Growth response of oaks to insect defoliation: Immediate and intermediate perspectives

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ABSTRACT

In this study, we investigate the immediate and short-term consequences of defoliation by the spongy moth *Lymantria dispar* on secondary growth of oaks (*Quercus robur* L. and *Quercus petraea* (Matt.) Liebl.), including the interplay between defoliation and water availability during the defoliation period within a large-scale field experiment in south-eastern Germany. Furthermore, the impact of defoliation on oak secondary growth is explored retrospectively based on tree core measurements.

Within the large-scale filed experiment, secondary growth of 880 oaks in 44 oak-dominated stands was monitored using permanent girth tapes over a three-year period following a spongy moth outbreak. Insecticide treatments were applied to half of the plots to obtain trees without defoliation, and canopy cover dynamics were subsequently monitored ground based and from satellites in all plots.

We found that moth defoliation significantly reduced oak secondary growth by 10–60% during the outbreak year, with the impact on secondary growth being directly proportional to defoliation intensity. The negative impact of defoliation on secondary growth was aggravated by increased water availability during the outbreak year.

In the post-outbreak year, secondary growth of oaks that had endured mild defoliation was no longer different from that of non-defoliated oaks. In contrast, oaks that had experienced substantial defoliation still exhibited a significant 10–30% reduction in secondary growth. Regardless of defoliation intensity, no further reduction in secondary growth was detected two years after the event compared to control trees. Our complementary retrospective analysis, utilizing core samples from oaks previously subjected to a defoliation event under distinct weather conditions, disclosed a strikingly analogous recovery of secondary growth from defoliation instigated by the spongy moth. Thus, validating that our experimental findings possess broad temporal transferability.

1. Introduction

Insect-induced defoliation is a significant disturbance affecting tree growth, with consequences ranging from reduced forest productivity (Clark et al., 2010) to alterations in canopy habitats and their climatic buffering capacities (Lovett et al., 2006; De Frenne et al., 2021). Interestingly, insect-induced defoliation events can also trigger beneficial ecological dynamics within forest stands, acting as agents of disturbance. For instance, such events can result in the alteration of the existing species composition and prompt the initiation of new cohorts,

thereby instigating diversification in previously mono-layered single species stands (Fajvan and Wood, 1996). While there's considerable literature on the subject (e.g., D'Andrea et al., 2019; Jacquet et al., 2012; Wiley et al., 2017), most studies delve into their investigations post-observation of defoliation. Replicated experimental studies complementing observation studies by interventions and comparing ramifications of defoliation on individual trees or entire forest stands with and without insecticide applications in replicated designs do not exist in North America or Europe (Leroy et al., 2021). Our research pioneers in this dimension, providing quantification of the amount of secondary growth reduction of deciduous oaks (Quercus robur L. and Quercus petraea Mattuschka) that occurs in the first year of a defoliation event and tracing the recovery trajectory over two post-defoliation years. Integrating insights from varying defoliation intensities, and factoring in the interplay of water availability, our study adds a richer, multidimensional perspective to the discourse (Gandhi and Herms, 2010; Jactel et al., 2012).

In the throes of climate change and the consequences for sustainable forestry and forest transformation towards robust mixed species stands, an increasing significance of the oak in Central Europe is envisaged (Mette et al., 2013; Pretzsch et al., 2013a), attributed to its inherent ecological characteristics, such as drought resistance and phenological plasticity (Kremer and Hipp, 2020; Schroeder et al., 2021). However, these forests experience more and more frequent outbreaks of defoliating moths, like the spongy moth Lymantria dispar (Lepidoptera: Erebidae). The spongy moth is one of the most critical defoliators of hardwood forests worldwide (Montgomery and Wallner, 1988). In its native range in temperate Europe and Asia, it can cause severe damage during outbreaks, though it is mostly known for its severe impacts and rapid expansion in North American forests, where it is invasive (McManus and Csóka, 2007). Over the last decades, severe defoliation events, range expansion, and increasing outbreak frequencies have been reported across Central Europe (Zúbrik et al., 2021; McManus and Csóka, 2007; Siliņš et al., 2021), Russian Far East and Central Asia (Gninenko and Orlinskii, 2003; Orozumbekov et al., 2009) and North Africa (Villemant and Ramzi, 1995).

The effect of spongy moth defoliation on oak secondary growth has been extensively documented across multiple oak species within North America, with reported growth losses varying from 30 to 60 % based on local environmental conditions and species variance (e.g., Fajvan et al., 2008; Henninger et al., 2007; Baker, 1941). In contrast, the documented effects of spongy moth defoliation oak growth in Europe are markedly less prevalent (but see Fratzian (1973) and Magnoler and Cambini (1973) who showed growth losses for up to three years following a defoliation event). However, all these studies typically delve into their investigations post-observation of defoliation utilizing tree growth data from the pre-defoliation years as a reference point, as opposed to employing a replicated experimental design to compare the growth of defoliated and non-defoliated trees directly. Furthermore, the enduring impact of defoliation on secondary growth reduction, specifically in terms of varying defoliation intensity and concurrent environmental stressors like water availability, remains largely unexplored in post-defoliation years (Gandhi and Herms, 2010; Jactel et al., 2012).

Existing research into the interactive effects between drought and defoliation are limited to young oaks or other tree species, leaving a considerable gap in the understanding of such interaction in mature European oaks (Gieger and Thomas, 2002; Quentin et al., 2012; Jacquet et al., 2014). According to the growth-differentiation balance hypothesis, moderate drought stress and herbivory can trigger a defensive shift in carbohydrate allocation, potentially enhancing the tree's acclimation to disturbances (Herms and Mattson, 1992; Matyssek et al., 2002). Nonetheless, the collective impacts of insect defoliation and drought stress are not fully comprehended, though it is proposed that defoliation could alleviate drought stress on tree metabolism by reducing transpirational demand (Quentin et al., 2012). Given these knowledge gaps, particularly regarding the post-defoliation recovery and the interaction

with water availability, further investigation is crucial.

