



Pine processionary moth defoliation affects secondary growth dynamics and tree vitality in *Pinus brutia*

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Abstract

Pine processionary moth (PPM) defoliation can reduce secondary growth and increase tree susceptibility to abiotic and biotic stressors. However, its effects on seasonal secondary growth dynamics and xylem and phloem anatomy are less understood. This study investigated the effects of PPM (*Thaumetopoea wilkinsoni*) defoliation on mature *Pinus brutia* trees in the Mediterranean region of Türkiye over two consecutive years. In 2018, cambial activity and secondary growth dynamics were monitored throughout the growing season in 65% PPM-defoliated and control trees using detailed histological observations. Anatomical characteristics of xylem and phloem were assessed both before wood formation started and after its cessation. In 2019, the same study was repeated on a new set of trees. PPM defoliation advanced the cessation of cell enlargement and wall-thickening phenophases, shortening wood formation by approximately two weeks. Despite this, tree-ring width reduced by only 15–20% and did not differ significantly from controls. Defoliated trees showed significantly lower earlywood to latewood (EW/LW) ratios, while other anatomical characteristics, such as cell wall thickness, were unaffected, which suggests reallocation of carbon to needle growth and storage early in the growing season. The observed decreases in the tree-ring to conducting phloem (TR/CPH) and EW/LW ratios indicate diminished vitality in defoliated trees. However, the observed reduction in ring width was far below that previously reported for 65% PPM defoliation, indicating the ability of the studied *P. brutia* individuals to cope with this level of defoliation stress. These findings improve our understanding of defoliation effects on secondary growth and highlight the need for more comprehensive studies to better predict forest responses to climate change and the projected increase in the frequency of PPM outbreaks.

Keywords Cambial activity · Insect defoliation · Radial growth · Tree vitality · Turkish pine

Introduction

Forests of the Mediterranean Basin provide a wide range of ecosystem services (e.g., carbon storage, water regulation, timber and non-timber products) but are increasingly threatened by climate change and human activities (Lefèvre and Fady 2016; Morán-Ordóñez et al. 2021). Natural disturbances such as droughts, wildfires, and outbreaks of herbivorous insects have become more frequent and severe in

recent decades, significantly affecting tree health and forest functioning (Gea-Izquierdo et al. 2014; Anderegg et al. 2015; Rubio-Cuadrado et al. 2021). These disturbances can weaken trees, making them more susceptible to additional stressors or even cause mortality in extreme cases (Desprez-Loustau et al. 2006; Lombardero and Ayres 2011; Güney et al. 2024). Pines (*Pinus* spp.) are a major component of Mediterranean vegetation and among the most ecologically and economically important tree species in Mediterranean forests (Bonari et al. 2021; Moreno et al. 2021). They serve as hosts for numerous herbivorous insects, among which defoliating insects represent a major economic threat (Battisti et al. 2016).

The pine processionary moths (PPM) *Thaumetopoea pityocampa* (Den. & Schiff.) and *T. wilkinsoni* Tams are the main defoliating insects of Mediterranean coniferous forests (Roques et al. 2015; Kerdelhué et al. 2024). *T.*

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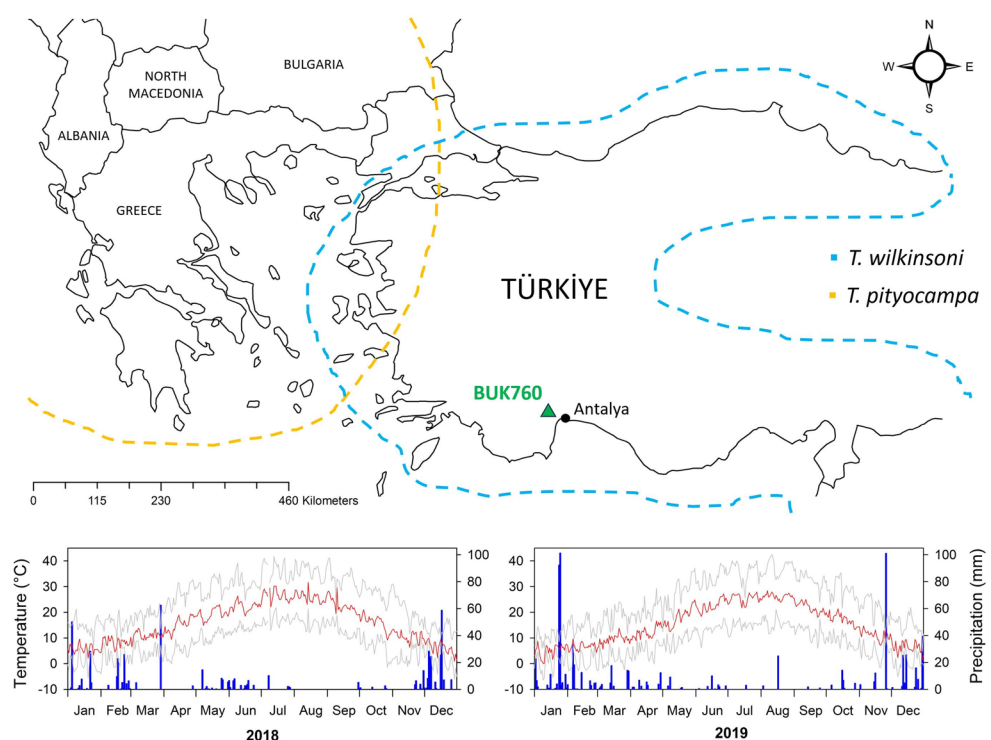
pityocampa is distributed in southern Europe, extends into western Türkiye, and is also found in North Africa, whereas *T. wilkinsoni* ranges from Türkiye to Israel (Kerdelhué et al. 2009; Fig. 1). Both belong to the ‘winter clade’ whose larvae hatch in autumn/winter, develop in winter, and feed on needles until March/April where they cause the most damage to the trees before descending to the soil for their pupal stage (Battisti et al. 2015). In Türkiye, *T. wilkinsoni* is the most widespread PPM and primarily infests *Pinus brutia* Ten. (Turkish pine). This species is the most common forest tree in Türkiye, especially in the Mediterranean and Aegean regions, covering approximately 23% (5.3 million ha) of the total forest area (Turkish General Directorate of Forestry 2023). It is fast-growing, widely used in industrial plantations (Batur et al. 2024), and accounts for ca. 30% of the country’s annual timber production (Turkish General Directorate of Forestry 2023). Given its important role in Turkish forests, understanding how PPM outbreaks affect *P. brutia* is essential for assessing both ecological and economic consequences.

