



Xylogenes is uncoupled from forest productivity

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Abstract

Key Message *Pinus leiophylla* production of radially enlarging tracheids is bimodal with peaks in June and October. The production of thickening tracheids and NDVI were coupled.

Abstract In drought-prone areas, xylem production and forest productivity are assumed to depend on the amount and timing of precipitation. However, few studies have addressed if xylogenes and proxies of forest productivity as the Normalized Difference Vegetation Index (NDVI) are coupled and respond to moisture availability. In these areas, drought seasonality and timing could lead to bimodal growth patterns. We tested if xylogenes was bimodal and coupled with climate and NDVI at the intra-annual scale in *Pinus leiophylla* from NW Mexico. We found a bimodal growth pattern with a major peak of production of radially enlarging tracheids in June and a secondary peak in October. The June peak preceded a coupled rise of the amount of cell-wall-thickening tracheids and the NDVI which peaked from September to October. The timing in the production of thickening and mature tracheids matched the NDVI pattern. This coupling suggests active carbon uptake after wet summer conditions and carbohydrate usage in tracheid maturation and cell-wall thickening. The production of radially enlarging tracheids, which determines the final ring width, was enhanced by warmer minimum temperatures whenever precipitation was abundant. In contrast, more mature latewood tracheids were produced in response to cool-wet summer conditions. The bimodal behavior of *P. leiophylla* radially enlarging tracheids illustrates xylem plasticity in response to seasonal drought. Xylogenes and NDVI data were uncoupled. Therefore, the assessment of forest responses to climate warming in similar drought-prone areas must explicitly consider shifts in productivity and the timing of wood production.

Keywords Drought · NDVI · *Pinus leiophylla* · Radial growth · Wood formation

Introduction

It is widely demonstrated that hydroclimatic variations influence forest productivity and tree growth in areas subjected to seasonal drought (Linares et al. 2009), but also in temperate forests under mesic conditions (Helcoski et al. 2019). Forest productivity and tree growth respond to particular time scales of drought and year-to-year hydroclimate

variability (Vicente-Serrano et al. 2013). However, we do not know how coupled are these responses at intra-annual scales despite this knowledge is needed to disentangle how productivity and wood formation will respond to warmer and drier climate conditions. For instance, in some drought-prone areas, it has been suggested that this coupling has strengthened and preceded growth decline, canopy dieback, and increased mortality rates (Allen et al. 2015; Camarero et al. 2015b, 2016).

Northern Mexico illustrates one of those drought-prone, vulnerable areas, where a great diversity of climatic, soil, and topographic conditions determine how diverse pine forests (Perry 1991; Sánchez-González 2008) respond to hydroclimate variability, drought stress, and atmospheric patterns (Seager et al. 2009; Pompa-García et al. 2015; Stahle et al. 2016). Dendroecological approaches have allowed quantifying how coupled are long-term changes in tree radial growth of pine species with respect to climate, specifically

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precipitation, evaporation, and drought (Villanueva-Díaz et al. 2007; González-Cásares et al. 2017; Pacheco et al. 2019).

However, most of those long-term tree-ring studies were based on annually resolved data, which limits our ability to understand intra-annual variability in wood formation. The tree ring can be divided into earlywood and latewood to refine the climatic signal and improve the study resolution (Björklund et al. 2017). Moreover, it is assumed that most of the ring is formed around the same month which biases our analyses on growth responses to climate (Vaganov et al. 2006). However, it is well known that the seasonal timing of climate events and the growing season have changed through time affecting forest productivity and tree growth (Touchan et al. 2012; Kulmala et al. 2017; Helcoski et al. 2019). For example, a longer season of xylem development (xylogenesis) in conifer forests across the northern Hemisphere has been linked to climate warming and implies large changes in forest productivity, since wood is a long-term reservoir of carbon fixed by trees (Cuny et al. 2015).

The detailed phenological analyses of tree-ring formation offer a window to elucidate how environment conditions drive xylogenesis processes (Camarero et al. 1998; Rossi et al. 2011, 2016). Xylogenesis results from metabolic processes as a response to specific environmental signals which determine water and carbon fluxes driving cambial activity and xylem formation (Vaganov et al. 2006; Cuny and Rathgeber 2016). Thus, xylogenesis is a key ecological indicator that has enabled understanding the impact of environmental changes on forests at fine temporal resolution, usually biweekly-to-monthly scales (Fonti et al. 2010; Popkova et al. 2018).

Deciphering xylem dynamics is crucial to understand how climate affects tree growth, phenology, and forest productivity (Michelot et al. 2012; Delpierre et al. 2019). First, growth duration influences stem wood production (Lempereur et al. 2015). Second, the rates of xylem cell production determine 75% of the variability of the final ring width, whilst the remaining 25% is attributed to duration of the growing season (Cuny et al. 2015). However, fixed carbon may take ca. 1 month until it is converted into cell walls during the phase of tracheid maturation, which is critical for other wood properties such as density (Björklund et al. 2017). Thus, it is highly relevant to focus on the timing and rates of cell production and how they depend on climate and affect forest productivity.