In this study, we investigated the relative effects of defoliation by the spongy moth on the secondary growth of deciduous oaks (Quercus robur L. and Quercus petraea Mattuschka). We address the defoliation effects on secondary growth as secondary growth and productivity are key characteristics for forest management and utilization (Dieler et al., 2017; Yaffee, 1999), ecosystem functioning (Haberl, 1997; McNaughton et al., 1989), and directly related to carbon sequestration, as well to other ecosystem services (Alcamo et al., 2003). To assess the relative effects of defoliation on secondary growth of oak trees, we examined two studies in the north-western part of Bavaria, Germany (Figure S1). In a defoliation experiment we selected 44 oak dominated stands with either a high or low defoliation risk predicted based on spongy moth population surveys, treating half of these stands with insecticides (Leroy et al., 2021). Concurrently, amid the spongy moth outbreak, we measured the secondary growth of 880 oaks (20 per plot) within these oak stands over three years and used T-Lidar to document the forest structure. We utilized satellite-based remote sensing data to monitor modifications in canopy cover throughout the outbreak, thereby accurately quantifying defoliation (Bae et al., 2022). We investigated the interactive effects of defoliation and water availability on the secondary growth of oaks. Specifically, we tested the following hypotheses concerting the effect of the defoliator outbreak on the secondary growth of oak:

(H1) The secondary growth of oak is significantly reduced by defoliation caused by spongy moths.

(H2) The magnitude of secondary growth reductions intensifies with defoliation intensity.

(H3) The impacts of defoliation on oak secondary growth are mitigated by high water availability, i.e., antagonistic effects of water stress and defoliation stress.

(H4) After a one-year defoliation event, significant secondary growth losses persist for multiple years following the defoliation event.

Finally, to substantiate the temporal generalizability of our experimental results regarding the recovery of secondary growth post-defoliation by the spongy moth, we juxtaposed the insights gleaned from the defoliation experiment with the effects of defoliation on the secondary growth of 100 oaks subjected to a spatially and temporally distinct spongy moth outbreak in 1994 in a retrospective analysis using tree cores.

2. Material and methods

2.1. Defoliation experiment

2.1.1. Study design

The defoliation experiment focused on a region of 2,400 km2 in the north-western part of Bavaria, Germany (Figure S1). This region comprises oak-dominated forests, including pedunculate and sessile oak, which were severely infested by the spongy moth between 2018 and 2020. It is noteworthy that, although the spongy moth outbreak spanned over three years at the regional scale, it was restricted to the first year of investigations (2019) in the selected plots. The selection procedures and environmental characteristics of the study plots of the defoliation experiment are described in detail in Leroy et al. (2021). Briefly, the risk of defoliation of individual stands was quantified based on an index that considered primarily the density of spongy moth egg masses per oak stem, and other variables such as tree's vitality and outbreak history. Eleven blocks were established, each consisting of four forest stands, two of which had high defoliation risk and two of which had low defoliation risk, resulting in a total of 44 forest stands. The forests within the same block had similar structural and compositional characteristics (Table 1). Within each block, one high-risk stand and one low-risk stand were randomly assigned one of two treatments: (1) early suppression of spongy moth populations with insecticides to prevent defoliation or (2) no intervention. We used the Lepidoptera-specific insecticide tebufenozide, which was applied via helicopter as Mimic® (Spiess-Urania

Table 1

Detailed description of the stand characteristics of defoliation experiment plots. N, number of trees per hectare; dq, quadratic mean diameter (cm); hq, height corresponding to dq (m); BA, stand basal area ($m^2 ha^{-1}$); V, standing volume (m³/ha).

Plot	Tree species[1]	Soil type[2]	N (ha^{-1})	dq (cm)	hq (m)	BA ($m^2 ha^{-1}$)	V ($m^3 ha^{-1}$)
AHC	Oak	C-S	713	20.2	15.9	27.5	218
AHM	Oak	R-C-Rd-P	339	27.7	19.6	23.5	230
ALC	Oak / Hbm	R-C-Rd-P	603	20.7	17.2	27.8	239
ALM	Oak / Hbm	R-C	476	23.5	17.6	30.1	265
BHC	Oak	C-S	314	27.5	18.8	22.5	211
BHM	Oak-Be	C-S	459	26.3	20.6	30.5	314
BLC	Oak	S-C	406	25.1	19.5	23.8	232
BLM	Oak	C-S	622	23.2	20.2	30.3	305
DHC	Oak / Hbm	S-C-Rd-P	615	23.8	18.2	40.1	365
DHM	Oak / Hbm	S-C-Rd-P	357	26.5	18.6	27.7	258
DLC	Oak / Hbm	S-C-Rd-P	753	21.6	17.2	38.9	334
DLM	Oak / Hbm	S-C-Rd-P	744	19.9	15.7	35.3	276
FHC	Oak-Be	C-P-R-Pd	243	31.1	21.2	22.7	240
FHM	Oak-Be	C-S-R-P	467	25.1	19.0	36.4	346
FLC	Oak-Be	C-Pd	200	40.9	26.8	27.8	373
FLM	Oak-Be	C-Pd-S	244	36.4	24.4	29.0	353
GHC	Oak-Be	S-C	438	23.8	16.0	28.8	231
GHM	Oak-Be	S-C	261	33.5	21.8	27.7	301
GLC	Oak / Hbm	C-S	513	22.0	17.2	30.1	258
GLM	Oak / Hbm	C-S	632	19.4	16.1	29.0	233
HHC	Oak-Be / Hbm	C	437	29.1	22.0	33.6	370
HHM	Oak-Be / Hbm	Rd-C-S	528	24.9	19.1	31.5	301
HLC	Oak / Ld	Rd-C	503	26.5	21.0	29.0	305
HLM	Oak / Ld	Rd-C	640	24.7	20.2	34.3	346
JHC	Oak (mixed)	R-C	552	25.5	19.8	35.2	348
JHM	Oak (mixed)	R-C	718	20.8	19.0	29.7	281
JLC	Oak (mixed)	S-C	382	26.7	22.1	25.8	285
JLM	Oak (mixed)	S-C	294	31.7	22.3	31.9	357
MHC	Oak / Hbm	C-S	512	27.2	21.2	41.7	443
MHM	Oak / Hbm	C-S	323	30.2	22.1	28.7	318
MLC	Oak / Hbm	C-S	503	27.7	20.7	39.1	405
MLM	Oak / Hbm	C-S	369	30.2	19.5	35.1	342
NHC	Oak / Mp-Hbm	R-P-S	475	25.0	17.8	28.6	254
NHM	Oak / Mp-Hbm	R-P-C	359	25.6	18.2	25.1	228
NLC	Oak / Mp-Hbm	G-S-C	433	25.1	18.1	30.1	273
NLM	Oak / Mp-Hbm	G-S-C	293	29.1	19.9	24.9	247
OHC	Oak / Mp	C-S	394	27.0	18.5	29.0	267
OHM	Oak / Mp	C-S	672	23.2	17.1	36.1	309
OLC	Oak / Ld	S-C	214	33.9	23.2	23.8	276
OLM	Oak / Ld	S-C	190	33.3	22.4	20.5	231
SHC	Oak-Be / Hbm	C-S	296	31.7	21.5	32.6	350
SHM	Oak-Be / Hbm	C-S	325	28.6	20.8	30.1	313
SLC	Oak-Be / Hbm	C	312	30.1	23.3	26.9	314
SLM	Oak-Be / Hbm	C-S	298	29.2	23.2	26.3	305

[1] Dominant tree species (overstory / understory); Oak (*Quercus* sp.), Be = European beech (*Fagus sylvatica*), Hbm = hornbeam (*Carpinus betulus*), Ld = linden (*Tilia* sp.), Mp = field maple (*Acer campestre*).

