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When parasites bite hardest: mistletoe effects on oak radial growth peak near climatic optima

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Hemiparasitic mistletoes reallocate host water and carbon, yet it remains unclear when their costs are greatest and whether parasites shift cambial timing or mainly constrain the amount of wood produced. We tested whether European mistletoe (*Loranthus europaeus*) alters the timing or magnitude of radial growth in ring-porous *Quercus robur*, and whether impacts peak under climatic stress or near hydrothermal optima for host performance. We continuously monitored oak trees across age classes, canopy positions, and infection statuses using 15-min electronic dendrometers over four growing seasons (2020–2023), paired with air temperature, soil temperature, and volumetric soil moisture. We quantified cambial phenology (onset, peak, cessation), seasonal infection-effect curves (non-infected minus infected), climate–growth correlations, and temperature–moisture response surfaces describing the realised hydrothermal niche of growth. Growth phenology was conserved among years and categories (onset DOY ~ 120–140; peak ~150–220; cessation ~250–270), and infection did not shift these phases. In contrast, mistletoe reduced the amplitude of cambial increment, most clearly in solitary, well-lit trees and in high-growth years. Suppression peaked at moderate air temperatures (~10–18 °C) with adequate soil moisture and diminished under suboptimal combinations of heat or cold and dryness, indicating that host–parasite competition is strongest near conditions that maximise host growth. Short-term climate sensitivities were broadly similar across infection status: during the peak season, growth was typically negatively related to temperature and positively related to soil moisture, and temperature–moisture niches were comparable among categories. However, young, solitary, non-infected trees tracked midsummer moisture pulses more strongly than infected trees, suggesting that infection shifts hosts from a resource-tracking to a stress-limited growth regime in exposed microclimates. European mistletoe thus imposes its greatest penalty near the host's hydrothermal optimum, limiting wood production rather than growth timing, and identifies the environmental window in which parasite impacts are most consequential for forecasting oak productivity under shifting temperature–moisture regimes.

KEYWORDS
cambial phenology, climate change, dendrometer, growth optimum, host–parasite interactions, *Loranthus europaeus*, microclimate, *Quercus robur*

1 Introduction

Parasitic plants are a distinctive and ecologically important component of terrestrial ecosystems, influencing the physiology, growth, and survival of their host plants, as well as community dynamics and ecosystem functioning (Cameron et al., 2008; Mathiasen et al., 2008). Among these, mistletoes are hemiparasites that photosynthesize but rely on their hosts for water and mineral nutrients (Ehleringer et al., 1985; Glatzel and Geils, 2009; Urban et al., 2012), often exerting significant impacts on host carbon balance, hydraulic status, growth, and reproductive output (Watson, 2001; Press and Phoenix, 2005). By altering host performance, mistletoe infection can also influence competitive interactions and forest structure, making it an essential driver of vegetation dynamics in many woodlands (Matula et al., 2015; Oladi et al., 2025; Gosling et al., 2024).

The effects of mistletoe on host trees can be highly context-dependent. Variation in host susceptibility, canopy position, tree age and size, and local environmental conditions can modulate the magnitude and even the direction of infection effects (Zakaria et al., 2014; Santiago-Rosario et al., 2023). Climatic conditions can further shape host–parasite interactions, as the physiological activity of both partners responds non-linearly to temperature and water availability (Glatzel, 1983). Consequently, mistletoe impacts may vary not only among sites but also within a growing season, reflecting seasonal shifts in host phenology and proximity to climatic optima for growth (Cocoletzi et al., 2020). Seasonal changes in nutrient composition of host and mistletoe xylem sap illustrate the dynamic nature of these interactions (Escher et al., 2004). Moreover, drought exacerbates growth decline in mistletoe-infested hosts (Tamudo et al., 2021), and mistletoe's failure to close stomata under dry periods further stresses the host (Walas et al., 2022). Increasing climate variability is likely to amplify these resource imbalances, with cascading effects on carbon, water, and nutrient dynamics in infected trees (González de Andrés et al., 2024; Baranowska et al., 2025).

In oaks, early-season radial growth often begins before leaf flush, when transpiration is minimal (Pérez-de-Lis et al., 2016; Lavrič et al., 2017; Szatniewska et al., 2022; Puchałka et al., 2024). This phenological timing suggests that differences between infected and non-infected trees may be smaller during the initial growth phase and more pronounced later in the season, when leaves are fully expanded, and transpiration demand is high. Furthermore, differences in growth appear to be greatest near the host's climatic optimum, when absolute growth rates are highest, and to diminish under suboptimal conditions such as extreme temperatures or low soil moisture, consistent with climate-modulated parasite impacts on hosts (Bell et al., 2020; Tamudo et al., 2021). This pattern accords with host–parasite theory for hemiparasites: under favourable conditions, both host and parasite exhibit high physiological activity, intensifying resource competition, whereas under stressful conditions the parasite may rely more heavily on its own photosynthesis (Press and Phoenix, 2005; Těšitel, 2016), with seasonal shifts in xylem solutes and stomatal behaviour further modulating outcomes (Escher et al., 2004; Walas et al., 2022). However, exceptions can occur, such as in shaded young trees, where infection effects may be reversed, suggesting complex interactions between microhabitat, host vigour, and parasite strategy (Queijeiro-Bolaños et al., 2016; Lázaro-González et al., 2019).

Recent studies reinforce this view of context-dependent outcomes. Queijeiro-Bolaños et al. (2016) demonstrated that the balance between competition and facilitation in dwarf mistletoe–pine systems shifts in response to host size, stand density, and environmental stress, with infection effects sometimes neutral or even positive under resource-limited conditions. Lázaro-González et al. (2019) further demonstrated that mistletoes can generate non-trophic, trait-mediated effects that propagate through ecological networks, altering both host physiology and interactions with other organisms. These findings suggest that mistletoe's effects on radial growth cannot be explained solely by resource extraction; they must also be considered in the context of environmental variation, seasonal host physiology, and indirect ecological effects.

Quercus robur and related oak species are foundational components of Central European forests, providing habitat and resources for a wide range of organisms (Lanta et al., 2025). They are also known hosts of the European mistletoe (Loranthus europaeus), whose infection prevalence can be high in specific stands (Matula et al., 2015; Doležal et al., 2010). Despite the recognised importance of this parasitic association, relatively few studies have examined its effects on host radial growth at fine temporal resolution, and even fewer have considered how these effects might vary seasonally or in relation to climatic drivers (Doležal et al., 2016). Such information is critical for understanding how parasitic plants interact with their hosts under current and future climates, particularly amid warming and shifting precipitation patterns (Tumajer et al., 2022).

High-resolution dendrometer measurements offer a powerful means to track tree growth dynamics in unprecedented detail, capturing subtle variations associated with infection, phenological stage, and microclimatic conditions (Zweifel et al., 2014; Deslauriers et al., 2007). Although widely applied to study seasonal rhythms and climate–growth relationships, they have not previously been used to examine the impacts of mistletoe infection on host tree growth. By combining multi-year continuous growth monitoring with microclimatic data, it becomes possible to disentangle the overall effect of mistletoe infection from its seasonal modulation and climatic sensitivity. High-precision electronic dendrometers, already well established in studies of boreal, temperate, and tropical trees (Worbes, 1995; Etzold et al., 2022; Plavcová et al., 2025), record radial stem size with sub-hourly resolution, enabling the assessment of growth rates from hourly to annual scales and the characterisation of tree water storage (De Swaef et al., 2015; Salomón et al., 2022). Recent applications have shown that growth in temperate trees occurs primarily at night when turgor conditions favour cell expansion (Zweifel et al., 2021). At seasonal scales, growth is restricted to favourable days within a broader climatic window (Etzold et al., 2022; Tumajer et al., 2022). These insights demonstrate the utility of dendrometer data in elucidating how environmental factors influence tree growth. Here, we extend this approach to the novel context of mistletoe–host interactions.