PPM defoliation is usually accompanied by a reduction in stem growth since the loss of photosynthetically active tissue limits carbohydrate availability (Hódar et al. 2003). Growth losses can reach up to 80% depending on defoliation intensity (Jacquet et al. 2012). Pines are able to recover from 100% PPM defoliation if there are no other limiting factors, such as drought or secondary herbivorous insect infestations (e.g., bark beetles), that further constrain tree health. In this context, young trees are more at risk than

mature ones (Hódar et al. 2003; Battisti et al. 2015). In addition to stem growth reductions, natural or simulated PPM defoliation can affect non-structural carbohydrate reserves and wood anatomical characteristics (Palacio et al. 2012; Jacquet et al. 2014; Puri et al. 2015; Güney 2019). For example, cell wall thickness decreased in *P. pinaster* Ait. due to PPM defoliation, causing a reduction of earlywood density (Polge and Garros 1971). However, these studies all focused on investigating features of fully formed and mature tree rings. Much less is known about how PPM defoliation affects the dynamics of cambial activity and xylem and phloem formation.

Monitoring of cambial activity and wood formation (i.e., xylogenesis) dynamics, including the timing and duration of the different developmental stages of xylem cells, allows capturing intra-annual growth variability and tree responses to environmental factors (Camarero et al. 2010; Gričar and Čufar 2008; Saderi et al. 2019). The onset of wood formation is mainly controlled by temperature and photoperiod (Huang et al. 2020), whereas the factors regulating its cessation are less well understood (Lupi 2010). Exogenous factors such as water availability (Vieira et al. 2014), temperature (Marchand et al. 2025), and photoperiod (Mu et al. 2023), and endogenous factors such as tree vitality (Schmitt et al. 2003) have all been proposed as important drivers of wood formation cessation. Studies on the effects of defoliation on wood formation timings are still limited, reporting contrasting results depending on species and defoliation type. For example, artificial defoliation simulating

Fig. 1 Map showing the distribution range of pine processionary moths *Thaumetopoea wilkinsoni* and *T. pityocampa* in southeastern Europe.



spruce budworm (*Choristoneura fumiferana* Clem.) feeding in *Abies balsamea* (L.) Mill. seedlings showed no significant effect on wood formation timings (Rossi et al. 2009), whereas drought-induced defoliation in *P. sylvestris* L. and *P. nigra* Arn. significantly delayed growth onset (Guada et al. 2016). In contrast to wood formation, phloem formation has been reported to be less responsive to environmental factors (Gričar and Čufar 2008). However, studies investigating the effects of stress factors on phloem formation are scarce (Swidrak et al. 2014; Balzano et al. 2020). Nevertheless, combined xylem and phloem data can serve as valuable indicators of tree vitality. Tree vitality is a theoretical concept generally referring to a tree's ability to live, grow, and respond to environmental stressors (Larcher 1994; Dobbervin 2005). For instance, studies have shown that trees with diminished vitality have a lower tree-ring width to conducting phloem width ratio (TR/CPH ratio, Gričar 2012; Kücü and Güney 2021). Furthermore, variations in tree vitality can also be reflected through changes in the percentage of latewood (%LW) (Kort 1993).

A more comprehensive understanding of tree secondary growth responses to PPM defoliation is essential for accurately assessing its impact on tree health and forest productivity, particularly in the context of climate change, which might increase both the frequency of PPM outbreaks and the severity of defoliation (Hódar et al. 2003; Battisti et al. 2015; Domingo et al. 2024).

In this study, cambial activity and wood and phloem formation were monitored in defoliated and non-defoliated (control) *P. brutia* trees to assess the effects of PPM defoliation on secondary growth dynamics. In addition, selected anatomical characteristics of the mature xylem ring and conducting phloem at the end of the growing season were analyzed to better understand how PPM defoliation affects secondary growth and tree vitality. It was hypothesized that PPM defoliation would (1) alter secondary growth dynamics and xylem and phloem anatomical characteristics due to reduced carbon assimilation; and (2) reduce tree vitality due to defoliation-induced stress, indicated by a change in %LW and a decreased TR/CPH ratio.

Materials and methods

Study site and tree selection

The study was conducted at the Bük Lütüf Büyükyıldırım Research Forest, located in Antalya Province, in the Mediterranean region of Türkiye. The study site (BUK760, 36°57'46" N, 30°24'5" E) was situated at an elevation of 760 m within a mature even-aged *P. brutia* stand. Trees were planted as one-year-old seedlings in 1989 and are

growing on ophiolite serpentine bedrock. The shallow soil is mainly sandy loam with a pH around 7.08–7.19 (Basaran et al. 2011). The average slope of the study site was 7°. The climate is semi-arid with hot, dry summers. According to records from a weather station located within the research forest (36°58'12.84" N, 30°26' 2.11" E, 475 m) and approximately 3 km from the study site, the long-term (1970–2008) mean annual air temperature and total annual precipitation are 14.1 °C and 398 mm, respectively (Basaran et al. 2011). Meteorological data for this station were obtained from the Turkish State Meteorological Service for the years 2018 and 2019 (Fig. 1). According to these data, the mean annual temperature and total annual precipitation in 2018 were 15.77 °C and 579.9 mm, respectively. In 2019, the mean annual temperature was slightly lower (15.19 °C), while total annual precipitation was higher (837.1 mm) than in 2018.

The trees selected for this study were all co-dominant (Kraft 1884) and appeared healthy without visible damage (Fig. 2). Trees monitored for the effects of PPM defoliation (D) on secondary growth dynamics and the anatomical characteristics of xylem and phloem were selected from individuals with at least one PPM nest present. Control trees (C) were selected from individuals without PPM nests. In January 2018, six trees were selected for each group (D₂₀₁₈ and C₂₀₁₈). Cambial activity and xylem and phloem formation were monitored in four individuals per group, while the anatomical characteristics of mature xylem and phloem at the end of the growing season were analyzed in all individuals. For a second monitoring during 2019, a new set of trees ($n=3$) was selected for each group (D₂₀₁₉ and C₂₀₁₉) in December 2018 to avoid any effects from previous defoliation and/or microcoring. Tree height (Table 1) did not differ significantly between control and defoliated trees in either 2018 ($t(6)=0.28$, $p=0.791$) or 2019 ($t(3)=0.45$, $p=0.678$). Similarly, DBH showed no significant differences between groups in 2018 ($t(6)=-1.88$, $p=0.109$) and 2019 ($t(3)=0.31$, $p=0.770$).

DBH, diameter at breast height; C, control trees; D, defoliated trees; n_m , number of trees selected for monitoring secondary growth dynamics; n_a , number of trees selected for analysis of xylem and phloem anatomical characteristics. Subscript numbers indicate the year of monitoring/sampling. Values represent mean $\pm$ standard errors.