Here, we characterize the xylogenesis of *Pinus leiophylla*, a species with high dendrochronological potential across the dry NW Mexico (Sheppard et al. 2008). This species has demonstrated to be particularly sensitive to hydroclimatic variations, because its growth depends on the previous winter precipitation (González-Cásares et al. 2017). The presence of intra-annual density fluctuations in its wood

also confirms that it shows a high intra-annual variability in xylem dynamics reflected by wood anatomy (Acosta-Hernández et al. 2019; Vieira et al. 2014). These factors suggest that this species could present a bimodal growth pattern as that documented in other pine species from drought-prone areas as the Mediterranean basin (Camarero et al. 2010), but also observed in other conifers as firs (Linares et al. 2009; Rathgeber et al. 2011) and in hardwood species (Gutiérrez et al. 2011).

Since xylogenesis depends on species, site climate conditions, and other factors as tree traits (Vieira et al. 2015), its quantification is a first step toward assessing tree phenology plasticity in response to hydroclimate. In boreal and temperate forests, remote sensing has demonstrated its usefulness to assess forest phenology as related to growth or productivity (Wu et al. 2014; Piao et al. 2015; Antonucci et al. 2017). Linking xylogenesis with time-series of vegetation indices as the Normalized Difference Vegetation Index (NDVI) is an effective way to investigate changes in tree growth and forest productivity and how they relate to climate (Correa-Díaz et al. 2019). This assessment also allows elucidating the interdependence of foliage production and xylogenesis. The NDVI is a proxy of canopy cover, tree phenology, and forest productivity (Myneni et al. 1995), albeit it has been scarcely associated with tree-ring data at the intra-annual scale (but see Lopatin et al. 2006; Correa-Díaz et al. 2019).

We hypothesize that *P. leiophylla* shows a bimodal growth pattern in response to the variable hydroclimate over its distribution area, i.e., by showing higher growth rates during the favorable seasons with wet and cool conditions. Such bimodality can be inferred from xylogenesis and linked with NDVI data. In this pioneering study in Mexico, we characterize how wood formation occurs in a pine subjected to seasonal drought and how xylogenesis is related to NDVI by quantifying the number of cambium cells and tracheids in different phases of development.

Materials and methods

Study site and species studied

The study area is located in El Salto (Pueblo Nuevo, Durango, NW Mexico), in the Sierra Madre Occidental (Fig. 1), at 23.4° N–105.2° W and an elevation of 2566–2598 m a.s.l. This area is situated in a volcanic plateau, and it is characterized by rugged topography (González-Elizondo et al. 2012). The main vegetation is represented by mixed pine-oak forests (González-Elizondo et al. 2007). Several pine species (*Pinus teocote*, *Pinus cooperi*, *Pinus durangensis*, and *Pinus strobiformis*) are present in addition to *P. leiophylla* (González-Elizondo et al. 2007).

