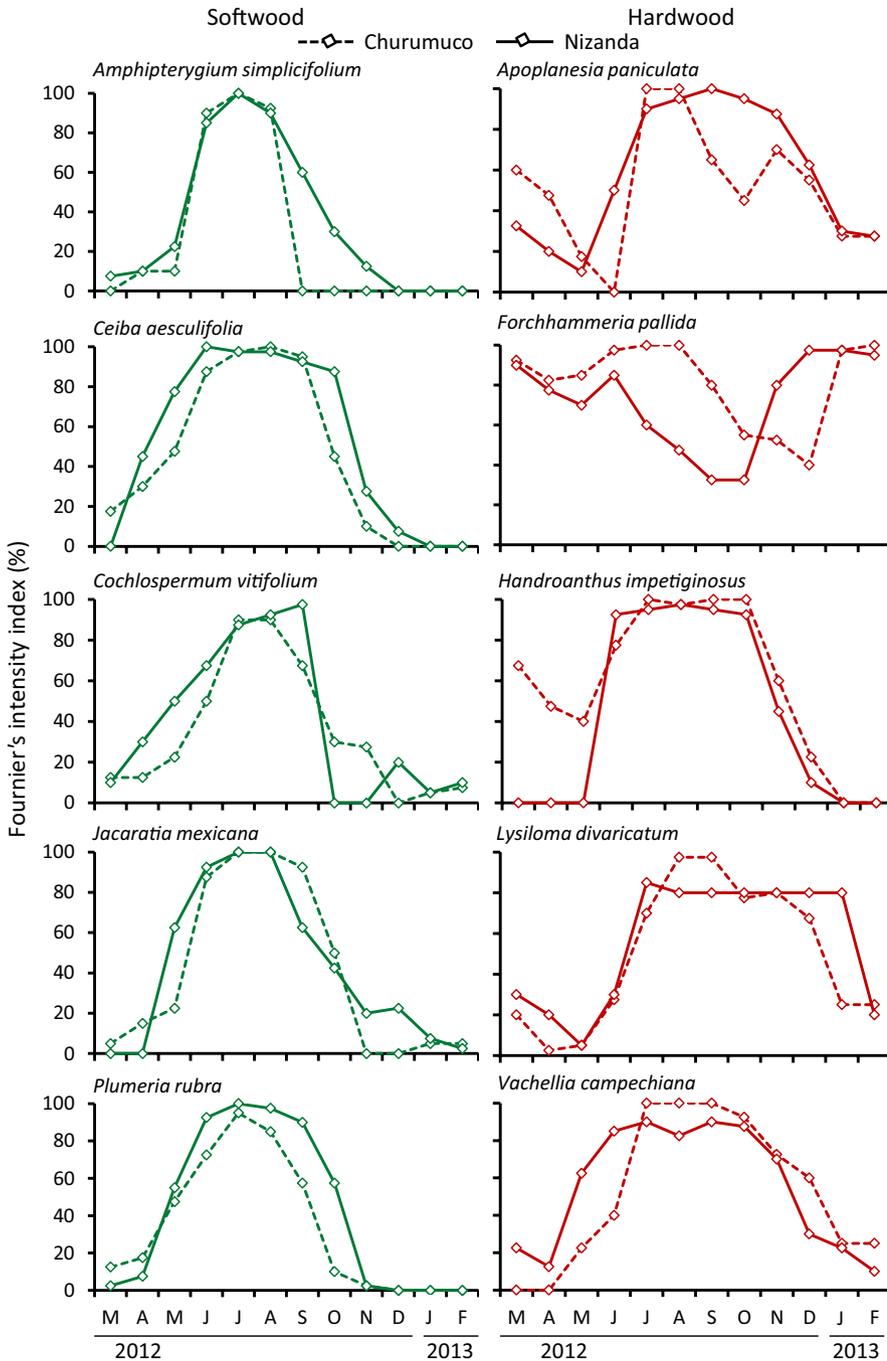


FIGURE 2 Fournier's intensity index for the leafing phenophase (open diamonds) of ten seasonally dry tropical forest tree species from Churumuco (broken lines) and Nizanda (continuous lines), southern Mexico, recorded from March 2012 to February 2013. Species are classified as softwood (left panels, green lines) or hardwood (right panels, red lines)

(December to April; Figure S3b). Regardless of wood density, fruiting peak lasted longer in Churumuco (June to April) than in Nizanda (July to November; Figure S3e-j).