Since the initial number of PPM nests on the selected trees (D) was relatively low, additional nests were manually transferred from nearby infested individuals in both years (in January), resulting in a final number of approximately eight PPM nests per tree. This led to a natural defoliation rate of approximately 30–40% by the end of March. The degree of defoliation was visually assessed independently by two observers and then averaged, starting approximately two

Fig. 2 Study site with **A** mature, even-aged *Pinus brutia* trees in the Bük Lütüf Büyükyıldırım Research Forest in Antalya, Türkiye. Images taken on **B** December 13, 2018 and **C** May 2, 2019 show the same tree from the defoliated group (D₂₀₁₉). At the end of April 2019, this tree had a defoliation rate of approximately 65%. The white circle marks one of the transferred pine processionary moth nests. **D** Twigs showing natural defoliation caused by the feeding of PPM larvae and **E** artificial defoliation by cutting the needles with scissors

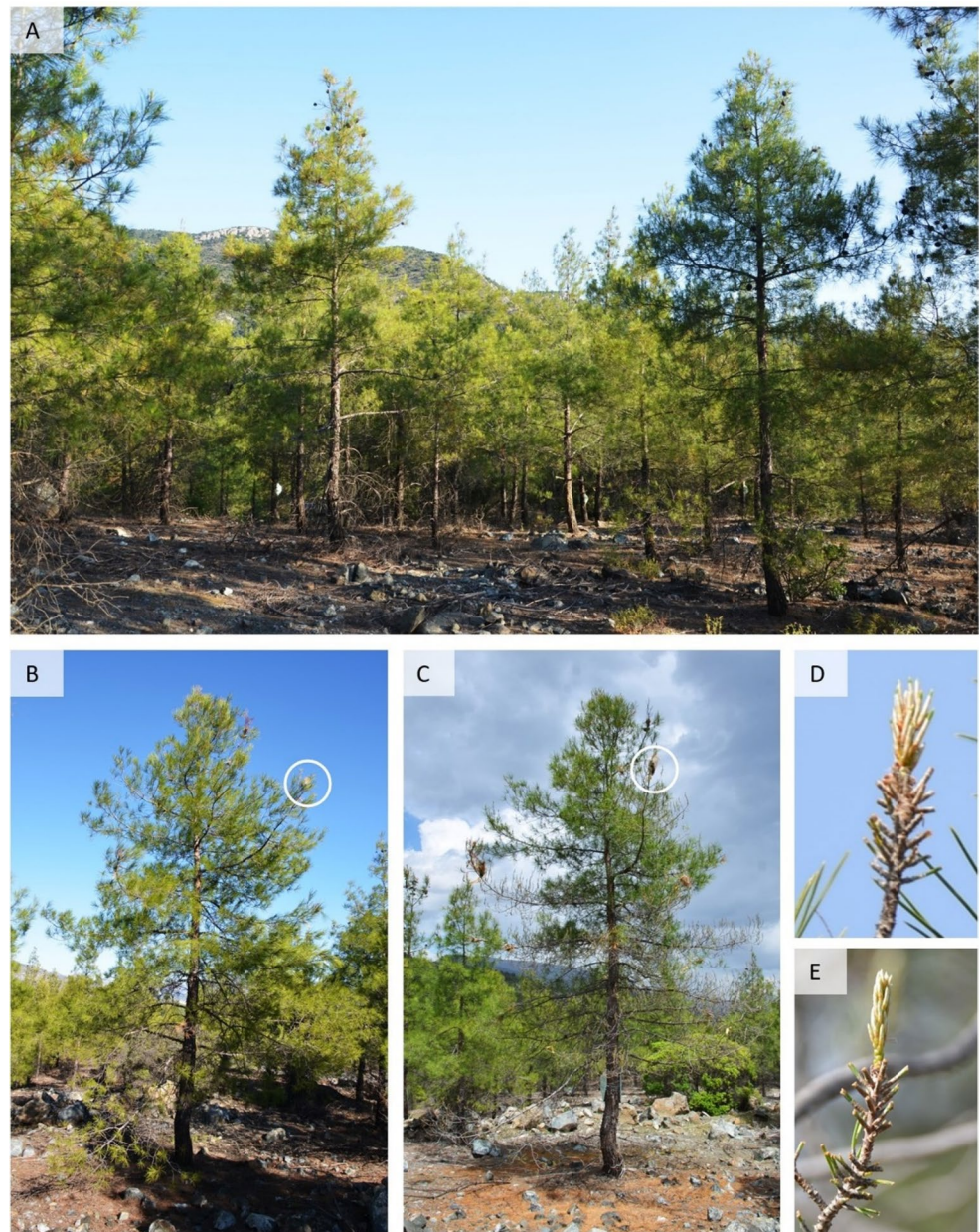


Table 1 Characteristics of *Pinus brutia* trees selected to study the effects of pine processionary moth defoliation on secondary growth dynamics and xylem and phloem anatomy

Group	n_m	n_a	DBH (cm)	Height (m)	Defoliation (%)
C ₂₀₁₈	4	6	17.8±0.6	7.7±0.2	0
D ₂₀₁₈	4	6	17.5±0.6	9.0±0.7	61±3.5
C ₂₀₁₉	3	3	17.7±0.3	8.2±0.5	0
D ₂₀₁₉	3	3	17.3±0.7	8.0±0.4	65±2.3

weeks after the PPM nests were transferred. Assessments were conducted every 1–2 weeks until the end of February and then weekly until PPM larvae ceased feeding. According to the meta-analysis by Jacquet et al. (2012), the average relative growth loss in conifers defoliated by PPM increases

with defoliation rate, but tends to level off at around 50%. Therefore, to ensure a defoliation rate exceeding this threshold, foliage was manually removed with scissors on two occasions during the first and second week of April, which corresponds to the period when PPM larvae cease feeding and allow for a gradual defoliation (Pestana and Santolamazza-Carbone 2011; Palacio et al. 2012). When cutting the leaves, care was taken to imitate the larvae as closely as possible, leaving a small part of the leaf base (Fig. 2d and e). Current-year leaves were not affected by PPM larvae or manual foliage removal, as they emerged after the larvae had descended to the soil. Ultimately, the defoliation rate averaged around 60–65% in both years (Table 1). This defoliation level was intended to enable detection of any effects

of PPM defoliation on secondary growth dynamics and anatomical characteristics, if such effects exist.

Tree sampling and sample preparation

In both years, microcores were collected weekly from the end of February until the end of September (on some occasions sampling intervals varied between 5 and 10 days) and then every 2–4 weeks until February of the following year. Microcores were extracted from the stem at breast height (1.3 m) using a Trephor (Rossi et al. 2006), following a spiral pattern and leaving approximately 5 cm between extraction points to avoid reaction wood (Deslauriers et al. 2003). Prior to sampling, the outer bark was carefully removed with a chisel. The microcores (2 mm in diameter and 15 mm in length), which contained parts of the phloem, the cambium and the most recent tree rings, were immediately placed in 2 ml Eppendorf vials filled with a 70% ethanol solution and stored at 5 °C until further use (De Micco et al. 2016). In the laboratory, microcores were dehydrated using a series of ethanol immersions (70%, 70%, 90%, 90%, 96%, 100%, 100%; each step lasting one hour). Subsequently, microcores were immersed in three successive xylene baths for

a total of 4.5 h, followed by two successive liquid paraffin baths at 65 °C for a total of 4 h (Deslauriers et al. 2015). The impregnated microcores were embedded in paraffin with the transversal side facing upwards. Transverse sections were cut to a thickness of 5–8 µm using a rotary microtome (Microm HM 340 E, Walldorf, Germany), double-stained with safranin and astrablue and mounted on microscope slides with Roti-Histokitt for anatomical observations under a microscope.