[2] Soil type; C = Cambisol, G = Calcareous gley, P = Pelosol, Pd = Podzol, R = Regosol, Rd = Rendzina, S = Stagnosol; Data source: Bavarian State Office for the Environment, https://www.lfu.bayern.de.

Chemicals, Hamburg, Germany) from May 3 to May 23, 2019, at the rate of 750 ml ha-1 (i.e., 180 g active ingredient ha-1), as part of an operational treatment campaign conducted in northwestern Bavarian forests at high risk of defoliation. Spraying was conducted over the whole area of each study plot. In both treated and untreated plots, all subsequent investigations were carried out within a 4.5 ha-subplot established around the plot centroid.

2.1.2. Tree sampling

In the defoliation experiment, we identified 20 central deciduous oaks (pedunculate and sessile oak) at distances of 25, 50, 75, 100, and 125 m from the plot centre in four transects following the cardinal directions in each plot. We measured the stem diameter, $d_{1.3}$, and stem basal area, *ba*, of the total of 880 central oaks using long-term girth tapes at 1.3 m above ground level in three consecutive years: 2019, 2020, and 2021. The annual stem basal area increment, *iba*, was calculated based on the two subsequent surveys' differences. For a description of the central tree characteristics under study see Table S1. We used terrestrial laser scanning (TLS) to measure tree positions, heights, and distances between trees to obtain stand characteristics. To estimate variables per

hectare, we calculated the expansion factor using the distance between the central oak tree and its fifth closest neighbour in all 80 six-tree samples per block. We then calculated the circular area for each six-tree sample using the measured distances as the radius and summed up all the areas of one block. Finally, we divided 10,000 by this area to obtain the expansion factor for calculating variables per hectare. See Table 1 for a detailed description of the stand characteristics per plot and Fig. 3 in Leroy et al. (2021) for a visual representation of the sampling design.

2.1.3. Quantification of defoliation intensity

We used foliage cover as a measure of defoliation and characterised the outbreak disturbance caused by the intensified feeding of spongy moths and caterpillar development during spring and summer (late April to early July; Leonard, 1981). For calculating foliage cover we employed Sentinel-1C-band SAR data to monitor canopy development and followed the methodology described in Bae et al. (2021) and Leroy et al. (2023). Specifically, we calculated the canopy development index (CDI; unit: dB) for each year at different points of time t_n as:

$$CDI_{t_n} = \gamma^0_{VV} t_n - \gamma^0_{VH} t_n$$

where γ^0_{VV} and γ^0_{VH} are daily mean values of two level-1 ground-range-detected high-resolution (GRDH) product polarisations within each plot at different points in time. These polarisations correspond to radar pulses that are vertically transmitted and vertically received (VV) and vertically transmitted and horizontally acquired (VH). The pixel spacing of these products is 10 m, and they measure the reflectivity of the radar target. To improve interpretability and reduce noise, we normalised the canopy development index, CDI, by dividing it with the baseline CDI measured at leaf-off t_0:

$$NCDI_{t_n} = \frac{CDI_{t_n} - CDI_{t_0}}{CDI_{t_0}}$$

The normalised canopy development index, $NCDI_{t_n}$, can be understood as an estimate of the proportional increase in canopy cover at different points in time (t_n) compared to leaf-off (t_0). CDI_{t_n} and $NCDI_{t_n}$ values on the plots under study were validated by optical (Sentinel-2) and terrestrial laser scanning (TLS) data as well by intensive caterpillar sampling from canopy fogging (Bae et al., 2022). Further details on the computation of the canopy development index can be found in Bae et al. (2022) and Leroy et al. (2023).

For each plot, we evaluated the intensity of defoliation by discerning the difference between the normalised canopy development indices at the first peak of leafing, $NCDI_{t_{peakleafing}}$, and at peak defoliation (prior to a resurgence in foliage cover due to refoliation), $NCDI_{t_{peakdefoliation}}$. This difference was subsequently normalised by it with $NCDI_{t_{peakleafing}}$. The derived metric provides a relative defoliation measure, spanning from 0 (indicating no defoliation) to 1 (denoting absolute defoliation).

2.2. Restrospective analysis

To test how far our results from the defoliation experiment can be replicated in other time spans, we also conducted a retrospective analysis using tree cores. Measurements for this retrospective analysis were taken at two additional oak stands that were subjected to a severe spongy moth outbreak in 1994 (Figure S1). The spongy moth population was back then suppressed with insecticides in one of them but the other was not treated and underwent substantial defoliation. However, since these two additional oak stands were not experimentally studied at the time of the 1994 spongy moth outbreak, there was unfortunately no data available on the exact intensity of defoliation in 1994.

Both stands were similar in every other regard (Table S2). In June 2021, 50 dominant trees in each stand (one control and one treated) were selected and sampled for retrospective analyses of defoliation effects on annual secondary growth increments. For each tree, we measured the current diameter at breast height ($dbh_{1.3}$) as well as the tree height. Annual secondary growth increments were obtained from each tree by taking two cores from the eastern and northern cardinal directions using a 5 mm borer (Haglöf, Sweden) at $dbh_{1.3}$. A total of 200 cores were collected from 100 trees, and after sanding and measuring, visual crossdating was performed to identify distinct growth patterns (Stokes and Smiley, 1996). Statistical cross-correlation functions in the dplR library of the R statistical environment (Bunn, 2008; R Core Team, 2022) were employed to verify the accuracy of crossdating. To remove age- and size related secondary growth trends, the raw ring-width series were transformed into dimensionless ring-width indices, rwi, by fitting a 30-year cubic spline with a 50 % frequency response cut-off (Cook et al., 1990; Fritts, 1976). Finally, the two rwi series per tree were averaged, resulting in 100 rwi series. A chronology was built for each plot by calculating the Tukey's biweight robust mean of all respective rwi.