4 | DISCUSSION

Here, we compared the vegetative and reproductive phenology of ten tree species, each represented by two distant populations (> 700 km) experiencing somewhat different climatic regimes. Despite the limited number of species examined, our results support the hypothesis that vegetative and reproductive phenological responses to environmental cues differ between HW and SW species, as they

show higher homogeneity for some phenophase attributes than for others across conspecific populations. Our results also provide evidence for a more integrated vegetative and reproductive phenology in HW than in SW species. Our findings allow us to advance toward a comprehensive evaluation of the relationship between endogenous (wood density) and exogenous (climatic) factors, and their regulatory role of the complex phenological behavior of SDTF trees.

4.1 | Leafing

Between-locality comparisons of the phenological curves for the leafing phenophase showed high, albeit not seamless, overlaps both

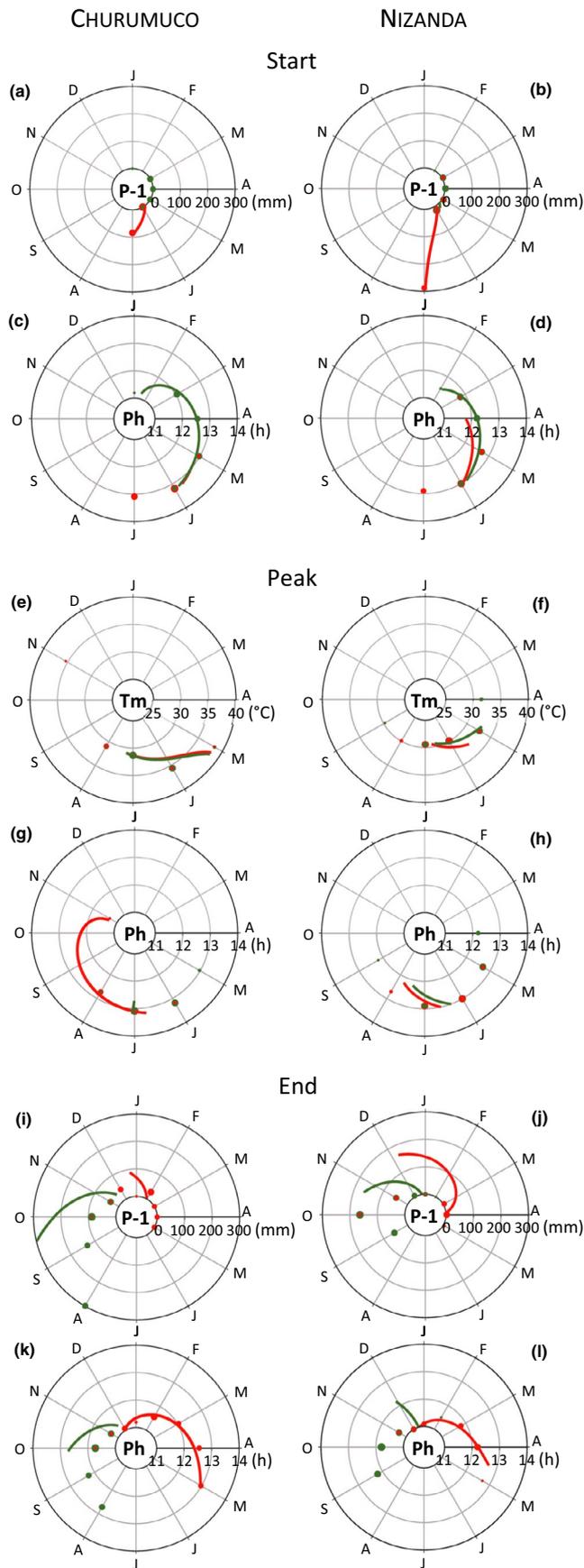


FIGURE 3 Best-supported models of the effects of climatic variables (exogenous factors) and wood density (endogenous factor) on leafing start, peak and end (response variables), to describe the phenological behavior of nine tree species in two seasonally dry tropical forest localities of Mexico, Churumuco (left panels) and Nizanda (right panels). The three best-supported models identified wood density as a factor partly explaining the variation in the leafing phenological response, thus all graphs include two lines (red, hardwood species; green, softwood species). The colored dots represent the data of the phenological trajectories for these two species groups (see Figure S1). The response variable (month of the year when the phenological attribute is recorded) was plotted as a circular variable to express the cyclic nature of the seasons. Leafing start: precipitation in the previous month (P-1; a, b), photoperiod (Ph; c, d). Leafing peak: maximum monthly temperature (Tm; e, f), photoperiod (g, h). Leafing end: precipitation in the previous month (i, j), photoperiod (k, l). For each model, climatic variables are arranged in decreasing order of importance in the model (see Table S3)