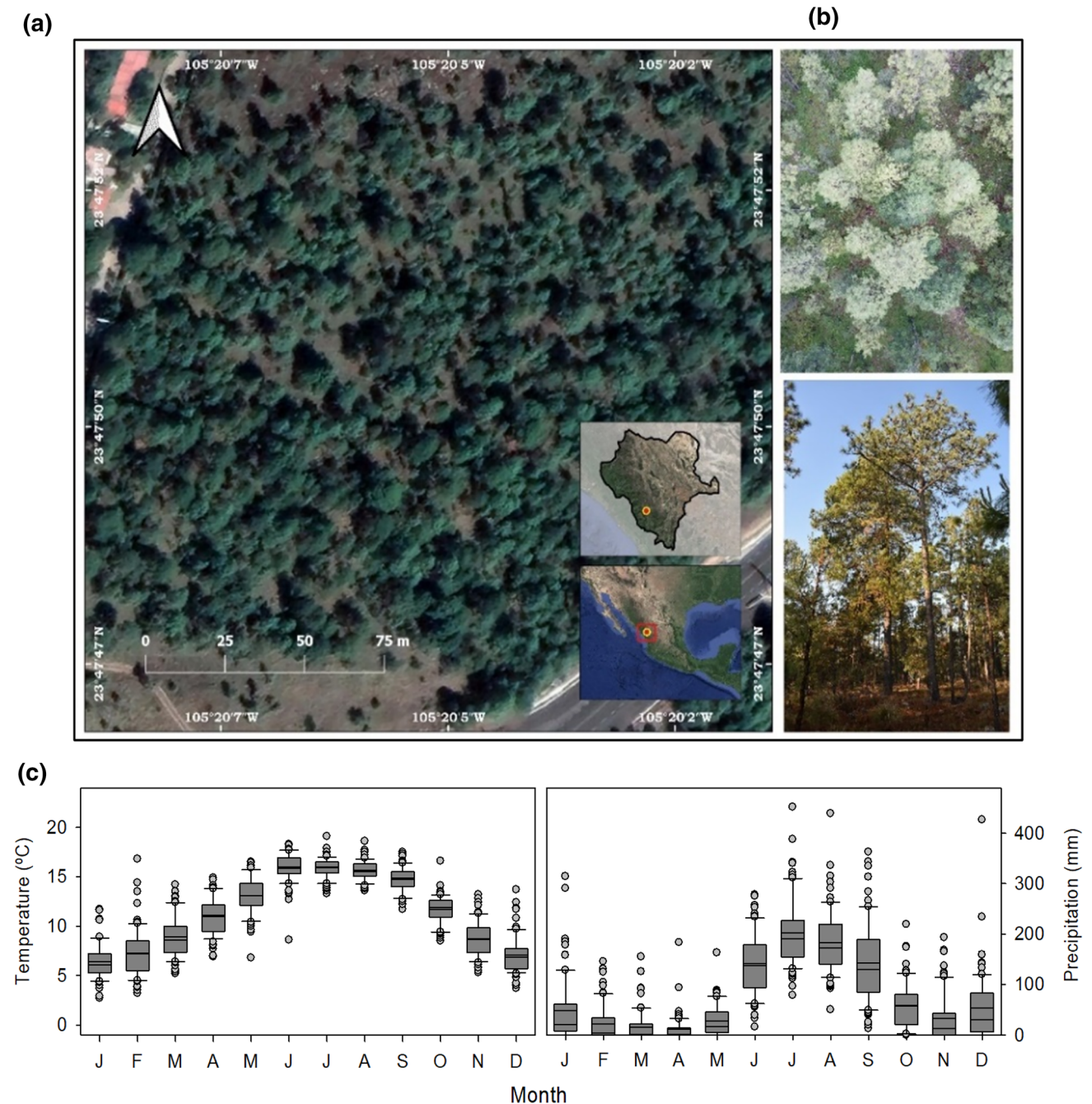


Fig. 1 Location of the study site (a), photograph of a sampled site (b), and monthly, climate conditions (c) obtained from the “El Salto” station (period 1946–2018)

In the study mixed stands, *P. leiophylla* accounted for more than 50% of basal area.

The climate is temperate sub-humid climate (Fig. 1), with marked seasonality characterized by humid and cold summers derived from the influence of the North American summer Monsoon (June–September) and winters with less intense rains during the cold season (November–February) (Adams and Comrie 1997). It presents an annual mean

temperature of 11.5 °C and mean annual precipitation of 1,200 mm (CNA 2018).

The soils correspond to the luvisol type, characterized by higher clay content in the subsoil (INEGI 2001). This is an area of great ecological, economic, and environmental importance, given the high diversity of plant species and the multiple services (timber, lumber, cattle raising, etc.) provided by forests to local people (Bickford et al. 2011).

The study species is *Pinus leiophylla* Schl. & Cham., which has been previously studied in other dendroclimatic studies (Acosta-Hernández et al. 2019). This tree species is distributed from the southern USA to southwest Mexico, mainly in mesic sites of the Sierra Madre Occidental (Perry 1991).

Xylogenesis

Sampling was done biweekly from April 2018 to April 2019. According to data from the “El Salto” station, climate conditions were normal during that period with a mean temperature of 11.7 °C and precipitation of 1258 mm. Microcores (15 mm long, 2 mm diameter) were taken using a Trephor microborer (Rossi et al. 2006) following a spiral trajectory on the stem at a height of 1.0–1.5 m from six trees. We selected dominant, apparently healthy well-shaped trees with symmetric crowns, and avoided scars and damaged stems and others visible injuries. Selected trees had a diameter (mean \pm 1SE) at 1.3 m of 28.0 ± 3.4 cm, a total height of 11.0 ± 0.6 cm and age (estimated by taking basal cores) of 56 ± 4 years.

In the laboratory, each microcore was vertically oriented following the fiber orientation before cutting. Then each sample was cut in 2–4 transverse sections with a 15–25 μ m thicknesses using a sliding microtome (Anglia Scientific AS 200, Cambridge, UK). The sections were stained with 0.05% Cresyl violet acetate which reacts with lignin (Antonova and Shebeko 1981), and observed under bright field and

polarized light after coloration within 10–30 min of staining at 100–500 magnification (Rossi et al. 2006). According to developmental stage, cells stained a different color and presented different shapes. Images were photographed with a digital camera (JVC 3.3 CCD GC-X3E; JVC, Yokohama, Japan) to distinguish earlywood and latewood tracheids following (Denne 1989). According to this author, latewood tracheids were considered those whose single cell-wall thickness multiplied by four was greater or equal to their lumen widths.

For each sample, the following cells were counted along five radial files: the number of cells in the cambial zone, radially enlarging tracheids, cell-wall-thickening tracheids, and the number of mature tracheids (Antonova and Stasova 1993). Cambium cells have similar and small radial diameters with thin cell walls. The first cells with evident radial diameter increments, but still containing a protoplast enclosed by a thin primary wall, were regarded as the first enlarging tracheids (Fig. 2a). The end of radial-cell expansion and the onset of secondary cell-wall formation corresponded to the appearance of pit borders and cell corner rounding (Fig. 2b). The secondary walls glistened when observed under polarized light. Tracheid lignification corresponded to a color change from violet to blue (Fig. 2c). Finally, tracheid maturation ended when traces of cytoplasm were not observed within the lumen. Mature cells showed completely blue cell walls.