2.3. Climate data

We used climate data from the German Meteorological Service (DWD Climate Data Center, 2021a, 2021b) for all our study plots. Gridded climate data included monthly precipitation (mm) and mean, maximum, and minimum temperature (°C) in a spatial resolution by 1×1 km for the entire period under consideration. To investigate the impact of water availability on the correlation between defoliation and secondary growth, we utilized the Standardised Precipitation Evapotranspiration Index (SPEI) (Vicente-Serrano et al., 2010). The SPEI is a statistical indicator, that indicates dry and humid periods based on the climatic water balance (CWB = precipitation – potential evapotranspiration). This index allows for assessing various drought durations, has low data requirements, and is responsive to global warming due to its multiscalar approach. To derive potential evapotranspiration we applied the Hargreaves equation (Beguería and Vicente-Serrano, 2017; Hargreaves, 1994). For describing water availability, we chose the September SPEI integrated over six months (SPEI6, April to September), as this period was shown to encompass the duration of the cambial activity of oak trees in central Europe (Puchałka et al., 2017).

2.4. Statistical analyses

We performed all analyses using R version 4.1.2 (https://www.r-project.org) and applied linear mixed models (LMMs) with the lme4 package (Bates et al., 2015) in combination with the package lmerTest (Kuznetsova et al., 2017). To check for overdispersion, heteroscedasticity and distribution of residuals, we used the packages DHARMa (Hartig, 2022) and lmfor (Mehtätalo and Kansanen, 2022). All statistical inference was performed using Wald tests and reported effect sizes are based on estimated marginal means (EMMEANs for the categorical predictor variable, e.g., calendar year) and estimated marginal means of linear trends (EMTRENDs for continuous predictor variable, e. g. defoliation intensity) calculated with the package emmeans (Lenth, 2022).

Effects of defoliation on secondary growth and mediating effects of water availability. We applied linear mixed effects models to the tree secondary growth data in 2019 to assess the effects of spongy moth-induced defoliation on secondary growth of oaks within the defoliation experiment. We tested whether secondary growth decreased significantly with increasing defoliation intensity and whether water availability played a mediating role in the growth response of oak to the defoliation (H1-H3). The model structure was as follows:

$$\begin{aligned}
\ln(iba_{ij;2019}) = {} & a_0 + a_1 \times \ln(basic\ area_{ij;2019}) + a_2 \times defoliation\ intensity_{i;2019} \\
& + a_3 \times water\ availability_{i;2019} + a_4 \times defoliation\ intensity_{i;2019} \\
& \times water\ availability_{i;2019} + b_i + c_i \times \ln(basal\ area_{ij;2019}) + \varepsilon_{ij}
\end{aligned}$$

$$(1)$$

where *iba* represented the annual stem basal area increment in 2019. The independent variables were the trees' basal area at the beginning of the vegetation period in 2019, the defoliation intensity, the water availability (SPEI6), and the two-way interaction of defoliation intensity and water availability. For defoliation intensity, we used values measured during the peak defoliation period (i.e., July 2019). The indexes i and j represented the ith plot and the jth tree in plot i. The fixed effects were covered by the parameters a_0-a_4. If the interaction term was significant, the contributing main effects were kept in the model even when not significant, following a protocol suggested by Zuur et al. (2009). To account for autocorrelation, random effect b_i and c_i ($b_i\ N(0, \tau_1^2), c_i\ N(0, \tau_2^2)$) were applied at the plot level. While the random effect b_i relates to the intercept a_0, the random effect c_i refers to the slope a_1. The uncorrelated remaining errors are ε_{ij} ($\varepsilon_{ij}\ N(0, \sigma^2)$). All predictor variables were standardized ($x_{standardized} = (x - \overline{x}_{sample})/sd_{sample}$) to facilitate the models' interpretability and allow for direct comparison between regression coefficients (Schielzeth, 2010).

Recovery of secondary growth from defoliation. Using the complete dataset of the defoliation experiment spanning from 2019 to 2021, we

tested the temporal effects of defoliation on secondary growth of the oaks in the years following the defoliator outbreak (H4) by formulating a mixed linear regression model as follows:

$$\ln(iba_{ijk}) = a_0 + a_1 \times \ln(basal\ area_{ijk}) + a_2 \times year_{ijk} + a_3$$
$$\times water\ availability_{ik} + a_4 \times defoliation\ intensity_{i;2019} + a_5$$
$$\times year_{ijk} \times defoliation\ intensity_{i;2019} + b_i + b_{ij} + (c_i$$
$$+ c_{ij}) \times \ln(basal\ area_{ijk}) + \varepsilon_{ijk} \qquad (2)$$

In this model, the indexes i, j, and k represented the ith plot, the jth tree in plot i, and the kth observation of tree j in plot i. The notation of the variables is the same as in Equation (1). To include potential growth trends, we introduced the variable year, which indicates the calendar year the trees grew. A significant estimate of a_2 would indicate that there was a temporal trend of the basal area - basal area increment relationship's level, while a significant value of a_5 indicates a temporal trend in the effect of the 2019 defoliation on tree secondary growth. The random effects in this model were b_i, b_{ij}, c_i, and c_{ij} ($b_i\ N(0, \tau_1^2)$, $b_{ij}\ N(0, \tau_2^2)$, $c_i\ N(0, \tau_3^2)$, $c_{ij}\ N(0, \tau_4^2)$). The first random effects, b_i and c_i, were related to the plot level and considered that all observations from the same plot were not statistically independent. The second random effects, b_{ij} and c_{ij}, refer to the tree level. Importantly, spongy moth abundances naturally collapsed in the untreated plots after 2019 leading to no outstanding level of defoliation in any plot in 2020 (Leroy et al, 2023), such that the outbreak turned out to be a single year event. Therefore, we only used defoliation intensity measured in 2019 in the model testing for outbreak effects over the 3 years of the study. Again, all predictor variables were standardized.