for HW and SW species. The similarity between the two curves of each species suggests consistent phenological signatures of the different species across their geographical ranges, in line with the view that phenological strategies are traits fixed over their evolutionary histories (Davies et al., 2013; Davis et al., 2010; Staggemeier et al., 2010). More importantly, however, the overlap between the two curves was always imperfect, with asymmetric discrepancies between the two wood density groups; while synchrony in leaf out was higher for SW species, HW species tended to be more synchronous in leaf fall, in agreement with our hypothesis (Table 2).

Overall, the results of the modeling of climatic and wood density effects on phenological attributes were also confirmatory of our hypothesis. First, the phenological behavior of SW species closely matched our expectations (see Figure 1c). Water storage in these species' wood allowed leaf out initiation in a period of low water availability, implying that leaf out is uncoupled from the onset of the rains, ultimately resulting in synchronous leafing between localities (ca. April). This result agrees with phenological observations from other SDTF regions (Borchert, 1994; Butz et al., 2018; Chapotin et al., 2006a, 2006b; Lima & Rodal, 2010) and suggests that leaf flushing in SW species is cued by an increase in photoperiod for growth initiation, rendering this attribute more predictable than others triggered by precipitation (Rivera et al., 2002; Wright & van Schaik, 1994). Furthermore, populations of SW species showed a clear early deciduous pattern in both localities, in line with their higher cavitation risk (Meinzer et al., 2008; Méndez-Alonzo et al., 2012; de Oliveira et al., 2015). It must be noted, however, that leaf abscission did not fully coincide with the end of the rains. In fact, although we expected an earlier leaf fall for Nizanda populations than for their Churumuco counterparts, given the late end of the rains in Churumuco, we observed exactly the opposite pattern. This result suggests that the sharp precipitation reduction is not the only environmental signal