In this study, we monitored the radial growth of oak trees with and without mistletoe infection over four consecutive growing seasons (2020–2023) using high-resolution dendrometers. We examined how infection effects on the onset, peak, and cessation of radial growth and daily tree increment varied with tree age, canopy position, and year-to-year climatic conditions, and whether these effects were modulated by seasonal phenology or by specific combinations of temperature and soil moisture. We also investigated whether infection effects were most pronounced near climatic growth optima, as predicted by host–parasite theory for hemiparasitic plants. Based on the ecophysiology of ring-porous oaks and hemiparasitic mistletoes, we tested four main hypotheses. H1: Mistletoe infection reduces the magnitude of host radial growth, but has little effect on the timing of cambial phenology; specifically, infected and non-infected trees should differ more in growth rate

and seasonal increment than in the onset, peak, or cessation of growth. H2: The negative effect of mistletoe is context dependent and is strongest in vigorous, resource-exposed hosts, particularly in young, solitary trees, whereas it is weaker in shaded canopy trees and in older trees. H3: Infection effects are greatest under climatic conditions favourable for host growth, that is, near the hydrothermal optimum defined by moderate temperatures and sufficient soil moisture, and diminish under suboptimal conditions such as drought, excessive heat, or cold. H4: Mistletoe alters the host's short-term responsiveness to climatic variation, especially by weakening the positive growth response to mid-season soil moisture pulses in exposed trees, indicating a shift from a resource-tracking to a more stress-limited growth regime. By integrating growth phenology, climate–growth relationships, and infection effects, our work provides new insights into the context-dependent nature of mistletoe–oak interactions in temperate woodlands.

2 Methods

2.1 Study area

The research was conducted in the National Nature Reserve (NNR) Čertoryje, located in the White Carpathians Protected Landscape Area along the Czech–Slovak border (Figure 1). The region forms part of a hilly chain (maximum altitude 970 m a.s.l.) composed of base-rich flysch sediments. The landscape is a mosaic of villages in narrow valleys, steep slopes covered by deciduous woodland, and grasslands on shallow slopes and plateaus. Traditional land use, preserved until the early 1980s due to the late arrival of communist-era land consolidation, has maintained a fine-scale habitat mosaic of meadows, pastures, small fields, orchards, and woodlots (Doležal et al., 2010). The climate is temperate with a mean annual temperature of 8.8 °C (1900–2024 average) and mean annual precipitation of 699 mm (Doležal et al., 2016). Grasslands cover approximately 20% of the protected area and are dominated by species-rich "Carpathian meadows" with exceptionally high plant diversity (Albert et al., 2019). The oak stands studied consist predominantly of *Quercus robur*, interspersed with other broadleaves, including rowan (*Sorbus aucuparia* and *S. torminalis*), maple (e.g., *Acer platanoides*), and hawthorn (*Crataegus* spp.). They exhibit varying degrees of infestation by European mistletoe (*Loranthus europaeus*).

2.2 Experimental design

We sampled 34 mature *Quercus robur* trees (Figure 1a; Supplementary Table S1) that covered eight combinations of age class (young, old), canopy position (solitary, closed canopy), and mistletoe

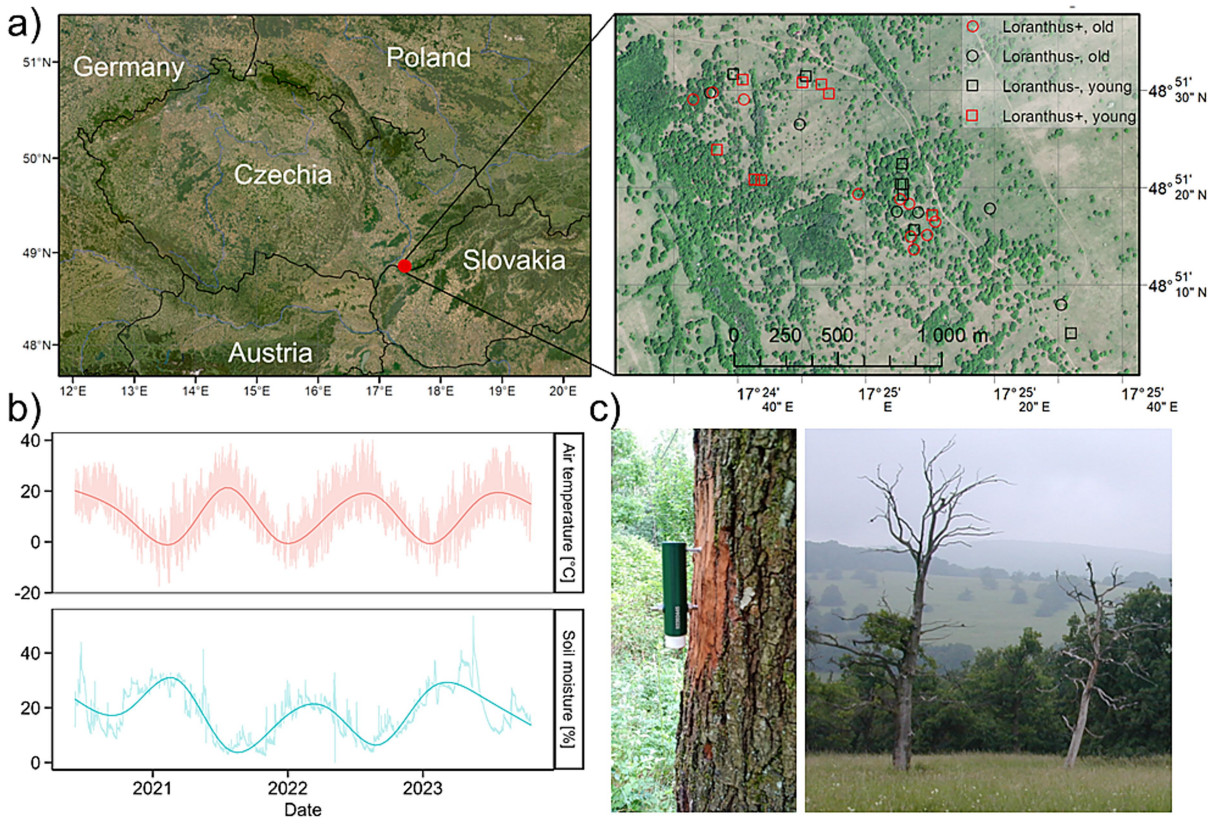

FIGURE 1
Study area (White Carpathians, Czech Republic). Savannah-like species-rich meadow with scattered oak groves and solitary trees at the woodland–grassland ecotone on base-rich flysch **(a)**. High-resolution satellite map of the site showing mapped oaks by mistletoe (*Loranthus europaeus*) status and age class: red = parasitized (*Loranthus*+), black = unparasitized (*Loranthus*−); circles = old trees, squares = young trees. **(b)** Site microclimate (2021–2023): air temperature (°C) and volumetric soil moisture (%), raw readings with a smoothed seasonal trend, both showing strong seasonality, warm, dry summers and cool, wetter winters. **(c)** Left: point dendrometer installed on an oak stem for continuous growth monitoring. Right: open woodland with severely declined/standing dead oaks illustrating canopy dieback in the landscape.

status (infected, non-infected). We aimed for four trees per combination (32 total), with two additional trees in the old × solitary × infected group ($n = 6$), which were instrumented with point dendrometers (TOMST, Praha, Czechia). Age classes were defined based on trunk diameter at breast height (DBH, smaller or larger than 30 cm) and number of growth rings at DBH counted on increment cores extracted using Pressler's borer (younger or older than 60 years), and growth form: "young" trees were relatively vigorous; "old" trees often showed signs of age-related decline such as the presence of dead crown branches. Solitary trees were free-standing individuals exposed to full light, whereas canopy trees grew within closed stands and experienced greater shading. Infected trees bore visible mistletoe clumps, with infection intensity ranging from moderate to high. The number of mistletoe plants on each of the target trees with dendrometers was counted; infested trees had more than five plants (up to a maximum of 15 plants on a single tree (Doležal et al., 2016).