The numbers of cell in five radial files per tree were averaged to assess the onset, the period of maximum production

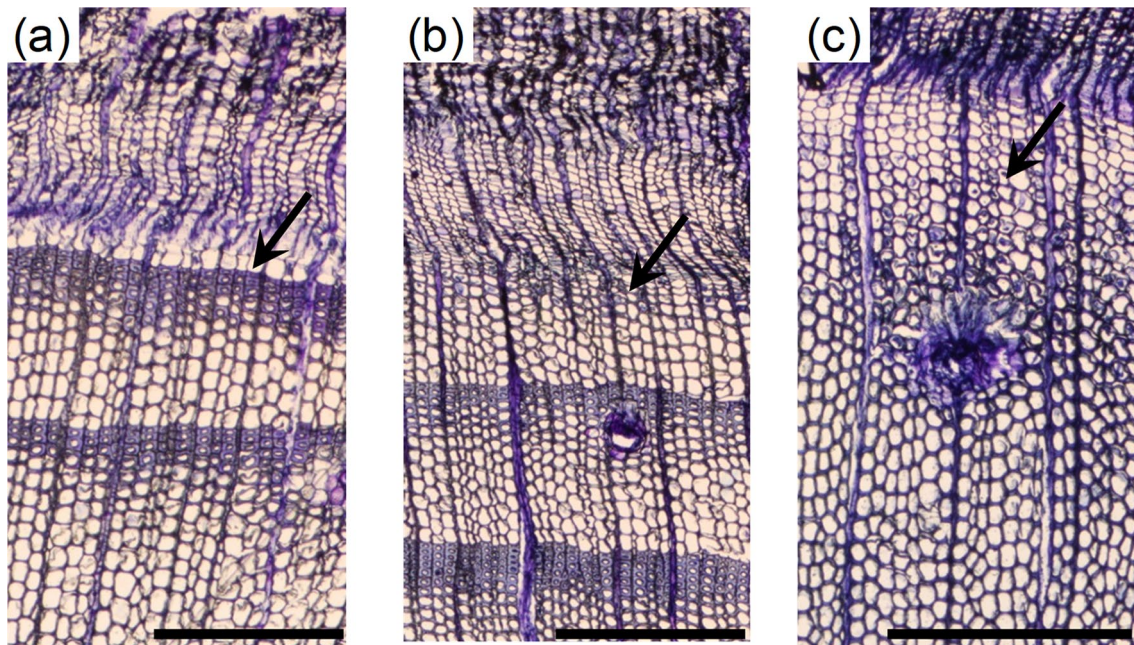


Fig. 2 Images showing the major phases (arrows) of xylogenesis in *Pinus leiophylla* during 2018 (a) radial enlargement of tracheids (early May), (b) thickening (mid-July), and (c) maturation (early September). The scale bars measure 0.1 mm

of mature cells and the end of xylem formation. The onset of xylem formation was regarded as the date when at least 50% of trees showed more than one row of cells in the cell-enlargement phase (Camarero et al. 2010). The ending of xylogenesis was considered the date when 50% of trees lacked tracheids corresponding to the cell-wall-thickening phase. We calculated the rate of production of developing tracheids (sum of enlarging and thickening tracheids) and that of mature tracheids (sum of mature earlywood and latewood tracheids) by subtracting successive values of summed tracheids and dividing them by the elapsed time between samplings (Camarero et al. 1998).

Quantifying NDVI variability

The NDVI for each 10-m pixel from 13QDG scene (3×3 pixels) was extracted from satellite images of Sentinel-2A mission MultiSpectral Instrument, which measures the reflected solar spectral radiances in 13 spectral bands ranging from the visible to the shortwave infrared bands with 5-day revisit time (Drusch et al. 2012). In this site, *P. leio-phylla* is dominant and forms mixed stands with *P. teocote*. We retrieved 24 biweekly images of the study area from March 15 2018 to May 15 2019 via Google Earth Engine (Gorelick et al. 2017). We neglected those images covered by clouds which corresponded to 20% of all images. The NDVI is the ratio between red (RED) and near-infrared (NIR) light reflected by a plant canopy (Myneni et al. 1995), and it was calculated as $NDVI = (NIR - RED) / (NIR + RED)$. Images were processed using QGIS software ver. 3.12.0 (QGIS 2020) and the “levelplot” of the R statistical software (R Core Team 2018).

Statistical analyses

Since variables followed normal distributions, we calculated Pearson correlations (r) between climate variables (mean maximum and minimum temperatures, and precipitation), NDVI values and the following xylogenesis variables: numbers of enlarging and thickening tracheids, and rates of production of total number of tracheids and mature tracheids. Prior to calculating correlations, the average number of cells in each of these phases was standardized with respect with the total number of tracheids formed in the previous (2017) ring to reduce the effect of the relative position of sampling on the stem (Rossi et al. 2003). To accomplish a similar temporal scale, all compared values were converted to biweekly values and climate data were converted into mean temperatures or total precipitation. These climate variables were averaged or summed over the 14 days prior to each sampling date. Analyses were carried out with the package caviar of the R statistical software (Rathgeber et al. 2018).

Results

Xylogenesis

The numbers of cambial cells reached maximum values in March–April, but showed less variations through time than radially enlarging cells which peaked during June (DOY, days of year 160–174), then decreased slowly until September and increased again showing a second peak in early October (DOY 286) (Fig. 3). The number of tracheids in the wall-thickening phase reached maximum values from September to October (DOY 258–263). The earlywood and latewood mature tracheids started rising from July to September (DOY 203–272) and from October to November (DOY 286–314), respectively.

The onset of xylem formation occurred from late March to early April (DOY 80–106). The cell-wall-thickening phase finished in December, representing the end of xylogenesis (DOY 342–256). The rate of production of enlarging plus thickening tracheids showed two peaks, the first ($0.38 \text{ cells d}^{-1}$) between late April and early May (DOY 118 to 131), and the second ($0.40 \text{ cells d}^{-1}$) between late August and late September (DOY 244 to 272) (Fig. S1, Supporting Information). The first peak reflected the increase in production of radially enlarging tracheids, whereas the second peak corresponded to the entrance of cells in the enlargement phase and a longer residence in the lignification phase. The rate of production of mature tracheids reached maximum values ($0.41 \text{ cells d}^{-1}$) in September–early October (DOY 272 to 286) (Fig. S1).