Retrospective analyses. We set up a mixed linear regression model to compare the effects of defoliation on secondary growth between the 2019 defoliator outbreak (Defoliation experiment) and a previous spongy moth outbreak in 1994 under different weather conditions. For comparison, we used the dimensionless ring-width indices, *rwi*, of the trees from the two additional plots five years before the defoliator outbreak in 1994 and five years after the defoliator outbreak. The following model describes the dimensionless ring-width indices, *rwi*, as a function of the calendar year, whether the trees were treated with insecticides or not (control group), and their interaction:

$$\ln(rwi_{ijk}) = a_0 + a_1 \times treatment_{ij} + a_2 \times year_{ijk} + a_3 \times treatment_{ij}$$
$$\times year_{ijk} + b_j + \varepsilon_{ijk} \qquad (3)$$

In this model, the indexes i, j, and k represent the ith plot, the jth tree in plot i, and the kth observation of tree j in plot i. The random effect, b_i ($b_j\ N(0, \tau_1^2)$) was applied on the tree-level. Finally, $\varepsilon_{ijk,s}$ represents independently and identically distributed errors ($\varepsilon_{ijk}\ N(0, \sigma^2)$).

3. Results

3.1. Defoliation experiment

3.1.1. Variation in secondary growth, defoliation intensity, and water availability

Our data shows considerable variation in both secondary growth and defoliation for the studied oaks during the 2019 defoliator outbreak (Table S1, Fig. 1). The untreated oaks (control) exhibited defoliation values measured at the peak defoliation period (July) ranging from 0 % to 97.4 %, averaging at 36.1 %. Trees that received insecticide treatment presented a lower range and average, with defoliation values varying from 0 % to 24.2 % and an average of 6.6 %, suggesting a protective effect of the insecticide treatment on foliage cover (Fig. 1). Nevertheless, in four plots where intense defoliation was anticipated during the site delineation, only minimal defoliation transpired, thus creating a gradient of defoliation intensities across the plots. Importantly, the population of spongy moths witnessed a natural decline in all plots post-
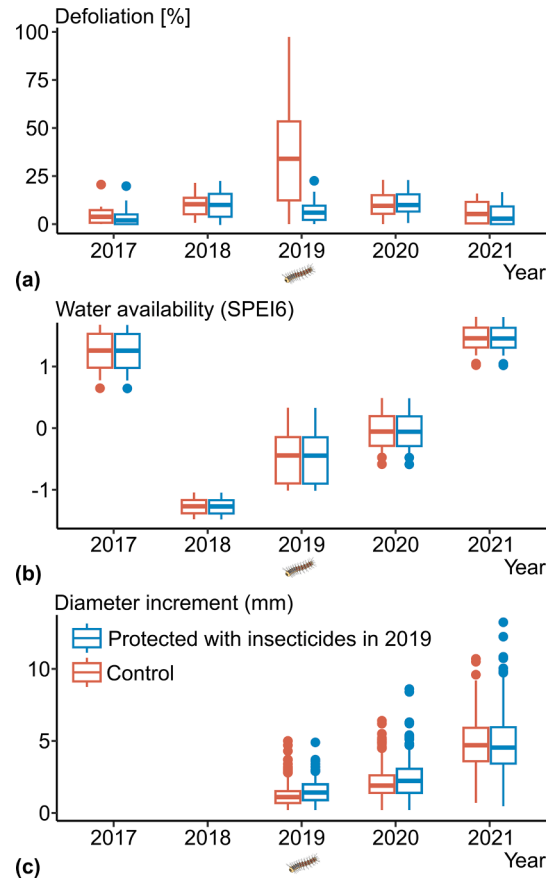
Fig. 1. Descriptive statistics captured in boxplots, encompassing (a) defoliation in percent, (b) water availability, quantified via SPEI6, and (c) stem diameter increment in mm. These variations were studied across two distinct scenarios: treated with insecticides in 2019 (blue) and no treatment with insecticides (control, red). The data, amassed from raw observational records, span two pre-defoliation years of 2017–2018, the year of the defoliator outbreak in 2019, and two post-defoliation years of 2020–2021. Note that diameter increment data were not available prior to the experiment start in 2019.

2019, resulting in an absence of any outstanding level of defoliation in 2020 (Fig. 1). Consequently, the outbreak manifested as a solitary annual occurrence.

Water availability, measured as SPEI6, remained consistent between the two groups, with values spanning from −1.01 to 0.31 (mean −0.52) in the year of the defoliator outbreak 2019 (Table S1). Secondary tree growth, quantified as diameter increment, was markedly lower in the outbreak year (2019) for both groups, but especially pronounced in the untreated oaks. Average oak diameter increment in control plots was 1.11 mm, considerably lower than the 1.55 mm observed in the insecticide-treated plots. In subsequent years, 2020 and 2021, secondary growth rate increased for both groups, almost paralleling each other in 2021 (Fig. 1, Table S1).

Comparative data analysis from 2017 to 2021 indicates that the differences in defoliation intensity observed during the outbreak year were not present in the years preceding or following the outbreak (Fig. 1). Delving into the defoliation intensity metrics for 2017 and 2021 reveals that during years characterized by endemic herbivory only, there emerges a baseline level of herbivory, attributable to all other leaf chewers within the canopy, approximating 5–10 % of foliage cover. Yet, the strikingly elevated levels of defoliation intensity in the epidemic phase (2019) underscore the marginal impact of the baseline level herbivory by other leaf chewers in the canopy during the spongy moth outbreak.

The patterns of water availability and oak diameter growth were

similar over this period (2019–2021), with a notably dry year in 2018 (SPEI6 values < -1), possibly leading to the low secondary growth values found in 2019.

3.1.2. Effects of defoliation on secondary growth and mediating effects of water availability (H1-H3)

We found that stem basal area and the defoliation intensity had a significant (p < 0.001) positive effect on stem basal area increment, suggesting that defoliation is a critical factor in secondary growth (Table 2). In addition, we examined the relationship between defoliation intensity and secondary growth in terms of water availability and the results showed that the water availability had a significant (p < 0.05) positive effect on stem basal area increment. We further find a significant (p < 0.05) negative interaction between defoliation intensity and water availability, indicating that the effect of defoliation on secondary growth was dependent on water availability (Table 2).

While the annual stem basal area increment of oaks that were completely defoliated in the outbreak year was reduced by an average of 55 % compared to non-defoliated oaks on plots with a better water availability, it was reduced by only 15 % on average on plots with poor water availability in 2019 (Fig. 2a). On plots with comparatively better water availability, even minor defoliation resulted in significantly lower annual basal area increments of oaks in the year of the outbreak (-10 %). On plots with low water availability, however, the secondary growth of oaks which experienced only minor defoliation was not significantly different from oaks that were not defoliated (Fig. 2a).