2.3 Dendrometer installation and measurements

On each tree, a high-resolution point dendrometer (TOMST, Prague) was installed at ~1.3 m height on the north-facing side of the stem to minimise direct solar heating. The installation took place in April 2020. The dendrometers recorded stem radius changes at 15-min intervals throughout four consecutive growing seasons (2020–2023). Instruments were checked regularly to ensure stability and accuracy, and the final recorded data were downloaded during April 2023.

2.4 Microclimatic measurements

Air temperature was recorded using TMS dendrometer sensors installed at breast height (1.3 m above ground), directly at the stem surface of each tree where radial growth was measured. These measurements, therefore, reflect the microclimatic conditions experienced by the cambial zone rather than free-air canopy temperatures. Soil moisture was measured at 10 cm soil depth using TMS T4 sensors (Wild et al., 2019), corresponding to the upper soil layer most relevant for short-term stem hydration and radial growth dynamics. Although canopy microclimate may differ from stem-level conditions, the selected sensor placement was appropriate for capturing the climatic drivers of stem growth, as measured by dendrometers. All variables were logged at 15-min intervals and synchronised with dendrometer data.

2.5 Data processing

The raw electric signals of stem size variation (recorded by dendrometers) and soil moisture (TMS T4) were converted into radius increment (µm) and volumetric soil water content (%) using the 'myClim' package (Man et al., 2023) in R (R Core Team, 2024). Converted dendrometer data were visually inspected for spurious values resulting from mechanical disturbance or sensor drift. Next, we used a zero-growth approach to calculate the radial growth rate (Zweifel et al., 2016). The growth rate (µm h^{-1}) for each tree at each 15-min timestep was defined as the difference between the stem radius measured by a given dendrometer at that timestep and the maximum stem radius recorded by that dendrometer since its installation. In case of negative differences, corresponding to periods of stem shrinkage, the growth rate was set to zero. We removed rare, unrealistic values of radial growth rate exceeding 150 µm per single timestep from further analysis. Mean daily growth curves were derived for each tree as daily means of radial growth rates at 15-min resolution. Seasonal growth curves, highlighting overall growth patterns beyond daily variation, were constructed by smoothing splines fitted to daily curves. Both daily and seasonal curves were aggregated into category means for further analysis.

2.6 Statistical analyses

First, seasonal growth phenology was quantified to identify the onset, peak, and cessation of growth for each tree, category, and year. Cambial phenology was derived from daily dendrometer-based radial growth series. For each tree and year, cumulative radial increment was calculated, and the start of season (SOS) and end of season (EOS) were defined as the days of the year when 5 and 95% of the final annual ring width were reached, respectively (Zweifel et al., 2016; Etzold et al., 2022). Growing season duration (DOS) was calculated as EOS − SOS. This threshold-based approach minimises the influence of short-term stem hydration effects on phenological estimates. Differences in SOS, EOS, and DOS among mistletoe infection status (infected vs. non-infected), age class (young vs. old), and canopy position (solitary vs. canopy) were tested using a linear mixed-effects model (LMM) with tree identity (series) and year as the random factors (Supplementary Table S2). The model was fitted using restricted maximum likelihood (REML) in the lme4 package, with significance testing based on Satterthwaite's approximation implemented in the lmerTest package.

Second, seasonal growth dynamics were analysed using daily radial growth rates (GRO; µm h^{-1}). Daily mean radial growth rates were used as the response variable in a linear mixed-effects model (LMM), while tree age class, canopy position, and mistletoe infection status were included as fixed categorical predictors, and DOY (day of the year), tree identity and year as the random factors (Supplementary Table S3). Tukey *post-hoc* tests were applied to assess pairwise differences among factor levels. Furthermore, mean daily growth curves were calculated for each category (age class × canopy position × infection status) and year. To quantify the effects of seasonal infection, we calculated the difference in mean daily growth rates between non-infected and infected trees within each category (non-infected minus infected). Positive values indicated faster growth in non-infected trees and were used to visualise the timing and magnitude of infection effects over the growing season.

Third, climate–growth relationships were assessed using Pearson correlation coefficients between 15-min radial growth rates and microclimatic variables (air temperature, soil temperature, and soil moisture). Correlations were computed for each tree and calendar month and then averaged within categories. In addition, mean radial growth rates were calculated across discrete climatic intervals (4 °C air-temperature bins and 5% soil-moisture bins) to identify climatic optima and to assess whether infection effects were strongest under optimal or suboptimal conditions. In addition to the monthly aggregation presented in the main text, climate–growth correlations were computed at a weekly resolution to assess the sensitivity of the results to temporal aggregation. Weekly correlations were derived directly from the original 15-min time series for consecutive calendar weeks, following the same procedure used for the monthly analyses. To complement correlation-based analyses and explicitly account for repeated measurements and hierarchical data structure,

we applied a linear mixed-effects model (LMM) to quantify the joint effects of climate and mistletoe infection on radial growth rate (GRO). The model was fitted again using restricted maximum likelihood (REML) in the lme4 package, with significance testing based on Satterthwaite's approximation in the lmerTest package. Air temperature and soil moisture were included as fixed effects, while random intercepts were specified for individual trees nested within infection status, calendar month, canopy position, tree age class, and mistletoe infection status, allowing separation of short-term climatic effects from seasonal forcing and inter-individual variability while avoiding pseudoreplication arising from the high temporal resolution of the data. Model performance was evaluated using marginal and conditional coefficients of determination (Supplementary Table S4).

Fourth, joint climatic effects were computed to visualise combined temperature–moisture influences on radial growth. We plotted matrices of mean growth rates for specific combinations of air temperature and soil moisture, with point size representing the frequency of occurrence and point colour indicating mean growth rate. These analyses were performed separately for infected and non-infected trees to identify potential differences in optimal climatic niches. The Mantel test was used to assess differences between infected and non-infected matrices.

All data processing and statistical analyses were conducted in R v.4.2.2 (R Core Team, 2024) using dplyr and lubridate for data manipulation, myClim for pre-processing of dendrometer and climatic data, ggplot2 for plotting, base stats for correlation analyses, lme4 and lmerTest for mixed-effects modelling, and vegan for Mantel tests. Figures were prepared with consistent axis ranges and colour scales to facilitate direct comparison among years and categories.

3 Results

3.1 Seasonal growth dynamics

Seasonal growth dynamics of oak trees, assessed over four consecutive growing seasons (2020–2023), revealed a consistent phenological pattern across all combinations of age class, canopy position, and mistletoe infection status (Figure 2). Radial growth typically began between day of year (DOY) 120–140, peaked in late spring to early summer (DOY 150–220), and declined towards the end of the growing season (DOY 250–270). This pattern remained stable across years and categories, with variation primarily occurring in the timing and magnitude of peak growth. Mistletoe infection did not alter the onset or cessation of growth in any year, but its effects were sometimes apparent in the amplitude of growth, particularly in favourable years.

Across all years, SOS typically occurred between DOY ~ 120–140 and EOS between DOY ~ 250–270, with limited inter-individual variation. Analysis of variance revealed no significant effects of mistletoe infection status, tree age, or canopy position on SOS, EOS, or DOS (all $p > 0.19$; Supplementary Tables S2, S5). These results indicate that cambial phenology was largely invariant among tree categories and primarily governed by seasonal climatic conditions rather than by parasitic infection or tree structural attributes.