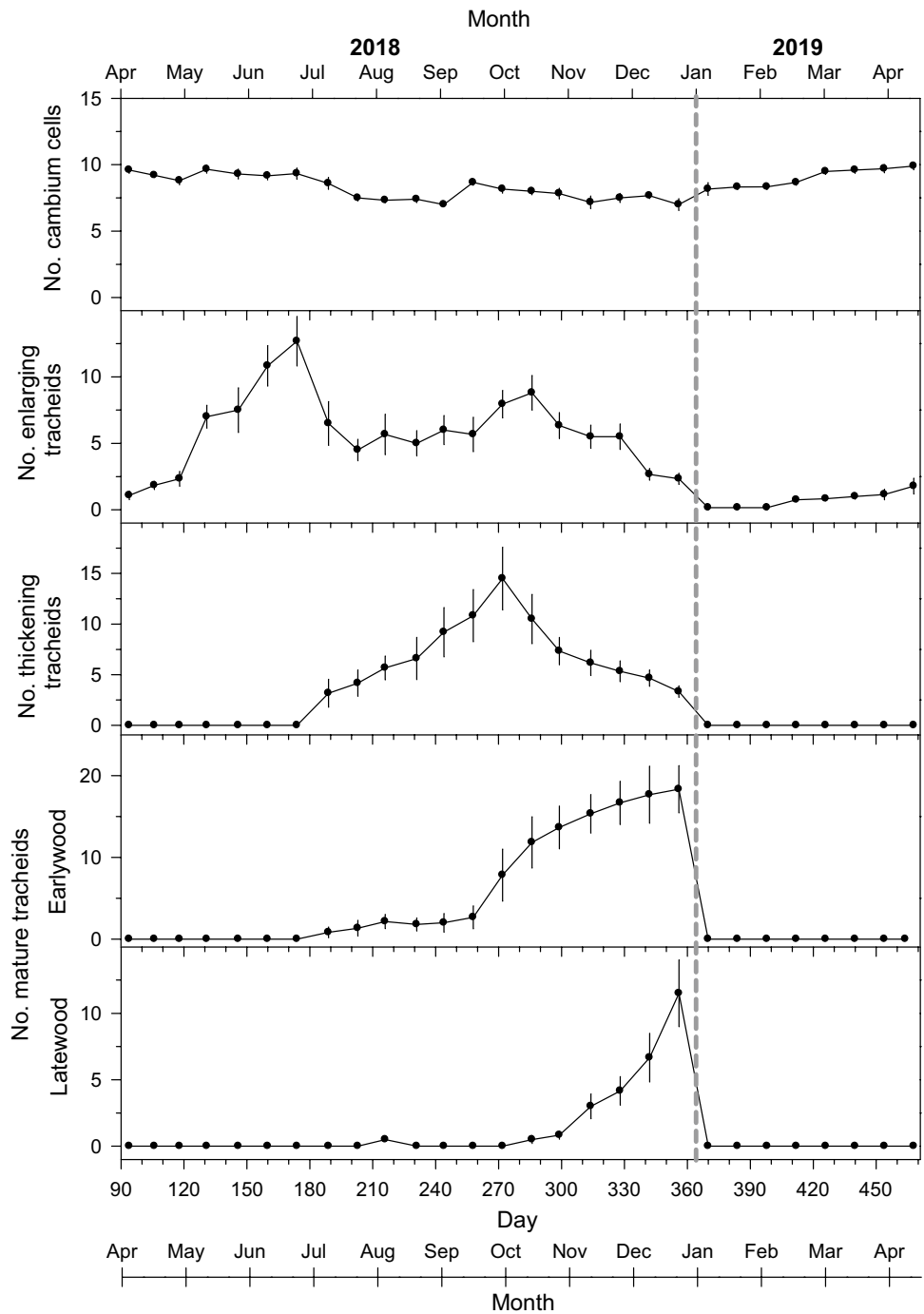
NDVI and xylogenesis

The obtained NVDI values ranged from 0.37 to 0.59 with minimum values in late winter–spring (February–May) and maximum values in autumn (September–October). The June peak of radially enlarging tracheids (Fig. 3) occurred about 1 month before than the most rapid rise of NDVI in July preceding the plateau of NDVI maximum values from August to October (Fig. 4). The timing of NDVI showed a similar pattern, albeit slightly lagged, with the temperature and precipitation patterns at the site study which reached maximum values from June to September and minimum values from December to May, respectively (Fig. 4).

Climate, NDVI, and xylogenesis

The number of cambial cells was positively associated with the biweekly means of maximum temperatures, but negatively associated with NDVI (Table 1). The amount of radially enlarging tracheids was also positively correlated

Fig. 3 Xylogenesis phases in *P. leiophylla* according to the production of cambial cells and different types of tracheids (radially enlarging, wall thickening, and mature tracheids) Values are means \pm 1SE. The dashed line indicates the end of the year 2018



to minimum temperatures (Table 1). Thickening tracheids were coupled with NDVI. The amounts of earlywood and latewood tracheids were negatively associated with both maximum and minimum temperatures, but NDVI and the number of earlywood tracheids were positively correlated. This explains why the rate of production of mature tracheids was positively associated with NDVI values ($r = 0.59$, $p = 0.01$). The rate of production of enlarging plus thickening tracheids was positively related to

maximum temperatures ($r = 0.52$, $p = 0.03$). The rate of production of mature latewood tracheids was negatively related to maximum temperatures ($r = -0.58$, $p = 0.01$), but positively related to precipitation ($r = 0.47$, $p = 0.04$). Correlations based on other periods (7- and 10-day-long periods prior to each sampling date) for calculating correlations between xylogenesis data and climate or NDVI averages and totals were lower than those obtained with 14-day periods (*results not presented*).