Histological analysis and cell measurements

Transverse sections (Fig. 3) were observed and photographed at 100x – 400x magnification using a light microscope (Leica DM750, Leica Microsystems IR GmbH, Germany). Cell counting was carried out on each sample to determine the numbers of cambial cells, xylem cells at different developmental stages, and phloem cells. Cambial cells were identified by their thin cell walls and small radial diameters. Enlarging xylem cells have thin and elastic primary walls and radial diameters that are at least twice that of a cambial cell. Cells in secondary wall formation (wall-thickening cells) exhibit a colour change from blue to red,

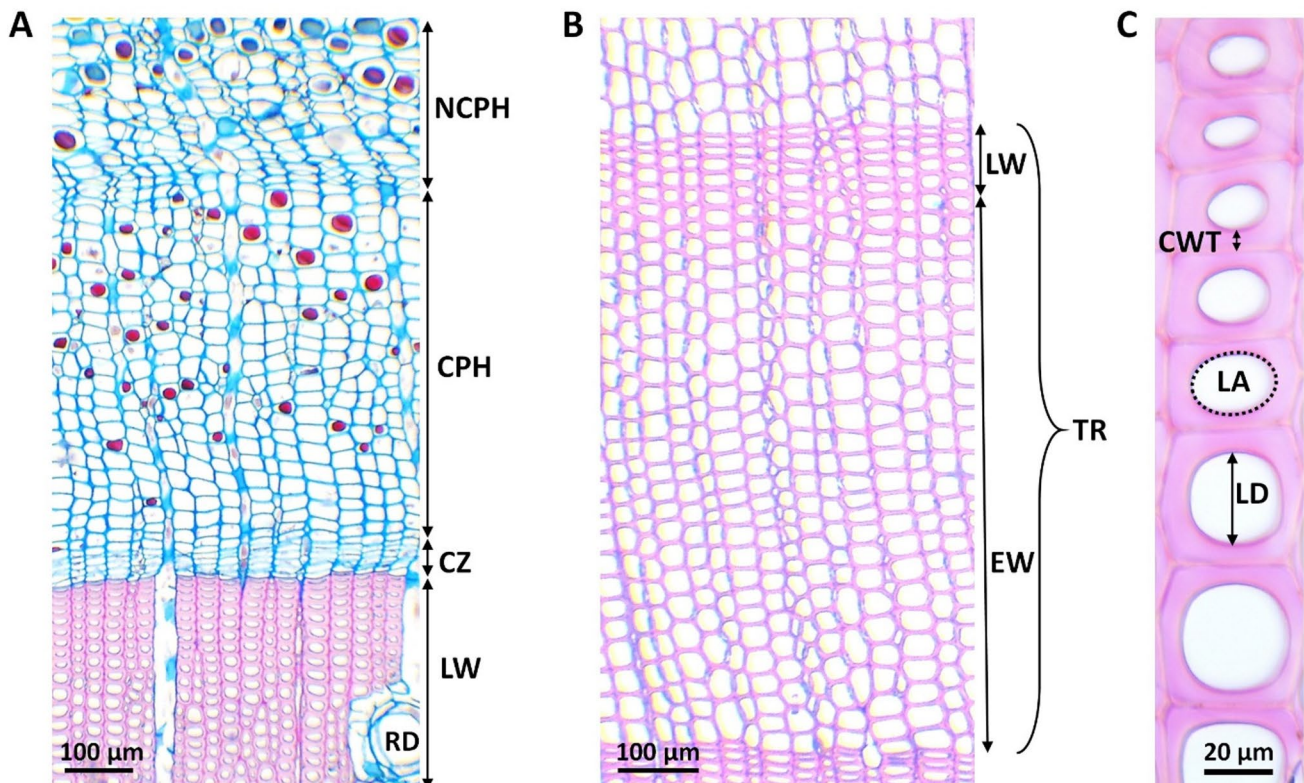


Fig. 3 Light micrographs of *Pinus brutia* cross sections. **A** Cross-section of a sample taken from one of the control trees on February 2, 2019, showing the latewood (LW) of the most recent tree ring, the cambial zone (CZ), and the phloem. The phloem includes the non-collapsed, conducting phloem (CPH) and the deformed, collapsed, non-

conducting phloem (NCPH). RD, resin duct. **B** Tree ring (TR) with earlywood (EW) and LW. **C** Radial row of tracheids illustrating the measurement of cell characteristics: lumen diameter (LD), lumen area (LA, dotted circle), and cell wall thickness (CWT)

starting from the cell corners, and shine under polarised light. Mature cells have a red colour throughout the cell wall, shine under polarised light, and do not contain a protoplast (Abe et al. 1997; Deslauriers et al. 2015). Phloem cells were identified by their larger radial diameters and slightly thicker, blue-stained secondary walls compared to cambial cells (Fig. 3a). As reported for several Mediterranean conifer species, phloem ring boundaries were not detectable (Gričar et al. 2016; Balzano et al. 2020; Sökücü and Güney 2021). Therefore, only the non-collapsed, conducting phloem (CPH) was analyzed, which is easily distinguishable from the deformed, collapsed, non-conducting phloem cells (Gričar 2012).

Cell measurements were carried out on sections of microcores collected in February of the year following ring formation, to ensure the tree rings were fully mature. Lumen area, radial lumen diameter, and radial cell wall thickness of tracheids (Fig. 3c) were measured using ImageJ image processing software (National Institutes of Health, Bethesda, MD, USA) in both the most recent and preceding tree ring (Vieira et al. 2014). Earlywood (EW) and latewood (LW) tracheids were classified according to Mork's criterion (Denne 1989):

$$\text{Mork's criterion (MC)} = \frac{4 \times \text{radial cell wall thickness}}{\text{radial lumen diameter}}$$

Cells were classified as EW if $MC \leq 0.5$, as transition wood if $0.5 < MC < 1$, and as LW if $MC \geq 1$ (Cuny et al. 2014). The same sections were used to measure the widths of the tree-ring (TR), EW, LW, and CPH (an overview of all abbreviations used in the text is provided in Table A1). Counts and measurements were conducted along three radial files and then averaged for subsequent analyses (Deslauriers et al. 2003; Vieira et al. 2014). For counting, the files with the largest cells were selected (Deslauriers et al. 2015).

The percentage of latewood (%LW) in TR width and the EW/LW ratio were calculated for mature tree rings of the year before defoliation occurred and the year of defoliation. The TR/CPH ratio was calculated using samples collected before the onset and after the cessation of wood formation.

Data analysis

To test whether defoliation had a significant effect on cell numbers over the monitoring period, a linear-mixed effects model was used with 'treatment' (control, defoliation), 'time' and their interaction as fixed effects and 'tree identity' as a random effect. Analyses were conducted separately for 2018 and 2019. To account for temporal dependencies between consecutive measurements, different covariance types were compared and 'autoregressive (AR(1))' was

selected based on Akaike's Information Criterion (AIC), which provided the best fit. Model residuals were visually inspected to verify normality. Post-hoc pairwise comparisons between treatments were conducted for each week using the Bonferroni correction.