Specifically, we found that when water availability was adequate, the impact of spongy moth defoliation on secondary growth increased significantly with increasing defoliation intensity. On the other hand, if

Table 2
Parameter estimates of the model analyzing the effects of defoliation on secondary growth and mediating effects of water availability in the year of the defoliator outbreak (2019) (Model 1) and of the model describing the recovery of secondary growth from defoliation (Model 2) of the defoliation experiment oaks.

Fixed Effect	Parameter	Estimate	se	p-value
Model 1 (growth reductions in the first year of the outbreak)				
Fixed part				
	a_0	**1.85**	0.0402	**<0.0001**
ln(basal area)	a_1	**0.337**	0.0263	**<0.0001**
Defoliation intensity	a_2	**−0.189**	0.0472	**<0.0001**
Water availability	a_3	**0.0903**	0.0429	**0.0414**
Defoliation intensity: Water availability	a_4	**−0.111**	0.0559	**0.0448**
Random part and residual				
	var(b_i)	0.206		
	var(c_i)	0.0847		
	cor(b_i, c_i)	0.444		
	σ^2	0.528^2		
Model 2 (recovery from defoliation)				
Fixed part				
	a_0	**1.91**	0.048	**<0.0001**
ln(basal area)	a_1	**0.39**	0.0236	**<0.0001**
Year [2020]	a_2	**0.562**	0.023	**<0.0001**
Year [2021]	a_2	**1.39**	0.0799	**<0.0001**
Water availability [SPEI6]	a_3	**0.0353**	0.0196	**0.0438**
Defoliation intensity [2019]	a_4	**−0.162**	0.0365	**0.0001**
Year [2020]: Defoliation intensity [2019]	a_5	**0.0859**	0.0185	**<0.0001**
Year [2021]: Defoliation intensity [2019]	a_5	**0.167**	0.0184	**<0.0001**
Random part and residual				
	var(b_i)	0.211		
	var(c_i)	0.0803		
	cor(b_i, c_i)	−0.405		
	var(b_{ij})	0.319		
	var(c_{ij})	0.14		
	cor(b_{ij}, c_{ij})	0.491		
	σ^2	0.356^2		

water availability decreased, the effect of increasing defoliation intensity also decreased. The post-hoc test by estimated marginal mean of linear trend (EMTREND) revealed that the interaction between defoliation intensity and water availability was significantly different from zero for water availability values (SPEI6) of −1 and −0.5 (with a decreasing trend with lower water availability), but not significantly different from zero for a water availability value of 0 anymore (Table S3). The EMTREND shows the mean change in the response variable annual stem basal area increment for a unit change in the continuous predictor variable, i.e. defoliation intensity, adjusted for other predictor variables in the model, i.e. water availability. We found that basal area increment decreased with increasing defoliation intensity, with an EMTREND of −1.48, −0.908, and −0.339 for water availability values of 0, −0.5, and −1, respectively (Table S3). Overall, these findings suggest that the effect of defoliation on secondary growth was strongest when water availability was, according to our data, high, but weaker under moderate or low water availability conditions.

3.1.3. Recovery of secondary growth from defoliation (H4)

Recovery of secondary growth from the defoliation event in 2019 was analysed for three consecutive years, from 2019 to 2021. First, we found a significant positive effect of stem basal area and the water availability, and a significant negative effect of the defoliation intensity in 2019 on annual stem basal area increment (p < 0.001). Furthermore, we found that the annual stem basal area increment was significantly higher in the years following the defoliator outbreak 2020 and 2021, compared to the year of the defoliator outbreak (Table 2). We also observed a significant interaction (p < 0.001) of the calendar year and defoliation intensity in 2019, indicating that the effect of defoliation intensity in 2019 on stem basal area increment varied depending on the year. Under average water availability conditions, the secondary growth losses were contingent upon the intensity of defoliation intensity during the outbreak year, ranging from 10 to 60 percent. In 2020, the first post-defoliation year, trees with minor defoliation intensity (25 %) no longer exhibited dissimilar secondary growth patterns compared to those that were not defoliated in 2019 (Fig. 2b). Trees with more severe defoliation displayed a 10 to 30 percent reduction in stem basal area growth during the first post-defoliation year. In 2021, the second post-defoliation year, we discerned no significant disparities in stem basal area growth between defoliated and non-defoliated trees, regardless of defoliation intensity in 2019 (Fig. 2b). Specifically, the post-hoc test by EMTREND showed a significant trend (p < 0.001) of defoliation intensity in 2019 on annual stem basal area increment in 2019 (defoliation intensity trend = -0.162; Table S4). In 2020, the first post-defoliation year, the trend was smaller but still significant (p < 0.05; defoliation intensity trend = -0.0765). However, in 2021, the second post-defoliation year, although a trend was still observed, it was not significantly different from zero (p = 0. 898; defoliation intensity trend = -0.0005) (Table S4). Overall, our results indicate that the effect of defoliation intensity in 2019 on secondary growth varied by calendar year, with a stronger effect in the year of the defoliation event and diminishing effects in subsequent years (Fig. 2b).
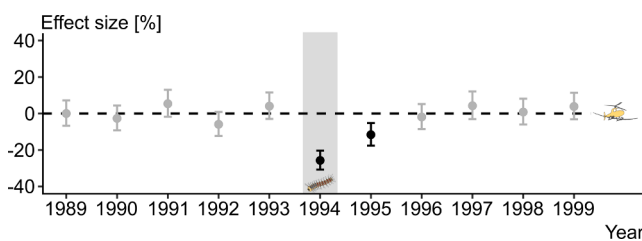
3.2. Retrospective analyses

We analyzed the effects of a defoliation event in 1994 on two additional selected plots, using data from 5 years prior and 5 years after the spongy moth outbreak in 1994 to allow for comparison with the effects of the defoliation experiment.