Fig. 4 Monthly climate variables (mean temperature and total precipitation) and NDVI during the period when *P. leiophylla* xylogenesis was assessed

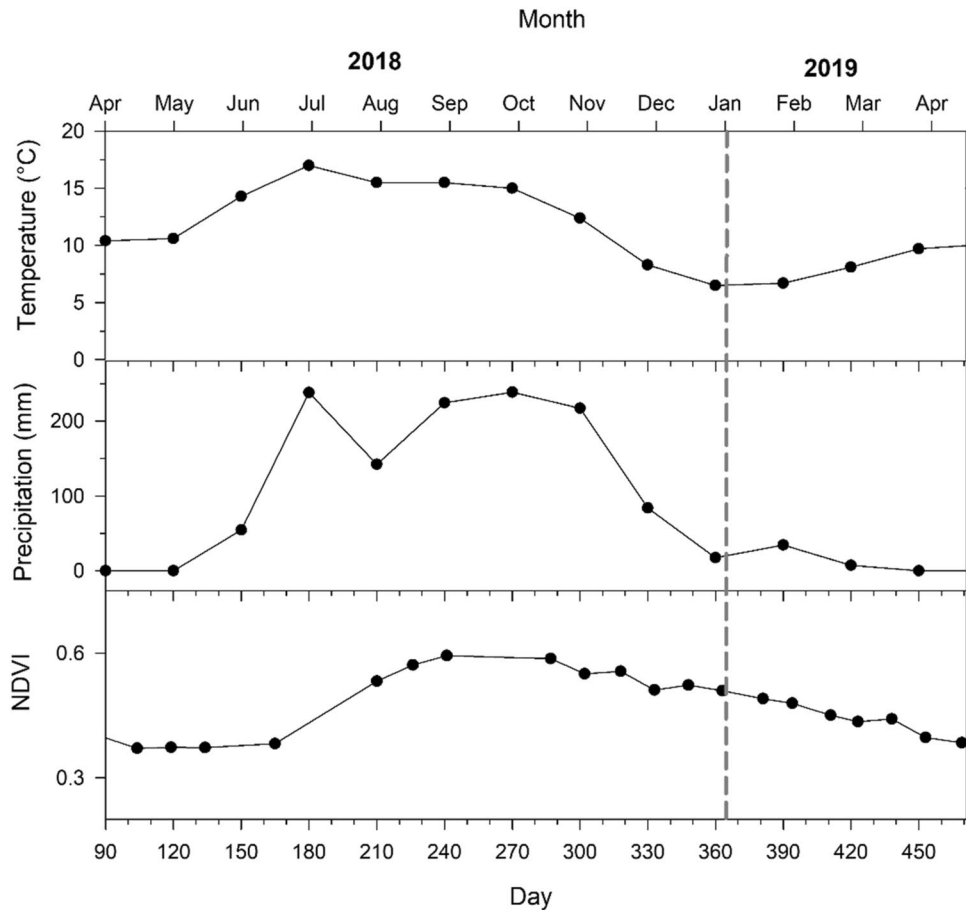


Table 1 Correlation values calculated by relating the number of cambium cells and tracheids in different development phases, biweekly climate (mean minimum and maximum temperatures, accumulated precipitation) and NDVI data

Cell type	Maximum temperatures	Minimum temperatures	Precipitation	NDVI
Cambium cells	0.55 (0.014)	0.44 (0.063)	0.13 (0.5908)	– 0.51 (0.0247)
Radially enlarging tracheids	0.51 (0.026)	0.63 (0.004)	0.25 (0.2926)	–0.09 (0.7133)
Thickening tracheids	–0.39 (0.0945)	0.30 (0.2110)	0.27 (0.2725)	0.89 (0.0001)
Earlywood mature tracheids	– 0.79 (0.0001)	– 0.53 (0.0183)	0.08 (0.7337)	0.57 (0.0091)
Latewood mature tracheids	– 0.73 (0.0004)	–0.70 (0.0008)	–0.02 (0.9233)	0.30 (0.2167)

The significance levels (p) are given between parentheses. Correlation values with $p < 0.05$ are shown in bold

Discussion

This study provided new insights on wood formation in a pine species from seasonally dry biomes. Our results show that the *P. leiophylla* xylogenesis was bimodal regarding radially enlargement tracheids, with peaks in spring–summer and autumn, which is consistent with other studies in similar drought-prone areas showing a similar growth plasticity (De Luis et al. 2007, 2011; Camarero et al. 2010; Touchan et al. 2012; Rossi et al. 2016; Ziaco et al. 2018). We further discuss the tight coupling found between the

amount of wall-thickening tracheids and NDVI, which both peaked in September–October.