3.2 Interannual and category-specific variation

In 2020, the year with the highest overall growth rates, young solitary trees reached seasonal peak growth rates of approximately 2–2.5 µm h^{-1}, with slightly lower peak amplitudes in mistletoe-infected

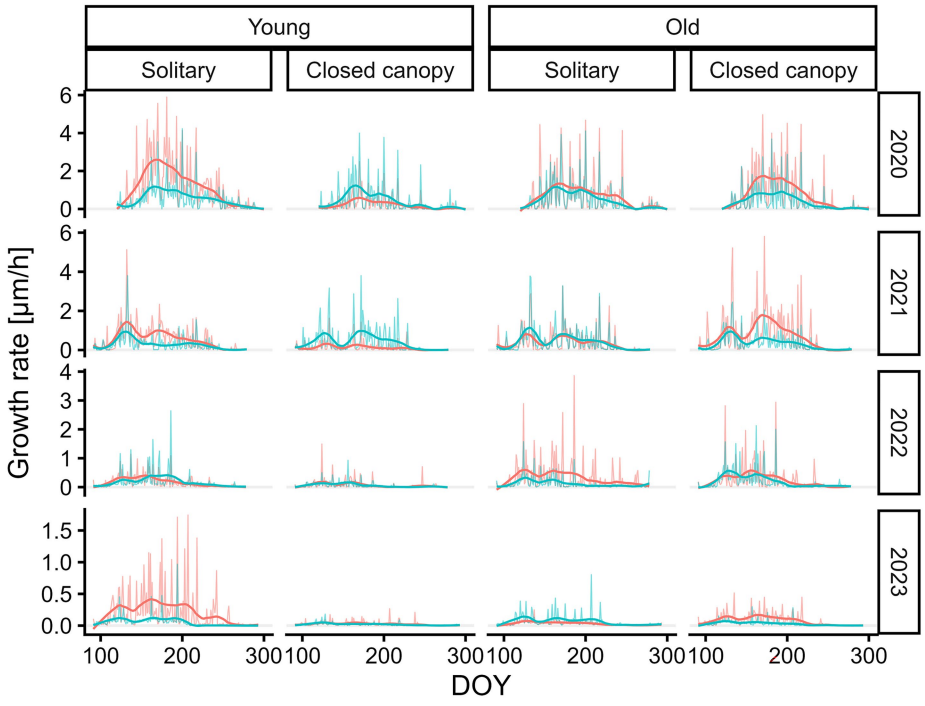

FIGURE 2
Daily and seasonal dynamics of radial growth rate (µm h^{-1}) in oak trees from 2020 to 2023 between days of year (DOY) 90 and 300, shown by age class, canopy position, and mistletoe infection status. Red and blue lines indicate non-infected and infected trees, respectively; thin lines show mean daily growth rates, and thick lines show smoothed seasonal curves. Note the different scales of the y-axis between years.

individuals (Figure 2; Supplementary Table S3). Old, solitary, and old closed-canopy trees showed intermediate peak growth rates (approximately 1.5–2 μm h^{-1}), whereas young closed-canopy trees exhibited consistently lower peaks of roughly 1–1.5 μm h^{-1}. Despite differences in amplitude, seasonal growth trajectories were broadly similar across categories. In 2021, peak growth rates were lower than in 2020, reaching approximately 1.5–2 μm h^{-1} in young solitary and old closed-canopy trees, and remaining below 1 μm h^{-1} in the other categories. The active growth period appeared shorter in most groups, as indicated by narrower seasonal curves. Growth dynamics in 2021 were frequently bimodal, with a pronounced mid-season reduction in growth evident across categories around DOY ~ 150. In 2022, maximum growth rates declined further, with young solitary trees peaking at approximately 0.7–0.9 μm h^{-1}, whereas all other categories reached only approximately 0.4–0.6 μm h^{-1}. Seasonal growth curves were flatter and more compressed, indicating overall suppression of cambial activity. By 2023, growth rates were uniformly low across all age classes, canopy positions, and infection categories, rarely exceeding 0.5 μm h^{-1}. Inter-category differences were minimal, and seasonal growth trajectories converged, reflecting that strong climatic limitation overrode the effects of age, canopy position, and mistletoe infection.

The influence of mistletoe infection on growth amplitude varied among years and tree categories. In high-growth years (2020–2021), infected trees often exhibited slightly lower seasonal and daily growth peaks, particularly among young solitary trees. However, in some cases, such as young canopy trees in all years and young solitary trees in 2022, infected individuals showed marginally higher average growth rates than uninfected ones. In low-growth years (2022–2023), differences between infection statuses were negligible, indicating that climatic constraints likely outweighed any parasitic effects.

Statistical analysis of daily growth rates confirmed these visual patterns (Supplementary Table S3). The linear mixed-effects model (LMM) revealed significant effects of mistletoe infection, tree age, and canopy position on daily growth (Figure 2). Mistletoe infection significantly reduced growth rates ($\beta = -0.0229$, $p < 0.001$), and trees growing under a closed canopy exhibited similarly reduced growth ($\beta = -0.0229$, $p < 0.001$). In contrast, older trees showed slightly higher growth rates compared to younger individuals ($\beta = 0.0091$, $p = 0.0029$). Importantly, inclusion of day-of-year as a random effect (1 | DOY) provided additional insight beyond the factorial ANOVA. The DOY-specific random effects indicated that growth differences between groups were not constant throughout the season. The largest positive deviations occurred during the summer, indicating that the greatest growth advantage of older, non-infected solitary trees emerged in mid-season. Conversely, early and late-season periods were characterised by predominantly negative deviations, reflecting overall growth limitation outside peak growing conditions.

Post-hoc Tukey HSD tests were consistent with the model estimates. Older trees exhibited marginally higher mean daily growth rates than young trees (mean difference = 0.0084 μm h^{-1}, $p = 0.0149$). Canopy trees grew significantly more slowly than solitary trees (mean difference = −0.0211 μm h^{-1}, $p < 0.001$), and mistletoe-infected trees exhibited reduced growth relative to non-infected individuals (−0.0211 μm h^{-1}, $p < 0.001$).

3.3 Seasonal patterns of infection effects

Difference curves (non-infected minus infected; Figure 3) revealed that positive values, indicating faster growth in non-infected trees, were most pronounced in 2020, especially in young solitary trees during the early-to-mid growing season (DOY 150–180; up to ~1.5 μm h^{-1}). Old canopy trees in 2020 also displayed moderate positive peaks (~0.75–1.0 μm h^{-1}). In 2021, differences were smaller and more transient, with occasional slight advantages for infected individuals in certain categories. In 2022, all categories showed differences mostly within ±0.3 μm h^{-1}, while in 2023, differences were minimal (<0.2 μm h^{-1}) and non-systematic. No consistent seasonal shift in infection effects was detected, suggesting that any influence of mistletoe on radial growth is not strongly tied to specific phenological phases of oak growth. The observed impacts are primarily context-dependent, emerging most clearly in high-growth years and varying according to tree age and canopy position.

3.4 Climate–growth relationships and variance structure

Radial growth responses to microclimatic variation were consistent across age classes, canopy positions, and mistletoe infection statuses (Figure 4). Monthly correlations between high-frequency growth rates and climatic variables showed predominantly negative associations with air and soil temperature during the main growing season (May–August), indicating reduced cambial activity under warmer conditions. In contrast, soil moisture generally exerted a positive influence on growth, particularly in early summer (June–July). These patterns were broadly similar between infected and non-infected trees, although young solitary oaks exhibited a stronger mid-summer moisture response in non-infected individuals. Climate–growth relationships derived at weekly resolution yielded patterns qualitatively consistent with the monthly analyses, including predominantly negative temperature effects and positive soil-moisture effects on radial growth (Supplementary Figure S1). However, weekly correlations showed higher variability and reduced clarity across categories, without altering the direction or interpretation of climate effects.

Linear mixed-effects modelling confirmed these contrasting climatic effects. Air temperature had a strong negative effect on radial growth rate (−0.0061 μm h^{-1} $°C^{-1}$, $p < 0.001$), whereas soil moisture had a positive effect (+0.00052 μm h^{-1} $\%^{-1}$, $p < 0.001$; Supplementary Table S4). Variance partitioning revealed that seasonal forcing (calendar month) accounted for the largest share of explained variability, followed by differences among individual trees. Canopy position and mistletoe infection accounted for substantially less variance, whereas tree age had a negligible effect. Random-effects estimates indicated slightly lower baseline growth in infected trees, although this effect was small relative to seasonal and inter-individual variability. Overall, these results show that oak radial growth is primarily governed by seasonal and tree-specific controls, with directionally robust responses to climate. Mistletoe infection imposes a secondary but consistent reduction in growth magnitude, becoming most apparent under conditions favourable for rapid growth, without fundamentally altering climate–growth relationships.