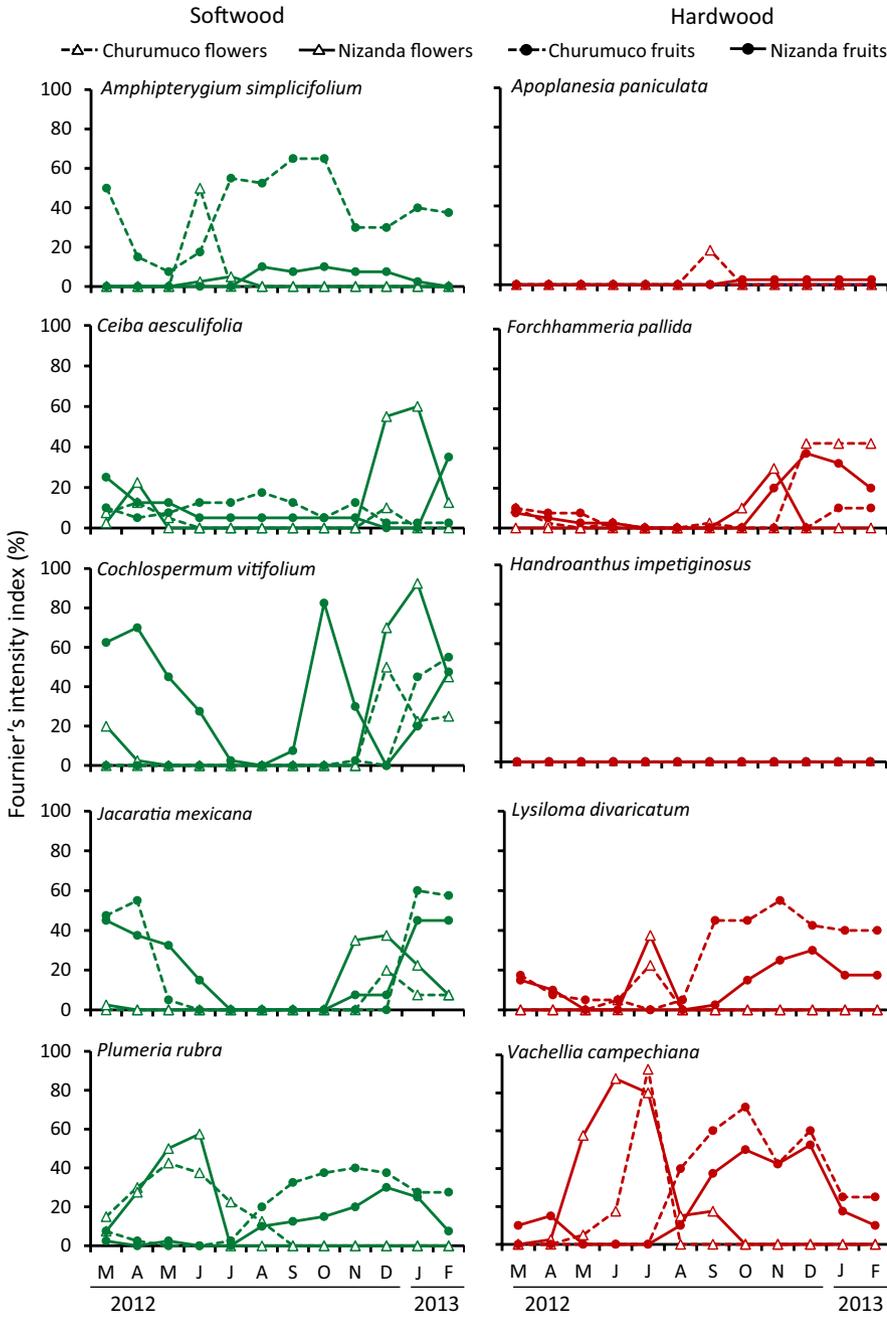


FIGURE 4 Fournier's intensity index for the flowering (open triangles) and fruiting (circles) phenophases of ten seasonally dry tropical forest tree species from Churumuco (broken lines) and Nizanda (continuous lines), southern Mexico, recorded from March 2012 to February 2013. Species are classified as softwood (left panels, green lines) or hardwood (right panels, red lines)

cueing the end of the growth season for these species, as suggested by other studies (e.g., Kushwaha & Singh, 2005; Sánchez et al., 2020; Seghieri et al., 2012), but that other cues are also involved, such as reduced photoperiod or increased temperature and the concomitant higher evapotranspiration.

Unlike the case of SW species, our results do not provide equally strong support to our hypothesis regarding the phenological leaf out behavior of HW species. Based on their limited water storage capacity, we expected leaf out to coincide with the onset of the rains, which would have resulted in trees from Nizanda flushing earlier than those from Churumuco. Although on average Nizanda populations of HW species did start leaf out a little earlier than those from Churumuco, intra- and interspecific variation was very large, blurring this pattern. The fact that leaf out in trees of HW species

was recorded under the widest possible range of total monthly precipitation in these regions (0 to 300 mm) suggests the existence of intermediate characteristics between the SW and HW extremes, possibly with anatomical arrangements that favor hydraulic efficacy and safety at the same time (Alvarado, 2020). For example, there is evidence that stem tissues of HW species are not necessarily devoid of water in the dry season, so that their growth does not depend so strongly on the rainfall pattern as previously thought (Osunkoya et al., 2007; Romero et al., 2020). Moreover, although root morphology in SDTF trees has been little explored, some studies show that the root systems of some HW species give them access to deep or permanent water sources during the dry season, thus modifying their phenological behavior (Hasselquist et al., 2010; Santiago et al., 2017; Valdez-Hernández et al., 2010). In any case, this result concurs

with previous statements that a dichotomic distinction between HW and SW species oversimplifies the enormous variability along the ecological continuum comprising these two functional groups (Méndez-Alonzo et al., 2012; Reich, 2014).

Unlike leaf out initiation, the observed leafing end pattern supports our hypothesis for HW species, as trees of this group from the two populations shed their foliage in April, displaying a synchronous late leaf fall pattern that is uncoupled from the end of the rains. These results agree with other studies (Chaturvedi et al., 2021; Galvão et al., 2021; de Oliveira et al., 2015) and suggest that resistance to xylem cavitation grants these species an extended growth season by retaining their leaves several months after rain cessation (Markesteyn et al., 2011).

The blurry leaf phenology patterns of HW species may be due at least partly to the inclusion of *Forchhammeria pallida* in this group, a species with inverted phenology that flushes the new leaves at the beginning of the dry season and displays foliage exchange during the rainy season, just at the photosynthetic activity peak of most other species. The phenological pattern displayed by this species seems to be induced by declining photoperiod (Chaves & Avalos, 2008) and thus it does not conform to the phenological behavior of the other HW species of study.