Dynamics of wood formation were assessed from cell count data using the R package CAVIAR (Rathgeber et al. 2011). Critical dates in wood formation dynamics were determined using logistic regressions and correspond to the point at which there is a 50% probability of a phenophase (e.g., enlarging) starting or ceasing. Critical dates include the beginning of the enlarging (bE), wall-thickening (bW), and mature (bM) phenophases, as well as the cessation of the enlarging (cE) and wall-thickening (cW) phenophases. The onset and cessation of wood formation were determined based on the presence of enlarging cells and the absence of wall-thickening cells, respectively (Rathgeber et al. 2011; Saderi et al. 2019). A phenophase is defined as having started(ceased) at the date when more(less) than 50% of the counted files contain cells of that phenophase. The duration of each phenophase was calculated using the critical dates: enlarging ($dE = cE - bE$), wall-thickening ($dW = cW - bW$), and wood formation ($dX = cW - bE$). Wood formation dynamics were modelled by fitting a Gompertz function to the cumulated cell count data using the *fitGompertzModels* function in CAVIAR. These models provide parameters such as (i) the dates at which 5% (tb) and 95% (tc) of the xylem cells are produced, (ii) the average (ra) and maximum (rm) rate of cell productions (in cell/day), and (iii) the duration of wood formation (dt) and timing of maximum cell production (tx). The overall fit of the models was assessed by calculating the Modelling Efficiency (EF), with values close to 1 indicating 'near-perfect' fit (Mayer and Butler 1993). A bootstrap permutation test with 10,000 iterations was used to compare the critical dates and durations of wood formation, as well as the parameters of the Gompertz functions, between control and defoliated groups, using the function embedded in CAVIAR (Rathgeber et al. 2011, 2018). The calculated achieved significance level (ASL) is interpreted in the same way as the p value, but results are considered significant if $ASL < 0.1$ (Rathgeber et al. 2011).

For the anatomical characteristics that were measured in the fully matured tree rings (TR width, LW width, CPH width, lumen area, lumen diameter, cell wall thickness, %LW, EW/LW, and TR/CPH), a two-way analysis of variance (two-way ANOVA) was used to test the effects of the factors 'treatment' (control, defoliation) and 'year' (2018, 2019) and their interaction. To account for individual variability and baseline differences, delta (Δ) values were calculated for each anatomical characteristic by subtracting pre-treatment values from post-treatment values. Before analysis, assumptions of normality and homogeneity of

variances were tested using the Shapiro–Wilk test and Levene’s test, respectively. Interaction effects between treatment and year were assessed, and estimated marginal means (EMMs) were calculated to interpret the main and interaction effects. Statistical significance was set at $p < 0.05$ and effect sizes were reported as partial eta squared (η^2) to quantify the magnitude of the effects. Linear-mixed effects models, the Shapiro–Wilk test, Levene’s test and two-way ANOVA were performed using SPSS v.20 (IBM Corp, Armonk, NY, USA).

Results

Cambial activity and seasonal variation in xylem and phloem cells

The seasonal variation in cambial activity and the number of xylem and phloem cells followed similar patterns in both defoliated (D) and control (C) trees across both years (Fig. 4). In 2018, the cambium seemed to be already active on the first sampling day (February 27, DOY (Day of Year) 58), as it showed a higher number of cells compared to those observed in winter (Fig. 4a). In 2019, cambial activity appeared to start approximately two weeks later (mid-March). The maximum number of cambial cells was observed around April 6 (DOY 96) and April 21 (DOY 111), in 2018 and 2019, respectively. Linear mixed-effects models revealed that treatment had no significant effect on cambial cell numbers in 2018 and 2019 (Table A2). However, a significant interaction between treatment and time was detected for cambial cells in 2019 ($p = 0.030$). This suggests that, although the overall main effect of treatment was not significant, the response to defoliation likely varied over time. Cambial cell numbers were significantly higher in D_{2019} in late March and April, and in C_{2019} in the first week of July. The number of conducting phloem cells did not significantly between treatments (Table A2). The conducting phloem consisted of 15.4 ± 3.5 cells on average, with higher values in spring and lower values observed in summer (Fig. 4e). Across both years, time had a strong and consistent effect on all cell types (Table A2), reflecting the expected seasonal progression of cambial activity as well as xylem and phloem development.

Wood formation dynamics

The first enlarging cells were observed in mid-March (DOY 75) in 2018 and one week later (DOY 82) in 2019 (Fig. 4). In both years, the onset of enlargement did not differ significantly between groups (Table 2). However, the enlargement phase ceased approximately one week earlier in defoliated

trees (D_{2018} and D_{2019}), resulting in a significantly shorter duration than in control trees. The number of enlarging cells peaked in April (Fig. 4b). Linear mixed effect models revealed a marginally significant interaction between treatment and time regarding the number of enlarging cells in 2019 ($p = 0.049$). Specifically, the number of enlarging cells was significantly higher in C_{2019} during the third week of May and the second half of June compared to defoliated trees. The wall-thickening phase began during the first week of April in 2018 and about two weeks later in 2019 (Fig. 4c). In both years, the number of wall-thickening cells peaked during spring and again in autumn. The wall-thickening phase ceased significantly earlier by approximately two weeks in defoliated trees (D_{2018} and D_{2019} , Table 2). Regardless of the study year, tree rings reached full maturity by mid-January of the following year. The onset of the mature phase was significantly earlier in defoliated trees (D_{2018} and D_{2019}) and the total duration of wood formation was significantly longer by approximately two weeks in control trees (C_{2018} and C_{2019}) in both years. Critical dates and durations of the different phenophases for each tree are shown in the supplementary information (Fig. A1–A4).

Analysis of wood formation dynamics based on Gompertz functions (Table 3, Fig. A5) showed that the time of maximum cell production occurred significantly earlier, by approximately 10 days, in defoliated trees (D_{2018} and D_{2019}) compared to control trees (C_{2018} and C_{2019}). Significant differences between the groups in the timing at which 5% of the cells were produced (tb) were only found in 2019. Although the mean final cell numbers (α) were lower in defoliated trees—20% lower in 2018 and 8% lower in 2019—these differences were not statistically significant. Mean values for the other parameters (tc, dt, ra, and rm) were also lower in the defoliated trees in both years, although no significant differences were found. Individual results of Gompertz curve fittings for each tree are provided in the supplementary information (Tables A3 and A4).