3.5 Climate optima and infection effects

Relationships between growth rate and climatic optima, analysed across discrete intervals of air temperature, soil temperature, and soil moisture, revealed clear non-linear responses (Figure 5). Growth rates peaked at moderate air temperatures (10–18 °C) and corresponding moderate soil temperatures, confirming these ranges as optimal for

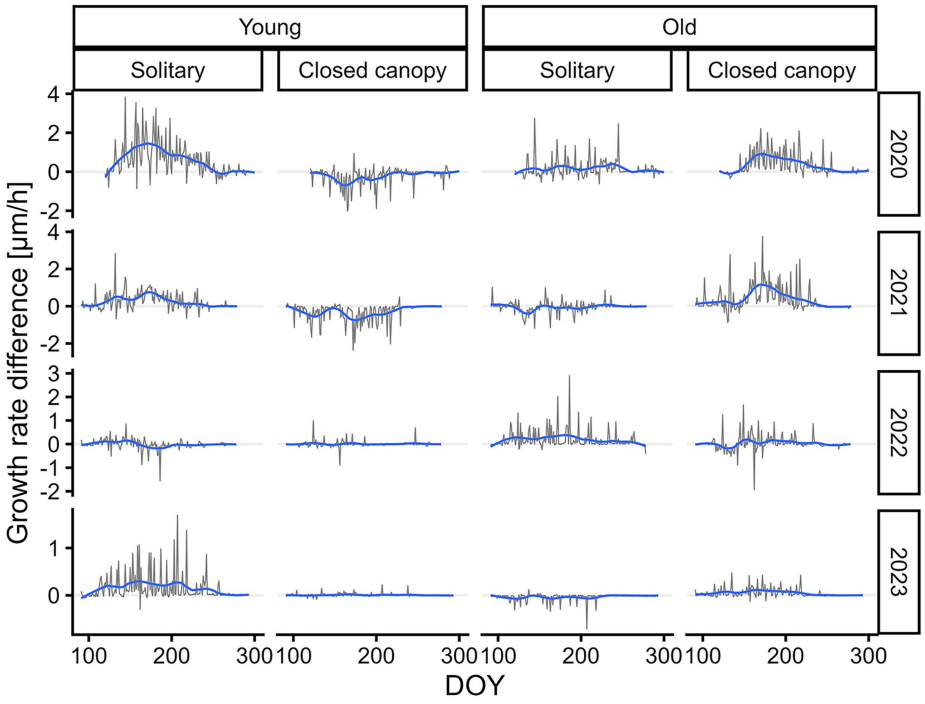

FIGURE 3
Daily and seasonal differences in radial growth rates between non-infected and mistletoe-infected oaks (non-infected minus infected) across age classes and canopy positions between days of year (DOY) 90 and 300 in calendar years 2020–2023. Positive values indicate faster growth in non-infected trees. Grey lines represent the mean daily growth rates; blue lines show their seasonal smoothing splines. Note the different scales of the *y*-axis between years.

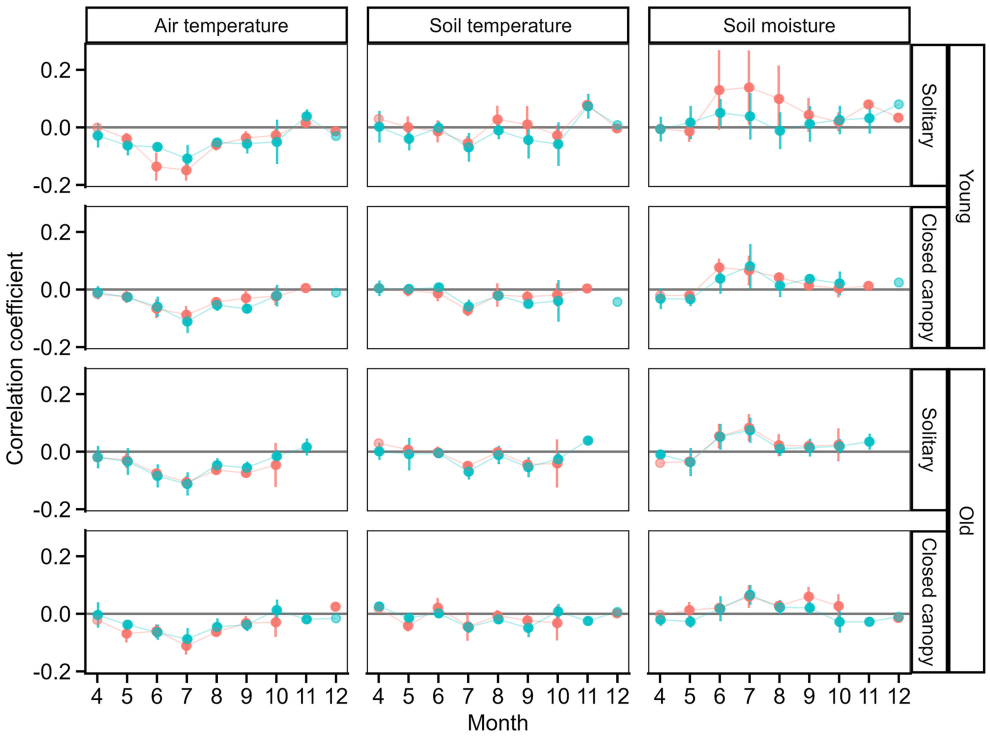

FIGURE 4
Mean (± SD) correlation coefficients between radial growth rate (15-min resolution) and air temperature, soil temperature, and soil moisture for young and old oaks in solitary and canopy positions calculated for each calendar month with growth occurrence within 2020–2023. Blue points and lines indicate trees with mistletoe infection, red points and lines show non-infected trees. Correlations were calculated for individual trees and then averaged within each category.

oak radial growth. Responses of growth to soil moisture availability were relatively flat. Differences between infected and non-infected trees were generally most evident near climatic optima, when absolute growth rates were highest. For example, in young solitary trees, non-infected individuals often outperformed infected ones at optimal temperatures and across full range of soil moisture. In contrast, under suboptimal conditions (low or high temperatures) the two groups grew at similar rates. A notable exception occurred in young canopy trees, where infected individuals matched or exceeded non-infected growth near optima of both temperatures and across a full range of soil moisture. These results indicate that mistletoe effects on host growth are not uniform; they are most pronounced under favourable climatic conditions, consistent with the idea that resource competition between host and parasite intensifies when both have high physiological activity. However, category-specific deviations from this pattern, such as the reversed trends in young canopy trees, highlight the complexity of host–parasite interactions in heterogeneous microhabitats.

3.6 Joint effects of temperature and soil moisture

The combined analysis of air temperature and soil moisture revealed that oak radial growth was highest under moderate temperatures (10–18 °C) and relatively high soil moisture levels (25–30%; Figure 6). Within this optimal range, mean growth rates frequently exceeded 1.0 µm h^{-1}, with maximum values approaching 1.5 µm h^{-1}. Growth declined sharply at both low (<6 °C) and high (>22 °C) temperatures, regardless of soil moisture availability. The frequency distribution of climatic conditions, as indicated by point size, showed that optimal combinations of temperature and moisture were relatively common during the measurement period, especially in late spring and early summer. However, the most common conditions for our site, characterised by air temperature 14–22 °C and soil moisture 5–15%, were rather suboptimal for tree growth, resulting in relatively low growth rates (< 0.5 µm h^{-1}). Patterns were statistically similar between infected and non-infected trees (Mantel R = 0.93, $p < 0.01$), with both groups exhibiting the same climatic optima. However, in optimal conditions (14–18 °C, 25–35%), non-infected trees exhibited slightly higher mean growth rates than infected ones. This difference diminished under suboptimal climatic conditions, suggesting that the competitive effects of mistletoe on host growth are most pronounced when environmental conditions favour maximal physiological activity.