These findings agree with our hypothesis, but more sites and longer monitoring periods should be considered to further support these statements. The bimodal pattern observed in radially enlarging tracheids is very important since these cells determine the growth rate and the final stemwood production (Vaganov et al. 2006). These tracheids were mainly formed in seasons such as spring (June) and autumn (September–October) with wet-mild climate conditions, which is partially unexpected for NW Mexico where the summer is relatively wet due to the influence of

the monsoon (Adams and Comrie 1997). Therefore, there is a disagreement between the bimodal growth pattern and the seasonal climate regime, particularly precipitation (Figs. 3 and 4) which explains why we found most significant correlations between xylogenesis data and temperature. In *Quercus ilex*, Campelo et al. (2018) found a bimodal pattern that follows the precipitation pattern in Mediterranean areas with peaks in spring and autumn. Interestingly, wet/dry conditions during the early or late growing seasons can modulate bimodality, since a wet spring enhances the corresponding early season (spring) growth rates and a wet summer also enhances the late-season (summer–autumn) growth rates, albeit in a lower degree (Ziaco et al. 2018). Cambial plasticity is common among pine species growing in drought-prone regions where bimodal growth patterns, characterized by a spring peak in tracheid production and a summer–autumn recovery, are driven by seasonal variation in soil water availability (Camarero et al. 2010; Vieira et al. 2015). The questions on how widespread bimodality is and what are the main climatic and ecophysiological drivers of bimodal growth remain still open. Additional environmental variables (soil water content, evapotranspiration rates, etc.) should be measured to answer these questions.

Our results on *P. leiophylla* agree with similar reports in conifers from cold biomes across the northern Hemisphere, showing that xylogenesis is active from late spring to early autumn (Rossi et al. 2016; Antonucci et al. 2017). The fact that cell production started before the rainy season indicates that the radial enlargement of the first formed tracheids was probably guaranteed by the water stored in the soil. A similar dependence of spring growth on prior-winter precipitation and soil water reserves has been observed in Mediterranean pine species as *Pinus halepensis* (Pasho et al. 2012). Thus, the rise in temperatures between May and June, whenever precipitation is not too low, seems to have triggered the rise in the production of enlarging cells (Figs. 3 and 4), which need enough turgor to expand and depend on soil water availability (Cuny and Rathgeber 2016). The radially enlarging tracheids reached two peaks of production, being the maximum during June when the highest photosynthetic activity occurs in response to longer and sunny days (Rossi et al. 2008). The second peak happened in October, suggesting that radial growth during the late growing season is very dependent on the precipitation associated with the summer Monsoon (Pompa-García and Antonio-Némiga 2015). However, we found no significant correlation between xylogenesis data and precipitation, excepting in the case of mature latewood tracheids, which suggests that either the other xylogenesis phases are associated with climate factors acting at longer temporal scales (months to seasons) or that the high year-to-year variability in NW Mexico precipitation (Seager et al. 2009) precludes finding this association with only 1 year of xylogenesis data. The link between late

growing-season precipitation and latewood production confirms the value of latewood width as rainfall proxy, and can be explained by an enhanced photosynthesis and use of photoassimilates to build new tracheids and lignify their walls (Griffin et al. 2013). It should be stated that the formation of earlywood depends on prior-year carbohydrates, whereas the formation of latewood depends on carbohydrates synthesized during the current growing season (Kagawa et al. 2006).

The period of seasonal wood formation in our study seems to be affected by temperature changes during spring and summer if precipitation is abundant. In a similar setting, Ziaco et al. (2018) found that the onset and ending of wood formation were driven by moisture constraints, but acknowledged that the main dynamics of tree-ring formation during spring are still controlled by temperature as in mesic temperate forests (Gričar et al. 2014). In addition, in boreal Scots pine (*Pinus sylvestris*) forests, radial growth was also very dependent on early season temperatures which controlled the soil water availability in spring and the start of the growing season and cambial activity (Henttonen et al. 2014). Therefore, even in areas subjected to seasonal drought air temperature is crucial to determinate the rate of tracheid production. Other factors not considered here may also explain the plasticity in xylogenesis such as tree-to-tree competition, tree vigor and age, genetics, or hydroclimatic variations at local scales (Michelot et al. 2012; Puchałka et al. 2017). However, they do not seem to be potentially relevant here, since we selected trees of similar vigor, size, and age, living in a relatively open stand. Including other climatic variables such as soil temperature and moisture and considering radiation and photoperiod (Rossi et al. 2016) could also contribute to better explain xylogenesis in this study, but, regrettably, we did not have access to those data.

The inclusion of NDVI as proxy of productivity and tree phenology confirms that the greenness and senescence of canopies were not coupled with the timing of wood formation, since NDVI depends more on primary growth, i.e., shoot and leaf production. Photosynthesis provides the carbon sources for radial growth and wood formation (Kulmala et al. 2017). Positive relationships were found between NDVI variability and the production of cell-wall-thickening and mature earlywood tracheids, which incur a high cost in carbon use (Cuny et al. 2015). The autumn peaks in production of wall-thickening tracheids and NDVI reflect active source and sink carbon activities, suggesting coupling between high photosynthesis rates and tracheid maturation and wall lignification. During this period, drought stress is probably reduced by the summer Monsoon rainfall. These ideas should be tested with ecophysiological measures of gas and water exchange. This result is also in line with the relationship between the duration of xylogenesis and high NDVI values reported by Antonucci et al. (2017). In this