Xylem and phloem anatomy

$\Delta TR/CPH$ was significantly influenced by year (two-way ANOVA, $p = 0.031$, partial $\eta^2 = 0.291$) and treatment ($p = 0.030$, partial $\eta^2 = 0.293$) with moderate effect sizes (Fig. 5, Table A5). The interaction effect between year and treatment was not significant ($p = 0.767$, partial $\eta^2 = 0.006$), suggesting the treatment effect was consistent across years. The model accounted for 45.8% of the variance in $\Delta TR/CPH$ ($R^2 = 0.458$). Based on absolute data, the TR/CPH increase was approximately 28% higher in C_{2018} than in D_{2018} after wood formation ceased in 2018 (Fig. A6). In 2019, D_{2019} showed a 10% decrease in TR/CPH , whereas C_{2019} showed a 7% increase.

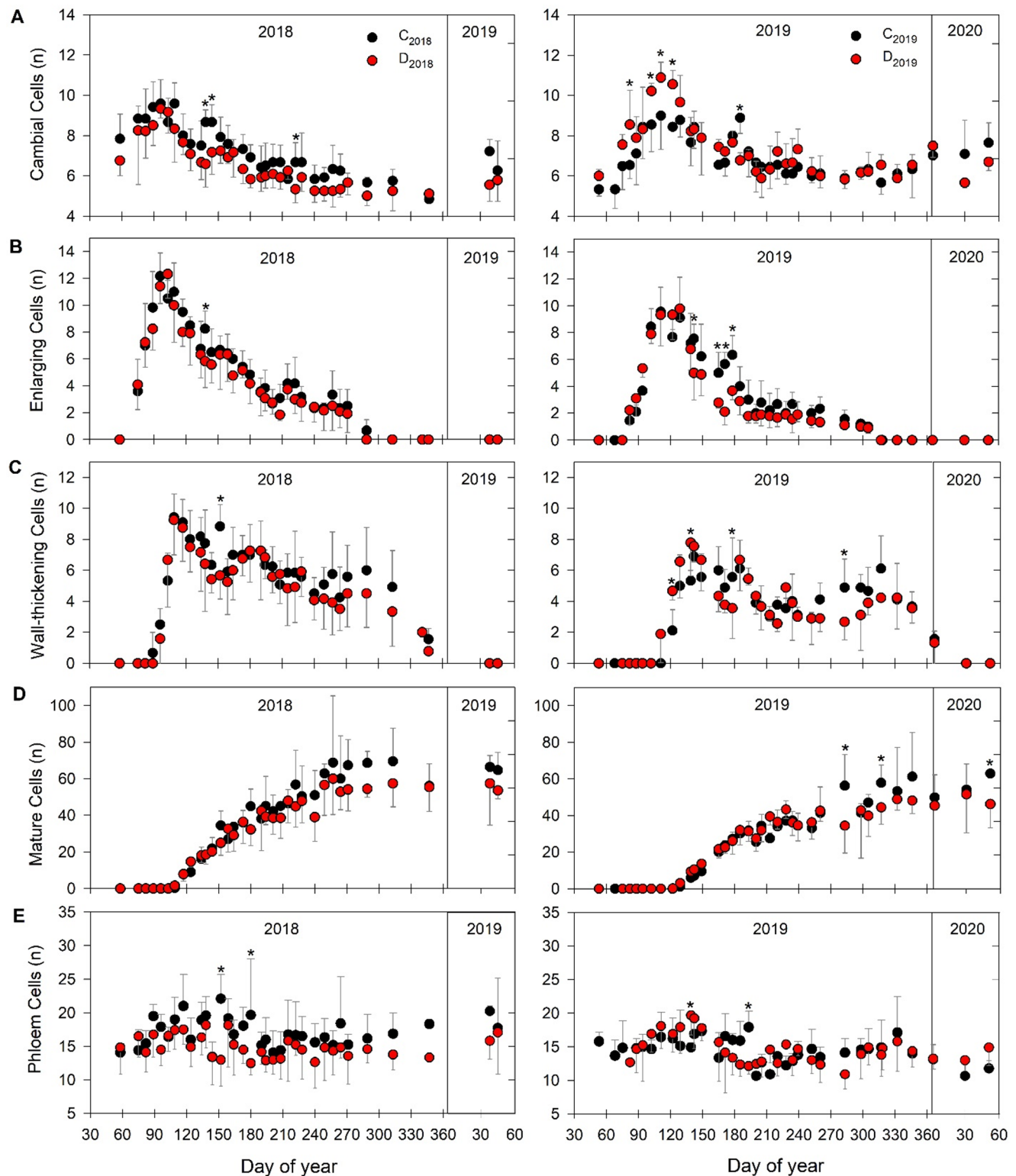


Fig. 4 Seasonal variation in the number of **A** cambial cells, **B** enlarging xylem cells, **C** xylem cells in secondary wall formation (wall-thickening cells), **D** mature xylem cells, and **E** non-collapsed, conducting phloem cells in control (C; black circles) and defoliated (D; red circles) *Pinus brutia* trees. The left panels show data from the groups (C₂₀₁₈ and D₂₀₁₈), which were selected to monitor cambial activity and secondary growth dynamics from February 2018 to February 2019.

The right panels display data from the groups (C₂₀₁₉ and D₂₀₁₉), which were monitored from February 2019 to February 2020, using a new set of trees. Data points represent means (circles), with standard deviations indicated by whiskers. Asterisks indicate significant differences ($p < 0.05$) between groups at individual sampling dates based on pairwise comparisons from the linear mixed-effects model.

Table 2 Critical dates (as day of year, DOY) and durations of wood formation computed from cell count data of control (C) and defoliated (D) *Pinus brutia* trees over the growing seasons of 2018 (C₂₀₁₈ and D₂₀₁₈) and 2019 (C₂₀₁₉ and D₂₀₁₉). Each year consists of a new set of trees

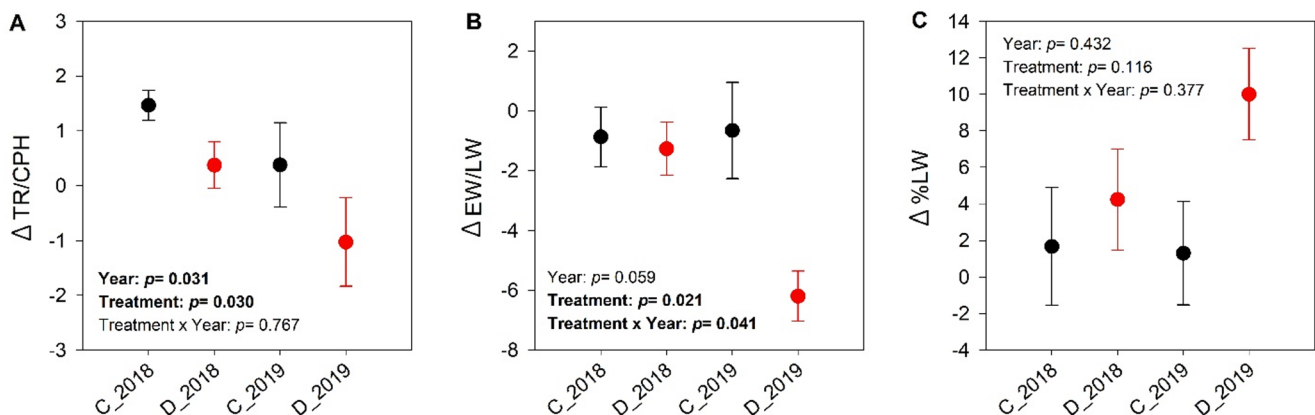
Group	bE (DOY)	bW (DOY)	bM (DOY)	cE (DOY)	cW (DOY)	dE (d)	dW (d)	dX (d)
C ₂₀₁₈	67±0	91±4	111±4	291±12	6±13 ^x	224±12	279±11	304±9
D ₂₀₁₈	67±0	95±4	108±2	280±0	357±13	213±0	262±15	290±13
ASL	n.s.	0.038	0.021	0.037	0.026	0.034	0.032	0.026
C ₂₀₁₉	79±0	119±3	130±4	311±0	12±8 ^y	232±0	258±7	298±8
D ₂₀₁₉	79±0	110±6	125±2	307±3	364±14	228±3	255±8	285±14
ASL	n.s.	0.019	0.044	0.011	0.096	0.009	n.s.	0.098