4 Discussion

Our multi-year, high-resolution monitoring of oak radial growth demonstrates that the effects of European mistletoe (*Loranthus europaeus*) on host performance are strongly context-dependent, varying

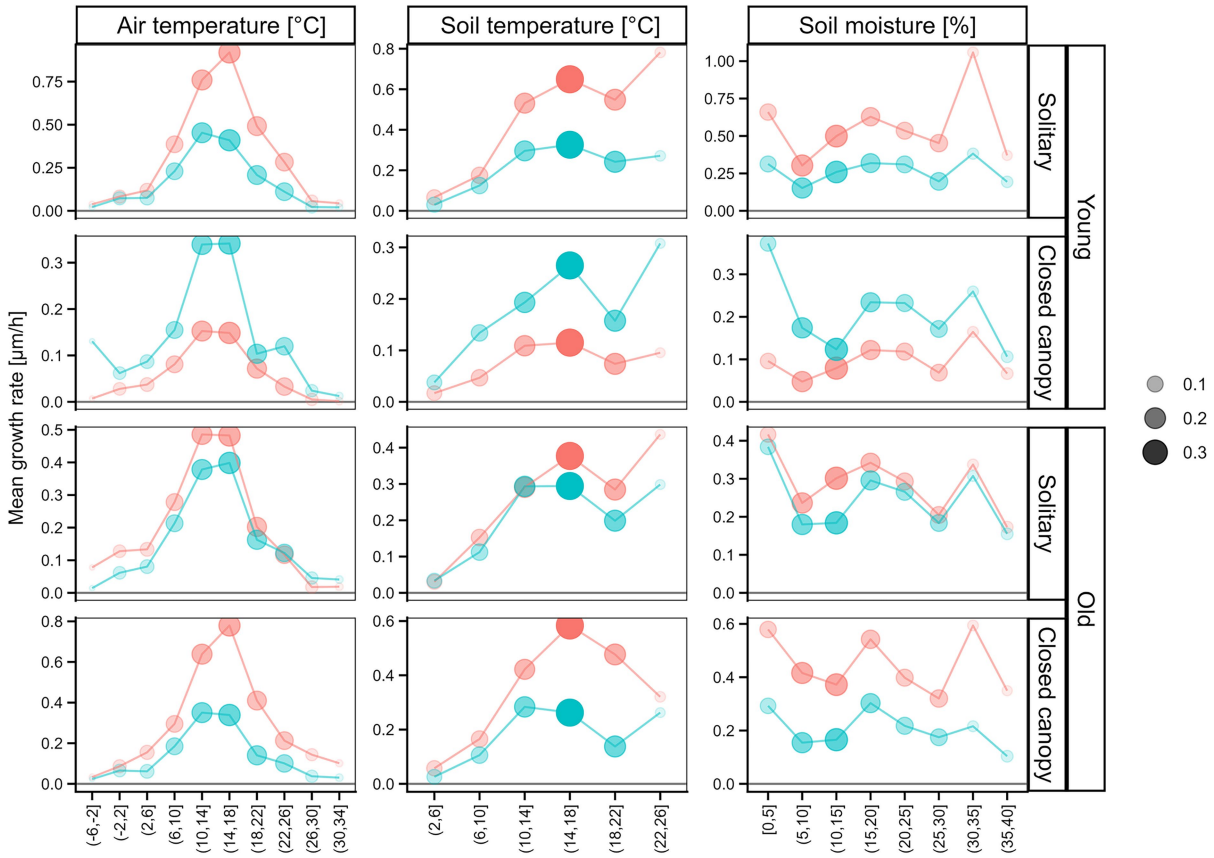

FIGURE 5
Mean radial growth rate of oak trees in relation to air and soil temperature and soil moisture across infection status (red = without mistletoe, blue = with mistletoe), age class, and canopy position. Data are binned into discrete climatic intervals; point size and its transparency reflect the relative frequency of each condition during the study period. Only bins with a relative frequency higher than 0.01 are shown. Note the different scales of the *y*-axes.

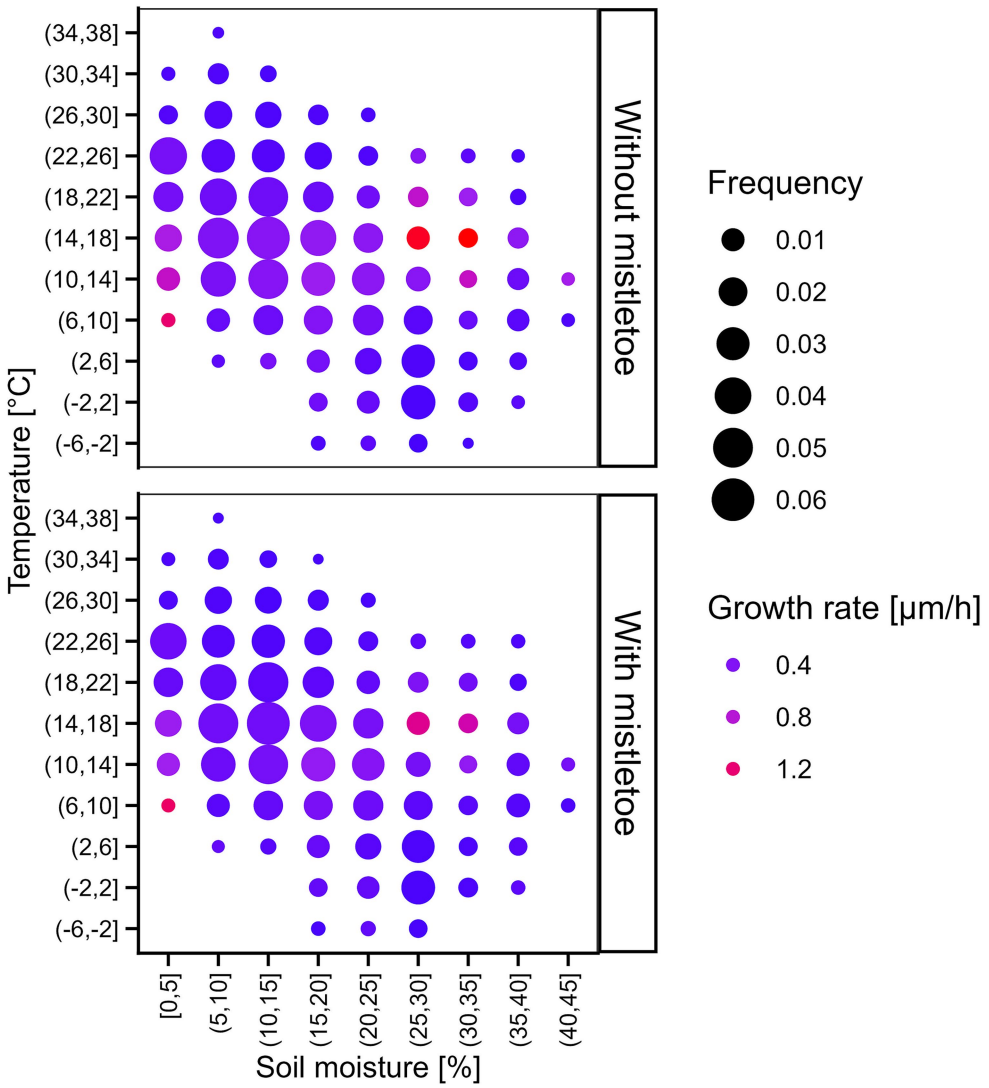

FIGURE 6
Mean radial growth rate (µm h^{-1}) of oak trees for specific combinations of air temperature (*y*-axis) and soil moisture (*x*-axis), shown separately for trees without mistletoe (top) and with mistletoe (bottom). Point size indicates the frequency of occurrence of each climatic combination during the study period, and point colour represents mean growth rate (purple = low, red = high). Only points with a relative frequency higher than 0.001 are shown.

with tree age, canopy position, climatic conditions, and their interactions. Across the four study years, mistletoe infection primarily reduced growth magnitude rather than inducing consistent shifts in growth timing. Differences between infected and non-infected trees were greatest under climatic conditions close to the operational optimum for oak growth, while under suboptimal or stressful conditions, growth rates converged. This pattern accords with theory for hemiparasitic plants, which predicts that resource competition intensifies when both host and parasite are physiologically active but weakens when environmental constraints limit resource fluxes through the host–parasite system (Těšitel, 2016).