sense, warm temperatures and high precipitation play an essential role as drivers of wood production in *P. leiophylla*. Our results highlight the presence of a link between canopy phenology, NDVI, and xylem growth which should be confirmed with more fine-resolution data on the timing of bud, needle, and xylem growth. However, studies comparing bud phenology and xylogenesis data to NDVI data at intra- and inter-annual scales are still scarce (but see Antonucci et al. 2015; Camarero et al. 2015a; Khare et al. 2019). Another limitation of our study is related to the NDVI spatial scale. Whereas xylem data are related to single trees, NDVI is obtained at fine-to-coarse scales (10 m in this study), representing the canopy phenology and greenness of several trees or stands, and including reflectance from soil, shrubs, leaf litter, etc. (Antonucci et al. 2017). These uncertainties could be solved by obtaining remote-sensing data for individual trees.

Ziaco et al. (2018) found in *Pinus ponderosa* that wet winter–spring conditions can make xylogenesis starting two months earlier than years with very dry spring conditions and abundant, monsoonal summer precipitation. These favorable conditions prior to cambial reactivation or occurring in the early growing season may be critical to enhance growth through a longer growing season as occurs with warm springs in cold-biome boreal or mountain forests (Deslauriers et al. 2008), but this should be further checked by comparing xylogenesis dynamics in wet vs. dry years and in other tree species. As a result, a more marked bimodality characterized by a more marked early season growth peak indicates that water ability has strong influence on growth rates of *P. leiophylla*, which is confirmed by previous tree-ring analyses in nearby sites. For instance, González-Cásares et al. (2017) demonstrated a high correlation between atmospheric patterns and tree growth. In another study, Acosta-Hernández et al. (2019) found that intra-annual density fluctuations (IADF) formed by *P. leiophylla* were associated with seasonal fluctuations in precipitation and temperature, suggesting a strong plasticity of wood formation in response to soil water variability. Thus, favorable conditions in late summer and autumn can trigger the resumptions of cambial activity which results in a second peak of growth and IADF formation (see Acosta-Hernández et al. 2017). This facultative ability is crucial for studying the response of *P. leiophylla* and other pine species to climate warning in drought-prone areas, where growing and dormancy periods shift in response to temperature and soil water availability. Consequently, xylem plasticity of *P. leiophylla* should be taken into account for quantifying productivity or in models of phenological timing events. More research is needed, including seasonal and daily scales of radial-increment monitoring using dendrometers and xylogenesis (Deslauriers et al. 2007; Vieira et al. 2014), application of the Vaganov–Shashkin model at daily resolution (Vaganov et al. 2006), and use of

chilling-influenced heat-sum phenology models (Delpierre et al. 2019).

Until now, most of tree-ring research in Mexico and in similar drought-prone areas assumed unimodal and fixed seasonal growth (see Villanueva-Díaz et al. 2007; Pompa-García et al. 2013; Stahle et al. 2016) and such formulations are based mainly in precipitation, but our results demand more efforts. Given that temperature is the main driver for triggering cambium activity in conifer forests (Deslauriers et al. 2008; Rossi et al. 2008; Gričar et al. 2014), future research should be based on monitoring temperatures to predict the timing of cambial resumption. In Mexico, many researchers have focused on linking seasonal growth to climate signals (Acosta-Hernández et al. 2017). However, to the best of our knowledge, this study is the first analysis of growth dynamics at intra-annual scales, with implications for dendrochronological studies in areas affected by summer monsoon. Preceding winter climatic conditions, particularly precipitation, plays a crucial role on controlling xylogenesis (Ziaco et al. 2018) and radial growth (González-Cásares et al. 2019). In addition, our results and those of Ziaco et al. (2018) confirm that summer and autumn climate conditions are critical to induce a bimodal growth pattern and may shift the main phases of wood production, indicating that this growth pattern is facultative but very common in the study region. Therefore, studies in this and other regions affected by shifting seasonal drought cannot assume that earlywood and latewood respond to fixed climatic windows (Cabral-Alemán et al. 2017).

Conclusions

Xylogenesis data, particularly the intra-annual production of radially enlarging tracheids, confirm the bimodal growth pattern in *Pinus leiophylla*, a major trees species in drought-prone Mexican forests. Growth peaked in June and October in response to mild and humid conditions, whilst NDVI peaked from late July to late September. Temperature played an important role on controlling growth whenever climatic conditions were not dry. Therefore, xylem production and NDVI were partially uncoupled. Changes in winter–spring and, secondarily, in summer–autumn climate conditions affect radial growth of the conifer. These results could help forests managers to develop criteria and strategies related to sustainable management given climate variability and considering forecasted climate warming. In this study case, mild and humid climate conditions during winter–spring and autumn are favorable for xylem activity in *P. leiophylla*. Consequently, if winter and spring become warmer and drier, the forests of this species could experience reductions in productivity.

Author contribution statement MP and JC planned and designed the research; MP was responsible for data collection and conducted fieldwork; JG acquired and analyzed the NDVI data; MC and JC conducted laboratory analyses; JC analyzed the data, with substantial contribution from MP; MP led the manuscript with contributions from all authors. All authors contributed critically to the drafts and gave final approval for publication.

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Data availability All data generated or analyzed during this study are included in this published article.

Code availability We used open source software.

Compliance with ethical standards

Conflicts of interest The authors declare that they have no conflict of interest.

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