^x DOY of the following year (=2019); ^y DOY of the following year (=2020). bE, bW, and bM represent the onset of the enlarging, wall-thickening, and mature phases, respectively; cE and cW represent the cessation of the enlarging and wall-thickening phases. dE, dW, and dX correspond to the durations of the enlarging and wall-thickening phases, as well as the duration of wood formation. Significant ASL (=Achieved significance level) values are in bold. Values represent mean±standard deviation

Table 3 Parameters of Gompertz functions fitted to xylem cell count data of control (C) and defoliated (D) *Pinus brutia* trees over the growing seasons of 2018 (C₂₀₁₈ and D₂₀₁₈) and 2019 (C₂₀₁₉ and D₂₀₁₉). Each year consists of a new set of trees. Individual results for each tree are provided in tables A3 and A4 of the supplementary information

Group	α (n_{cells})	tb (DOY)	tc (DOY)	dt (days)	tx (DOY)	ra (cell/day)	rm (cell/day)
C ₂₀₁₈	72.3±11	67±10	276±55	209±63	123±10	0.33±0.07	0.55±0.13
D ₂₀₁₈	58.9±20	65±7	238±54	173±59	112±11	0.31±0.01	0.51±0.01
ASL	0.111	0.353	0.148	0.183	0.066	0.230	0.272
C ₂₀₁₉	57.7±7	80±8	321±18	242±26	145±2	0.22±0.04	0.36±0.06
D ₂₀₁₉	53.4±8	72±4	307±18	236±20	135±3	0.20±0.02	0.34±0.02
ASL	0.222	0.059	0.147	0.335	0.013	0.248	0.195

Significant ASL (=Achieved significance level) values are in bold. Values present mean±standard deviation. α =upper asymptote for the final cell number, tb=date (as day of year=DOY) at which 5% of the cells are produced, tc=date at which 95% of the cells are produced, dt=time required for major period of wood formation (time between tb and tc), tx=date of maximum cell production, ra=mean cell production rate, rm=maximum cell production rate

**Fig. 5** Results of two-way ANOVA testing the effects of treatment (C=control, black circles; D=defoliation, red circles), year (2018 and 2019) and the interaction 'treatment x year' on **A** tree-ring width to conducting phloem width ratio (TR/CPH), **B** earlywood to latewood ratio (EW/LW), and **C** percentage of latewood (%LW) in *Pinus brutia*.

For $\Delta\text{EW/LW}$, there was a significant main effect of treatment ($p=0.021$, partial $\eta^2=0.325$) and a significant interaction between year and treatment ($p=0.041$, partial $\eta^2=0.266$, Table A5). The interaction indicates that the effect of defoliation on the $\Delta\text{EW/LW}$ ratio varied between years, with D₂₀₁₉ showing a marked decrease compared to other groups (Fig. 5). This decrease corresponded to an increase in ΔLW , where a moderate effect of defoliation was

The delta (Δ) values represent the difference between the year of treatment and the preceding year. Values for the trees monitored in 2018 ($n=6$ per group) and 2019 ($n=3$ per group) are shown as means and standard errors. Significant values ($p<0.05$) are indicated in bold

observed (partial $\eta^2=0.167$, Table A5). Regarding absolute values, the reduction in EW/LW and the increase in %LW were approximately 25% and 35% greater, respectively, in defoliated trees than in controls in the year of defoliation (Fig. A6).

Defoliation had no significant effect on TR width ($p=0.857$, Table A5). However, although TR width increased in 2018 relative to 2017 in both C₂₀₁₈ and D₂₀₁₈,

the average increase was 20% greater in C_{2018} compared to D_{2018} (Fig. A6). In 2019, average TR width increased by 3% in C_{2019} and decreased by 12% in D_{2019} relative to the previous year. Differences in LW width, CPH width, and tracheid lumen diameter, lumen area, and cell wall thickness were not significant (means for control and defoliated trees and different years are presented in Fig. A6).

Discussion

This study investigated the effects of PPM defoliation on secondary growth dynamics, xylem and phloem anatomy, and tree vitality in mature *P. brutia* trees using histological observations of periodically collected stem microcores. The results partially supported the hypotheses. The loss of two-thirds of the previous year's needles significantly affected the timing of maximum cell production and wood formation cessation but not onset. Furthermore, PPM defoliation significantly affected the TR/CPH and EW/LW ratios, indicating diminished tree vitality.

PPM defoliation had no significant effect on growth onset, which is consistent with the fact that most defoliation occurred after the onset of wood formation, defined by the presence of the first enlarging xylem cell. Instead, growth initiation appeared to be primarily driven by environmental factors, particularly temperature (Güney et al. 2015; Huang et al. 2020). In 2019, the onset of cambial activity and wood formation phenophases were delayed by about two weeks (Fig. 4; Table 2), likely in response to colder late-winter temperatures, with January and February 2019 averaging 0.7 °C and 1.7 °C lower than in 2018, respectively. Over the monitoring period, seasonal variations in the number of cambial, xylem, and CPH cells were similar between defoliated and control trees (Fig. 4) and resembled patterns reported for several Mediterranean conifer species (Linares et al. 2009; Balzano et al. 2020). The cambium exhibited higher rates of cell division in spring under favorable conditions and entered dormancy during winter. A bimodal growth pattern in which cambial activity peaks during spring and autumn, as observed in several Mediterranean pines from drought-prone environments (Camarero et al. 2010; Pacheco et al. 2018), was not present in the studied *P. brutia* trees.

In contrast to growth onset, PPM defoliation led to a significantly earlier timing of maximum xylem cell production and earlier cessation of the enlargement and wall-thickening phenophases, thereby shortening wood formation by approximately two weeks (Tables 2 and 3). According to Rossi et al. (2012), changes in the timing of one phenophase can propagate through the growing season and influence the timing of cell maturation. This could partly explain the earlier cessation of wood formation observed here, as

early-season defoliation led to an earlier start of the maturation phase, which in turn advanced the successive phenological events. The earlier cessation of wood formation did not lead to a significant reduction in TR width, which decreased by only 15–20%. This suggests that the overall rate of cell production was maintained even though the duration of wood formation was shorter, which aligns with the present findings (Table 3).