4.1 Phenology and timing of growth

Although radial growth in *Quercus robur* began early in the season, before full leaf expansion, we found no statistically significant differences in the timing of growth onset, cessation, or duration between infected and non-infected trees. Rather than indicating an absolute absence of phenological effects, these results provide evidence for the absence of detectable phenological shifts within the resolution and scope of this study; however, minor timing differences cannot be entirely excluded. This outcome is biologically plausible for a ring-porous species such as *Q. robur*, in which cambial reactivation and earlywood formation rely strongly on stored carbohydrates accumulated in the previous growing season and occur under relatively low transpiration demand. Such physiological control limits the potential for temporal avoidance strategies in response to parasitism, even when subsequent growth performance diverges. As leaf area, transpiration, and resource flux increase later in the season, mistletoe effects are therefore more likely to emerge through reductions in growth magnitude rather than shifts in growth timing (Pérez-de-Lis et al., 2016; Lavrič et al., 2017; Etzold et al., 2022; Szatniewska et al., 2022).

4.2 Context dependence of mistletoe impacts across host vigour and climate

Infection effects were most pronounced in young, solitary trees exposed to full light, indicating that high host vigour amplifies

competition between host and parasite. Under open-canopy conditions, an elevated vapour-pressure deficit, combined with sustained mistletoe transpiration demand, likely increases hydraulic tension in the host, thereby constraining the conversion of favourable climatic conditions into stem growth. Similar state-dependent outcomes have been reported in systems where the balance between competition and facilitation shifts with host size, stand density, and environmental stress (Queijeiro-Bolaños et al., 2016). At the opposite end of the ecological spectrum, recurrent drought may push host–parasite interactions beyond reversible physiological limitation towards structural constraint. In *Quercus brantii*, post-2011 droughts coincided with reduced vessel size, increased vessel density, and persistently depressed growth in infected trees (Oladi et al., 2025), suggesting long-term xylem reconfiguration. Together, these findings indicate that mistletoe impacts vary along a climatic gradient from transient, physiology-mediated limitation to more permanent anatomical adjustment under chronic stress.

4.3 Physiological mechanisms linking infection to growth suppression

Mistletoe infection consistently reduced radial growth magnitude in our dataset without altering growth timing, and this suppression was strongest under climatic conditions favourable to host growth. In addition, infected trees, particularly young solitary individuals, exhibited weaker responsiveness to mid-summer soil moisture variability than non-infected trees, indicating a reduced capacity to translate short-term resource availability into cambial increment. These patterns are consistent with well-documented physiological contrasts between mistletoe-infected and non-infected oaks. Across multiple systems, infected hosts exhibit reduced stomatal conductance, transpiration, and carbon assimilation relative to non-infected trees, whereas mistletoes maintain high transpiration rates and low water-use efficiency (Urban et al., 2012; Kubov et al., 2020; He et al., 2021). For example, during a drought year, infested *Quercus petraea* reduced stomatal conductance and transpiration to approximately two-thirds of the values observed in non-infested trees, while Loranthus europaeus sustained substantially higher transpiration, imposing a persistent hydraulic load on the host (Kubov et al., 2020). Similar hydraulic asymmetry and diffusion limitation of photosynthesis have been reported across host–mistletoe systems, with infected trees showing elevated intercellular CO_2 concentrations despite reduced conductance and lower intrinsic water-use efficiency (Urban et al., 2012; He et al., 2021). Together, these coupled hydraulic and carbon constraints provide a mechanistic explanation for our central finding that mistletoe primarily reduces radial growth, with suppression peaking under conditions that would otherwise promote rapid cambial activity. A chronically elevated transpiration demand imposed by mistletoe likely constrains host water status and turgor, thereby limiting cell expansion and wood formation even when external conditions are favourable. This mechanism also offers a parsimonious explanation for the weaker mid-summer soil-moisture responsiveness observed in infected trees, consistent with a shift from a resource-tracking to a more stress-limited growth regime.

4.4 Stand structure, parasite aggregation, and density-dependent effects

In our dataset, the magnitude and even the direction of mistletoe effects on radial growth varied strongly with stand structure and host condition. Growth suppression was most pronounced in solitary, well-lit trees, whereas in shaded canopy trees, particularly younger individuals, infected trees sometimes matched or even exceeded the growth of non-infected counterparts. These results indicate that mistletoe effects are highly context-dependent and not uniformly negative across microhabitats. This pattern is consistent with known spatial and ecological controls on mistletoe distribution and host–parasite interactions. Mistletoe occurrence is typically higher in large, exposed, and weakly competitive trees, and spreads over short distances, leading to aggregation on solitary individuals (Matula et al., 2015). Such patterns likely reflect bird-mediated dispersal, with frugivorous birds preferentially using free-standing trees as perches. In these exposed crowns, high resource flux allows parasite demand to translate directly into measurable reductions in growth, in line with previous observations in Central European oak systems (Doležal et al., 2016).

The weak or neutral infection effects observed in shaded canopy trees suggest that microhabitat conditions strongly modulate the physiological costs of parasitism. Under closed-canopy conditions, lower radiation load, reduced vapour pressure deficit, and cooler soils likely buffer hydraulic stress for both host and parasite, thereby reducing relative growth penalties. In addition, growth in young canopy trees is often strongly light-limited, meaning that the proportional carbon and water demand imposed by mistletoe represents a smaller fraction of host resource flux than in exposed environments. Trait-mediated and phenotypically plastic host responses may further contribute to this context dependence, as mistletoe infection can induce changes in host allocation patterns, water-use strategy, or crown architecture, generating non-trophic effects that are neutral or even weakly positive under buffered conditions (Lázaro-González et al., 2019).

Beyond stand structure, parasite density likely represents an additional key axis of variation. Intraspecific competition among parasite ramets can modify realised virulence (Nabity et al., 2021), such that spatial variation in clump number and size translates into density-dependent draw on host xylem flow. This mechanism provides a plausible explanation for why growth penalties were strongest in exposed, vigorous crown sectors and weaker under shaded or resource-limited conditions. It also highlights the distinction between infection probability and infection intensity (Matula et al., 2015), and helps explain the category-specific and interannual variability observed in our dataset. More broadly, these findings support a framework in which host condition, stand structure, and parasite density jointly determine the magnitude and persistence of mistletoe impacts on tree growth (Doležal et al., 2010; Gosling et al., 2024).

4.5 Climatic modulation of infection effects

Climatic conditions strongly modulated mistletoe impacts. Growth–climate relationships confirmed moderate air (10–18 °C) and soil temperatures as the optimal range for oak radial growth. Infection-related growth reductions were generally greatest in this range, particularly for solitary trees, and diminished under suboptimal conditions such as high temperatures or drought. A mechanistic link to leaf-level physiology is evident in Kubov et al. (2020): under drought, infested oaks restricted stomatal conductance and transpiration, whereas mistletoe maintained high conductance, thereby elevating host water limitation and depressing assimilation relative to non-infested trees. This is consistent with Bell et al. (2020) and Tamudo et al. (2021), who showed that warm or dry conditions can intensify the effects of hemiparasites by increasing host water stress.

However, in some systems, the greatest negative impacts occur during favourable years when host and parasite compete at peak activity. He et al. (2021) similarly reported that host–parasite contrasts were most evident in the wet season, whereas during the driest period, infested and uninfested oaks showed similar midday water potentials. In their system, parasites maintained lower (more negative) water potentials and higher conductance only when moisture supply permitted, mirroring our largest radial-growth penalties under moderate temperatures with adequate soil water. Together, these results indicate that hemiparasite demand scales with environmental supply: when transport capacity is high, competition for water and nutrients translates directly into reduced host growth; when supply is constrained, both partners are equally limited and differences collapse.