We found a strong effect of the calendar year on ring width indices, rwi, indicating that secondary tree growth varied significantly from year to year (Table S5). In addition, we found a significant interaction effect of treatment and calendar year during 1994 and 1995 (Table S5). Our analysis showed that the secondary growth of non-defoliated and defoliated trees did not differ significantly prior to their defoliation in 1994. However, the defoliation event in 1994 significantly reduced ring
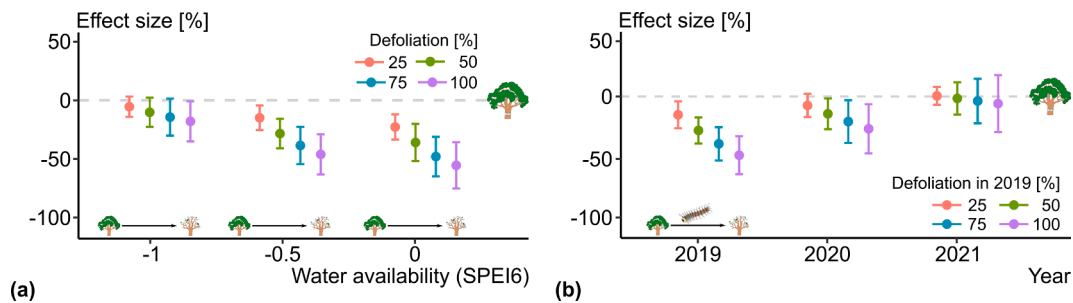
Fig. 2. (a) Effect sizes derived from Equation (1), delineating the influence of divergent defoliation intensities on secondary growth of oaks from the defoliation experiment during the defoliator outbreak in 2019 under assorted water availability conditions. (b) Effect sizes derived from Equation (2), delineating the influence of divergent defoliation intensities in the year of the defoliator outbreak 2019 on secondary growth of oaks from the defoliation experiment throughout the defoliator outbreak in 2019 and the two post-defoliation years 2020 and 2021. The 95% confidence intervals underscore variability among trees. The dashed horizontal line at value 0 identifies trees that were subjected to insecticide treatment or remained untouched by the defoliation. Note that in case of (a) the basal area of the trees and in case of (b) both the basal area of the trees and the water availability were uniformly maintained at the mean for this predictions. See Figure S2 for a visualization of stem basal area increment versus defoliation in 2019 and varying water availability values (Fig. S2a) and recovery years (Fig. S2b), respectively.

Fig. 3. Effects sizes derived from Equation (3), illustrating the impact of defoliation on the dimensionless ring-width indices, *rwi*, of the oaks from the two additional plots for retrospective analysis, five years pre-defoliation, during the year of the defoliator outbreak in 1994, and 5 years post-defoliation. The 95 % confidence intervals underscore variability among trees. The dashed horizontal line at value 1 identifies trees that were subjected to insecticide treatment in 1994. See Figure S3 for a prediction of ring-width indices of trees that underwent substantial defoliation in 1994 and trees which were protected from defoliation with insecticides over all shown years.

width indices values in the control plot trees in both 1994 and 1995 compared to the treated group (Fig. 3). Specifically, in the year of the defoliator outbreak 1994, the ring width indices values of the control plot trees were reduced by 20–30 % compared to the treated group. In the first year after the defoliation event (1995), the ring width indices values of the control group were reduced by 10–15 %. However, in the second year after the defoliation event and subsequent years, the ring width indices values of the control group were no longer significantly different from the treated group (Fig. 3).

4. Discussion

Our large-scale, three-year defoliation experiment explored the effects of spongy moth defoliation on oak secondary growth across 44 stands, illuminating key findings. A significant impact on stem basal area increment was noted even when only a small proportion of the foliage was consumed, with secondary growth losses of 10–60 % in the outbreak year correlating to defoliation intensity (H1, H2). Defoliation effects were amplified with high water availability, while moderate to low water availability lessened the impact, despite only minor fluctuations in water availability values (H3). Notably, defoliation consequences extended beyond the outbreak year, with secondary growth losses of up to 40 % in the first post-defoliation year yet were negligible by the second post-defoliation year (H4). Comparative analysis with a 1994 defoliation event revealed similar temporal patterns. In both the outbreak and subsequent year, defoliation decreased ring width indices (rwi) by 20–30 % and 10–15 % respectively compared to treated trees, while differences were insignificant in the second post-defoliation year,

reinforcing our recent findings from the defoliation experiment. Thus, our study underscores the sustained influence of defoliator outbreaks on oak secondary growth and offers insight into the impacts of insecticides on management.

4.1. Defoliation significantly reduces secondary growth

Our findings unequivocally reveal that spongy moth defoliation can cause substantial losses in stem basal area growth in oak trees within a short time of the defoliation event, with effects persisting one year beyond the year of defoliation. In this investigation, secondary growth loss exhibited a linear relationship with defoliation intensity, culminating in approximately 40 % to 60 % secondary growth loss in severely defoliated trees during the outbreak year. Spongy moth defoliation primarily inhibits secondary tree growth through diminished leaf biomass (Clark et al., 2010; Fajvan and Wood, 1996; Naidoo and Lechowicz, 2001), as reduced photosynthetic leaf area and carbohydrate supply constrain carbon allocation to secondary tree growth, consequently leading to decreased secondary growth (Ferretti et al., 2021; Jacobs et al., 2022; Waring, 1987).

Our observations regarding defoliation's effect sizes on secondary growth correspond with the conclusions of other studies that examined the impacts of spongy moth defoliation on oak tree secondary growth. Our finding of 40–60 % secondary growth loss in severely defoliated trees during the outbreak year overlaps with the broad range (29.6 – 56.0 %) reported by Naidoo and Lechowicz (2001) for northern red oak (Quercus rubra L.), sugar maple (Acer saccharum Marsh.), and white ash (Fraxinus americana L.) in southwestern Quebec, and is congruent with radial growth losses of about 40 % after near-total defoliation from outbreaks of spongy moth found by Rubtsov (1996) for red oak in a Russian study and Hennigar et al. (2007) in New Brunswick, Canada. The peak losses in our study are more consistent with the higher values reported by Minott and Guild (1925) (52.2 %) and Baker (1941) (58.0 %) for various oak species in New England following intense defoliation. The substantial volume losses reported by Fajvan et al. (2008) (54 % for white oaks (Quercus alba L.), 40 % for red oaks) during spongy moth outbreaks underscore the potential magnitude of these defoliation events' impacts. It is interesting to note the lesser growth losses of 33–43 % reported by Baker (1941) in plots of black and white oak and 32–50 % reported by Brown et al. (1979) and May and Killingbeck (1995) in plots of white oak and scrub oak (Quercusilicifolia Wangenh.) in Rhode Island forests. These disparities in secondary growth loss could be attributable to differences in the examined species, the level of defoliation, or local environmental factors.

Our observation that secondary growth loss magnitude is directly proportional to the quantity of foliage removed by insect herbivores, as well as the persistence of secondary growth loss into the first post-

defoliation year aligns with the prevailing consensus (e.g. Baker 1941; Muzika and Liebhold 1999; Kulman, 1971). Nonetheless, in a *meta*-analysis about the effects of defoliation by the processionary moth on pine or cedar growth, Jacquet et al. (2012) reported that the influence of defoliation intensity seemed to stagnate at intensities exceeding 50 %.