Although wood formation ceased significantly earlier in defoliated trees, it may not represent a severe carbon limitation. In *P. brutia*, PPM defoliation ended around peak cambial activity and before bud break (Battisti et al. 2015; and personal observation), reducing immediate photosynthetic capacity. However, moderate growth reductions in PPM defoliated trees (see Palacio et al. 2012 and Puri et al. 2015 for natural and artificial PPM defoliation, respectively) often occur without significant declines in carbohydrate concentrations and carbon supply becomes limiting only under severe defoliation (Palacio et al. 2014). Even 100% defoliated trees were able to restore non-structural carbohydrate levels to control values by the end of summer following needle regrowth (Puri et al. 2015). Therefore, the observed shortened wood formation duration in defoliated *P. brutia* likely reflects a temporary downregulation of sink activity or a shift in resource allocation toward needle growth and storage early in the growing season rather than a direct carbon source limitation (Wiley and Helliker 2012; Simard et al. 2013). The timing and vigor of current-year needle emergence likely allowed partial recovery of photosynthetic capacity, supporting ongoing xylem cell production by sustaining cambial sink strength and the duration of wood formation (Huang et al. 2014). This compensatory mechanism likely explains why cell wall thickness and cell sizes remained unaffected in defoliated *P. brutia*. If carbon assimilation had been strongly impaired, reduced growth rates and changes in anatomical characteristics would be expected, as observed in other studies, where disturbances such as insect defoliation (Polge and Garros 1971; Peters et al. 2020; Camarero et al. 2023) or drought (Kiorapostolou et al. 2020) limited carbon investment into secondary wall thickening, resulting in lower wood density.

Similarly to the findings in this study, Peters et al. (2020) showed that, in *Larix decidua* Mill. trees defoliated (~80%) by the larch budmoth (*Zeiraphera griseana* Hübner), cessation of cell wall-thickening occurred 17 days earlier than in control trees without affecting ring width but causing significantly thinner cell walls, especially in the latewood. However, unlike PPM defoliation, budmoth defoliation started at the peak of the enlargement phase and trees were re-foliated after 40 days, leading to prioritization of leaf recovery and carbon storage over wood formation.

The 15–20% reduction in TR width observed in this study contrasts with the 50% reduction reported by Jacquet et al. (2012) for similar defoliation levels. Previous studies on *P. brutia* have shown that growth reductions following PPM defoliation can range widely, from 20 to 60%, based on defoliation intensity (Chatziphilippidis and Avtzis 1994; Carus 2004; Kanat et al. 2005; Erkan 2011; Batur et al. 2024). The relatively small reduction in TR width in this study is closer to values reported under much lower PPM defoliation intensities (i.e., 5–24%; Jacquet et al. 2012).

The absence of significant changes in TR width, cell wall thickness, and lumen size in the present study suggests that the studied *P. brutia* trees were comparatively resilient despite the 65% defoliation, possibly due to rapid recovery through compensatory increases in photosynthetic capacity of remaining and newly emerging needles.

PPM defoliation also had no significant effect on the number of CPH cells and CPH widths (Fig. 4 and A6). This stability is consistent with previous studies that report that phloem production is more endogenously controlled and less responsive to environmental stress than wood formation (Gričar et al. 2014; Swidrak et al. 2014). Such regulation ensures the continued transport of carbohydrates, nutrients, and signaling compounds, which are essential for growth and stress adaptation (Esau et al. 1957; Dinant and Lemoine 2010).

Despite the relatively small reduction in TR width, defoliated trees showed a significant decrease in the TR/CPH ratio (Fig. 5), indicating a decline in tree vitality consistent with previous studies (Gričar 2012; Küçük et al. 2021). Such a decline can increase tree vulnerability to drought, pathogens, and other biotic stressors (Franceschi et al. 2000; Secchi et al. 2017). This is particularly relevant because in its natural habitat, *P. brutia* is regularly exposed to drought (Deligöz and Cankara 2020) and is susceptible to herbivorous insect attacks (e.g., bark beetles, Ibiş and Sarıkaya 2012). PPM defoliation also caused a significant decrease in EW/LW ratios. This supports the assumption that defoliation constrained carbon allocation to earlywood formation (Palacio et al. 2012) followed by partial recovery later in the season, leading to tendentially higher %LW. These findings align with Houdas et al. (2024), who observed higher %LW in *P. nigra* Arnold and *P. sylvestris* L. after PPM defoliation. Thus, the decline in vitality observed in this study is characterized by lower TR/CPH and EW/LW ratios. However, the interpretation of vitality indicators appears challenging, as they cannot be directly measured and no standardized classification yet exists (Rohner et al. 2021). Moreover, results may vary among species and stress types. For example, according to Kort (1993), lower vitality in *Pseudotsuga menziesii* (Mirb.) Franco, indicated by higher needle-loss percentages (not caused by defoliating

insects), was associated with lower %LW. Another study showed that heavily stressed *Picea abies* L. trees exposed to air pollution showed a significant reduction in %LW (Wimmer 2002). These contrasting results suggest that %LW and EW/LW ratio must be interpreted carefully, taking into account species-specific physiology, timing and severity of stress, and other environmental factors.

The findings of this study contribute to a better understanding of how PPM defoliation influences secondary growth and vitality in *P. brutia*. Although the number of monitored trees was limited, the strict selection of comparable trees (same age, size, and location) ensures that the observed differences are primarily attributable to PPM defoliation. Future studies encompassing larger sample sizes and multiple sites would allow for a more comprehensive assessment of variability across populations.

Conclusions

This study provides a first insight into how PPM (*T. wilkinsoni*) defoliation affects secondary growth dynamics and tree vitality indicators in *P. brutia* based on repeated histological observations over two consecutive years. A 65% reduction in the previous year's needle biomass at the beginning of the growing season led to a significantly earlier cessation of wood formation and decreased TR/CPH and EW/LW ratios, indicating negative impacts on tree vitality. The findings of this study suggest that the effects of defoliation on secondary growth are not yet fully understood and may depend on the timing and severity of defoliation as well as on species- and site-specific factors. However, understanding these dynamics is important as PPM outbreaks are projected to intensify and expand geographically under climate change (de Boer and Harvey 2020). Significant reductions in wood formation duration could limit carbon allocation into woody biomass and hydraulic capacity, thereby constraining growth recovery after defoliation and increasing vulnerability to other stressors. More comprehensive future studies should therefore explore how defoliation intensity, timing, and interactions with other stressors (e.g., drought) influence secondary growth across regions and pine species. Such knowledge will be crucial for better predicting forest resilience and carbon balance in Mediterranean ecosystems under increasing biotic and climatic stress.

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Data availability Data are available from the author upon reasonable request.

Declarations

Conflict of interest The author declares no competing interests.

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