4.2 | Flowering and fruiting

SDTF tree species display a wide range of reproductive strategies variously related to the combination of environmental cues and vegetative phenology (Borchert et al., 2004; Lacerda et al., 2018; van Schaik et al., 1993). In fact, both flowering and fruiting are known to be also influenced by many other plant traits, including pollination type, seed dispersal, and germination strategies (CaraDonna & Inouye, 2015; Cortés-Flores et al., 2017; Primack, 1980). The role of such assortment of factors in plant phenological regulation explains why intra- and interspecific variation in the timing of reproductive phenophases was larger than for leafing, which resulted in the failure of the models to reveal differences in flowering initiation between HW and SW species. Interestingly, however, the phenological behavior of some species strongly suggests that the timing of the vegetative phase does have an influence on the timing of flowering and the subsequent fruiting (Rivera & Borchert, 2001; Rivera et al., 2002). This is the case of the SW species *Ceiba aesculifolia*, *Cochlospermum vitifolium*, and *Jacaratia mexicana*, all of which seem to require a sign of the approaching drought, for example a sensible reduction in soil humidity, to make a rather abrupt switch from vegetative growth to flower production (Borchert et al., 2004). These three species flower shortly after shedding their foliage, probably responding to a reduction in photoperiod (Venter & Witkowski, 2019) or to the presence of its pollinators (Lobo et al., 2003). Moreover, some studies have concluded that the temporal separation of leafing and flowering is related to plant tissue rehydration following leaf abscission (Borchert, 1994; Borchert et al., 2004; Rivera & Borchert, 2001).

For HW species, making inferences on the relationship between vegetative and reproductive phases was not straightforward. This may be mainly due to the absence of reproductive activity in *Handroanthus impetiginosus* and to the inverted leaf phenology of *Forchhammeria pallida*. Nonetheless, it is worth noting that *Lysiloma divaricatum* and *Vachellia campechiana* (and to a lesser extent *Apoplansia paniculata*), showed overlapping periods of leaf and flower production during the rainy season. Again, the phenological records for these HW species hints at the possibility that flowering initiation is mainly determined by rainfall and the resulting increase in soil water availability (Lima et al., 2021; de Oliveira et al., 2015). While suggestive, these results are inconclusive given the limited number of species used in the analysis. Therefore, confirmation of the phenological patterns discussed here will require expanding the taxonomic coverage in future studies adopting this approach.

4.3 | A reflection on the analysis of plant phenology

Phenology is frequently examined through the description of discrete events (e.g., date of flowering initiation, or time of the year when fruiting peaks). Unfortunately, this approach fails to recognize phenology as a continuous, integrated process (Inouye et al., 2019). To advance toward a comprehensive understanding of phenological behavior, here we proposed the Phenological Overlap Index (POI). This index allows comparing two phenological curves between individuals, species and even communities; this has a large potential for the analysis of phenological data, as POI acknowledges the continuous nature of plants' phenological events.

The roles of endogenous and exogenous factors in modulating the shape of a given phenological curve are not necessarily the same for the different key moments it includes. Inferences on the role of environmental factors on SDTF tree phenology depend upon the phenological attribute being examined (i.e., start, peak, or end), as each attribute has a unique ecological significance that may be difficult to interpret in the light of the entire phenological curve. Our results emphasize the complexity of phenological studies and the relevance of using proper analytical procedures to answer questions that will broaden our understanding of plant phenological behavior (Brown et al., 2015; Inouye et al., 2019; Moussus et al., 2010; Staggemeier et al., 2019).

5 | CONCLUSIONS

Based on the comparison of phenological patterns observed in SDTF tree species classified in two functional groups (softwood and hardwood) and with populations experiencing climatic regimes that differ in some factors (e.g., rainfall) but not in others (e.g., photoperiod), we conclude that the role of environmental variables in cueing their growth and reproduction cycles is interrelated with

their wood density, a key endogenous factor linked to plant hydraulics in these water-limited ecosystems. The interplay of environmental factors and wood density allows us to anticipate a large variety of phenological responses among tropical trees to climate change related to their ability to cope with drought mediated by wood density.

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AUTHORS' CONTRIBUTIONS

ALLN contributed to the research design, data collection, data analysis, and writing; EJG contributed to research design, data analysis, modeling, and writing; JCF contributed to writing; GIB contributed to funding acquisition and data collection; AMR contributed to data collection; JAM contributed to research design, funding acquisition, and writing. All the authors contributed equally to the interpretation of results, commented on earlier drafts, and agreed with the final manuscript.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Dryad Digital Repository at <https://doi.org/10.5061/dryad.bcc2fqzdp> (Luna-Nieves et al., 2022).

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