Our findings indicate that the secondary growth of oaks, which experienced minor defoliation in 2019, was not different in the first year post-defoliation compared to oaks that were not defoliated. Deciduous trees, storing carbohydrates in woody tissues, can quickly recover from defoliation by mobilizing these reserves for secondary foliage (Chapin et al., 1990). Furthermore, reduced growth phases can lower resource consumption, leading to resource accumulation in the soil. This can result in a significant growth surge when conditions improve (Körner, 2002; Pretzsch et al., 2013b). However, oaks that underwent more substantial defoliation still exhibited a significantly reduced secondary growth (10 to 30 percent) compared to their non-defoliated counterparts in the year following the defoliation event. We attribute the continued reduced secondary growth of heavily defoliated oaks in the first post-defoliation year to the fact that recovery from significant defoliation can result in profound shifts in carbon allocation amongst the tree's various functions, wherein carbohydrate storage is prioritized over secondary growth (Wiley et al., 2017). Notably, our findings show that two years post-defoliation, the secondary growth of defoliated oaks matches that of non-defoliated ones, consistent with studies showing that growth losses were evident for not longer than three years (Fratzian 1973; Magnoler and Cambini 1973; Twery 1987).

However, besides these immediate effects, recurrent defoliation can have lasting impacts, such as an increased risk of stem embolism impairing water transport (Aguadé et al., 2015; Hillabrand et al., 2019). Moreover, it can influence annual tree ring patterns, potentially impacting timber quality and the tree's resilience to future stresses (Pretzsch, 2021; Hilmers et al., 2022; Schmied et al., 2022).

4.2. Interactive effects of water availability and defoliation on oak annual secondary growth

Interestingly, our results indicate that the effect of defoliation on secondary growth is reduced under conditions of limited water availability. This is consistent with reviews that predict antagonist effects of biotic and abiotic stresses on growth in woody plants (Hawkes and Sullivan, 2001; Wise and Abrahamson, 2007) and confirms our initial hypothesis of antagonist effects, i.e., that water stress would reduce the impact of defoliation on secondary growth by reducing water losses through transpiration by the tree crown. Furthermore, Kolb et al. (1999) found higher stem biomass in potted Douglas-fir seedlings submitted to western spruce budworm defoliation under low- than under high-moisture conditions, which is compatible with antagonist effects of water stress and defoliation. In Eucalyptus globulus (Eyles et al., 2009; Quentin et al., 2012) and in red oak (Quercus rubra) seedlings (McGraw et al., 1990), tree growth was unaffected by defoliation under different water treatments, which might be due to compensatory responses to defoliation and drought. However, these observations contrast with the results of a *meta*-analysis that showed larger impacts of defoliation on growth in water-stressed trees (Jactel et al., 2012) and an ecology review reporting the additive effects of harsh environmental conditions and insect herbivory on plant performance (Valladares et al., 2007), which is consistent with the findings by Haavik et al. (2015) that successive drought events combined with persistent insect activity pose an important threat to oak vitality.

The observed interactive effects of water availability and defoliation on oak secondary growth have important implications for forest management and conservation. As climate change is projected to increase the frequency and severity of droughts in many regions (IPCC, 2021), understanding the combined impacts of water stress and defoliation on oak secondary growth can inform adaptive management strategies. We postulate, consonant with the growth-differentiation balance

hypothesis, that oaks situated in arid environments exhibit superior physiological and morphological acclimation to stress and perturbations (Herms and Mattson, 1992; Matyssek et al., 2002). Concurrently, in the face of limited resources, these oaks may not only manifest heightened defensive capabilities but also exhibit augmented root-to-shoot ratios and subterranean storage capacities to counterbalance defoliation and facilitate recuperation (Hochwender et al., 2012; Reich et al., 1980). Additionally, certain research illustrates trees' acclimation to drought in naturally arid areas (Brito et al., 2019; Grote et al., 2016; Ruehr et al., 2019). Such findings could imply an improved adaptability to defoliation in trees situated in inherently dry sites.

5. Conclusions and management implications

Our results provide new evidence for trade-offs in the management of spongy moths in oak forests from the perspective of secondary tree growth. Overall, our research corroborates that defoliation by the spongy moth significantly influences the secondary growth of oak trees in the year of the defoliator outbreak, even if only a minor portion of the foliage is consumed. Our findings also elucidate that the loss of growth is more pronounced at sites with greater water availability. Our results indicating a linear correlation between defoliation intensity and growth losses imply that estimations of defoliation by spongy moths could be seamlessly integrated into tree growth models, facilitating the prediction of the impacts of spongy moth outbreaks on carbon sequestration in temperate forests. Nonetheless, our findings reveal that the secondary growth two years post-defoliation is no longer disparate between defoliated and non-defoliated trees, thereby bearing significant implications for forest management and nature conservation. The determination of whether to administer chemical treatments to infected stands during spongy moth infestations ultimately hinges on a multifaceted evaluation, contingent upon the objectives of forest policy and management. Factors such as biodiversity conservation, recreational appeal, landscape aesthetics, carbon sequestration, and other ecosystem services must be judiciously considered, along with stand performance in terms of growth stability and productivity.

CRediT authorship contribution statement

Torben Hilmers: Conceptualization, Data curation, Formal analysis, Methodology, Visualization, Writing – original draft, Writing – review & editing. **Benjamin M. L. Leroy:** Conceptualization, Data curation, Writing – review & editing. **Soyeon Bae:** Data curation, Formal analysis, Writing – review & editing. **W. Andreas Hahn:** Writing – review & editing. **Sophia Hochrein:** Writing – review & editing. **Martin Jacobs:** Data curation, Writing – review & editing. **Hannes Lemme:** Funding acquisition, Writing – review & editing. **Jörg Müller:** Conceptualization, Funding acquisition, Writing – review & editing. **Gerhard Schmied:** Methodology, Writing – review & editing. **Wolfgang W. Weisser:** Conceptualization, Funding acquisition, Project administration, Writing – review & editing. **Hans Pretzsch:** Conceptualization, Funding acquisition, Methodology, Writing – review & editing.

Declaration of Competing Interest

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

Data availability

Data will be made available on request.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi. org/10.1016/j.foreco.2023.121465.

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