Our climatic optima for oak growth (moderate temperatures with ample moisture) also map closely onto a VPD framework in which *Q. robur* achieves maximal growth around 12–16 °C and a vapour pressure deficit (VPD) ≤ 0.1 kPa (Tumajer et al., 2022). In this humid, growth-conducive niche, we observed the largest infection penalties, consistent with the expectation that parasite–host competition is most consequential when VPD permits sustained cambial activity. As VPD increases or temperature deviates from its optimum, *Q. robur* growth declines sharply. It becomes 'event-driven,' which helps explain why differences between infected and non-infected trees converge under suboptimal conditions. The stronger mid-summer moisture responsiveness of our young solitary, non-infected trees accords with this mechanism, where short moisture pulses can be exploited, infection dampens the conversion of water availability into growth. This is consistent with parasite-imposed hydraulic load observed under monsoon conditions (He et al., 2021).

Physiological evidence supports this mechanism. Escher et al. (2004) demonstrated pronounced seasonal shifts in the amino compound composition of xylem sap in *Viscum album* and its hosts, reflecting changes in nutrient demand and uptake patterns throughout the year. Walas et al. (2022) further showed that *V. album* maintains stomatal opening under drought, sustaining its own carbon gain but exacerbating host water loss. Our finding that growth suppression is most evident near climatic optima suggests that, when water and nutrient transport are at their maximum, parasite demand directly constrains host cambial activity. Conversely, during stressful conditions, the partial photosynthetic independence of hemiparasites (Tennakoon and Pate, 1996) may reduce the degree of competitive suppression. Superimposed on these climate effects, density-dependent interactions among parasite ramets (Nabity et al., 2021) may explain why infection penalties are most pronounced in well-lit, fast-growing hosts that can physiologically support many actively transpiring shoots.

Importantly, we did not detect a consistent seasonal pattern in infection effects attributable to phenological offsets between host and parasite. Although *Q. robur* initiates radial growth early in spring, before leaf flush and at low transpiration rates, differences between infected and non-infected trees were not systematically smaller in early than in late season, again consistent with the partial decoupling of cambial onset from leaf phenology in oaks (Pérez-de-Lis et al., 2016; Lavrič et al., 2017; Szatniewska et al., 2022; Puchałka et al., 2024), and suggesting that short-term temperature–moisture conditions rather than fixed phenophases primarily drive infection effects.

A notable pattern emerged in young solitary oaks: the mid-summer moisture dependence was stronger in non-infected trees than in those infected by mistletoe. This suggests that healthy young trees can capitalise on short moisture pulses to grow, whereas infection dampens the translation of moisture availability into growth. Mechanistically, mistletoe adds a persistent transpiration load and induces earlier stomatal closure and/or lower leaf–shoot hydraulic conductance in the host (Urban et al., 2012); thus, infected trees remain chronically water-limited and less responsive to inter-monthly variability in soil moisture. The effect is magnified in solitary trees where VPD, wind exposure, and radiation are higher than under the canopy, and where young trees likely have shallower rooting and smaller storage pools. Under a closed canopy, microclimatic buffering (lower VPD and cooler soils) reduces moisture stress for all trees, and differences in infection are correspondingly small. This summer divergence in young solitary trees can be viewed as evidence that mistletoe infection converts growth from "resource-tracking" to "stress-limited" mode: once a chronic hydraulic/carbon drain is imposed, additional water does not proportionally increase growth.

4.6 Implications for oak decline under climate change

Our findings highlight the importance of considering fine-scale climatic variability and host condition when predicting the effects of mistletoe on oak growth. Projected increases in temperature and altered precipitation regimes are likely to shift the frequency of conditions near the climatic optimum for oak growth. If optimal conditions become less frequent, the competitive suppression of host growth by mistletoe may diminish; however, under scenarios where favourable conditions coincide with high parasite prevalence, impacts on host productivity could be substantial. The physiological imbalances induced by mistletoe, affecting carbon allocation, water relations, and nutrient status, are likely to interact with climate extremes in complex ways (Kubov et al., 2020; González de Andrés et al., 2024). This could exacerbate decline episodes, particularly in fragmented stands or on drought-prone sites where host recovery capacity is low (Doležal et al., 2016; Gosling et al., 2024). From a silvicultural perspective, our results suggest that mistletoe impacts are unlikely to be uniform across stand structures and that management should focus on exposed, solitary, and heavily infested trees, which appear to experience the strongest growth suppression. In open oak woodlands, wood-pastures, and fragmented stand edges, targeted monitoring of mistletoe abundance may help identify trees at elevated risk of decline before severe crown deterioration becomes visible. Where conservation objectives allow intervention, selective pruning of heavily infested branches or the gradual release and regeneration of less affected individuals may reduce long-term productivity losses. More broadly, management that lowers drought stress and avoids abrupt canopy opening around vulnerable oaks may help buffer host trees against the combined effects of mistletoe infection and increasingly variable hydrothermal conditions (Matula et al., 2015; Doležal et al., 2010).

4.7 Limitations and future directions

Several limitations should be acknowledged. First, sample sizes within individual age × canopy × infection categories were necessarily modest because long-term, high-frequency dendrometer monitoring is logistically demanding. Although the factorial design and four-year replication increase the robustness of inference, limited replication reduces statistical power to detect subtle interaction effects. Second, mistletoe infection was treated as a binary factor, whereas parasite effects are likely

to vary continuously with infection intensity, parasite biomass, or leaf area. Because such quantitative measures were not available, we could not test for dose-dependent responses. Third, while the growth suppression associated with mistletoe infection was consistent, the underlying physiological mechanisms, including mistletoe transpiration, host hydraulic conductance, and photosynthetic responses (Marshall and Ehleringer, 1990), cannot be resolved directly from our dataset. Finally, infection status may partly covary with pre-existing host vigour or microsite conditions, so some of the observed differences may reflect both parasite effects and prior differences in host condition. Future work combining dendrometer monitoring with direct physiological measurements, quantitative estimates of parasite load, and lag-aware modelling would strengthen causal inference and improve predictions of host–parasite dynamics under climate change (Baranowska et al., 2025).

5 Conclusion

Our four-year, high-frequency records show that European mistletoe does not alter the timing of radial growth in *Quercus robur*; onset, peak, and cessation were remarkably consistent across years and categories. However, it reduces the magnitude of growth in a strongly context-dependent manner. Suppression was clearest in years and microhabitats that favoured rapid host growth, peaking near the climatic optimum (approximately 10 to 18 °C air temperature with adequate soil moisture), and was especially pronounced in solitary, well-lit trees. When conditions were suboptimal (hot and dry or cold and wet), infected and non-infected trees converged in performance. Short-term relationships between climate and growth were stable across infection status; temperature effects were weakly negative during the main season, and soil moisture effects were positive. This pattern suggests that mistletoe does not alter how growth tracks weather so much as it amplifies competition precisely when host physiological activity is at its highest. The stronger midsummer moisture responsiveness of young solitary non-infected trees further indicates that infection shifts hosts from a resource-tracking regime to a more stress-limited growth mode under exposed conditions.

Data availability statement

The original contributions presented in the study are included in the article/Supplementary material, further inquiries can be directed to the corresponding author.

Author contributions

JD: Project administration, Formal analysis, Methodology, Data curation, Funding acquisition, Writing – original draft, Writing – review & editing, Conceptualization, Investigation, Resources. VL: Conceptualization, Writing – review & editing, Methodology, Investigation. KK: Investigation, Writing – review & editing. LP: Validation, Investigation, Writing – review & editing. JT: Visualization, Formal analysis, Writing – original draft, Data curation, Writing – review & editing, Investigation, Software, Conceptualization, Resources.

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Conflict of interest

The author(s) declared that this work was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Generative AI statement

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