



Shifts in intra-annual growth dynamics drive a decline in productivity of temperate trees in Central European forest under warmer climate

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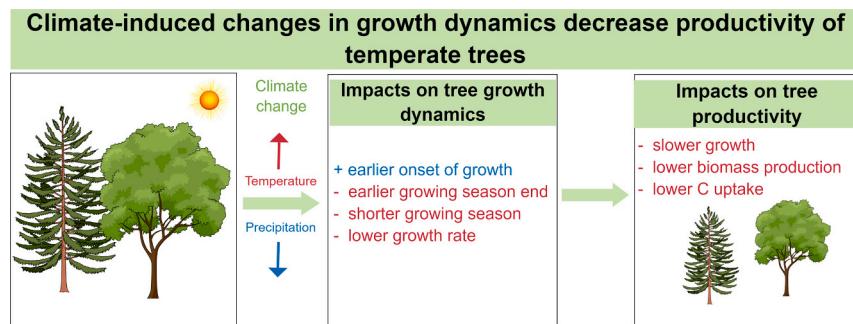
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HIGHLIGHTS

- Climate change alters tree growth dynamics, decreasing their productivity.
- Warmer climate shortens the growing season and decreases growth rates.
- Changes in intra-annual growth dynamics drive a decline in tree productivity.
- The most productive tree species are affected most negatively by warmer climate.

GRAPHICAL ABSTRACT



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ABSTRACT

Climate change shifts tree growth phenology and dynamics in temperate forests. However, there is still little information on how warming climate changes intra-annual growth patterns and how these changes affect the productivity and carbon uptake of temperate trees. To address this knowledge gap, we used high-precision growth data from automatic dendrometers to quantify the impacts of unusually warm weather in 2022 (hot year) on growth phenology, dynamics and aboveground biomass (AGB) production in eight common temperate species (both conifers and broadleaved) in the Czech Republic. Mixed-effect models were used to investigate inter-annual changes in the start, end, and length of the growing season and intra-annual growth dynamics. We also modelled how changes in growth phenology, growth rates, and tree size affected yearly AGB production of individual trees. In the hot year, the growth started 5 days earlier, peaked 22 days earlier and ended 20 days earlier than in the climatically normal year, resulting in a shorter growing season with fewer growing days. AGB production decreased 36 % in the hot year, mainly due to fewer growing days and lower maximum growth rates, but with significant variation among tested species. The decline in AGB production in the hot year was most significant in the most productive species, which were also the species with the greatest reduction in the number of growing days. Tree size strongly enhanced AGB production, but its effect did not change with climate variation. Our findings suggest that climate change is likely to advance but also shorten the growing season of temperate trees, resulting in lower biomass production and carbon uptake. The results also indicate that the fast-

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growing and highly productive temperate tree species will have their growth reduced most by climate change, which will increasingly limit their high carbon sequestration potential.

1. Introduction

Forests are an important carbon sink (Ciais et al., 2008; Nabuurs et al., 2013; Pan et al., 2011), and by sequestering carbon, they help to slow the pace of atmospheric CO₂ accumulation and climate change (Keenan et al., 2014). The magnitude of carbon uptake by forests largely depends on how much carbon trees bind into their biomass during their growth (Pugh et al., 2019). However, climate change has changed tree growth and productivity in recent decades (D'Orangeville et al., 2018b; Keenan et al., 2014; Myneni et al., 1997). Therefore, understanding the underlying mechanisms of tree growth and productivity responses to current and future climate variation is crucial for predicting the impacts of the warming climate on forest carbon sequestration (Steppe et al., 2015). Despite the imminent importance of these productivity and carbon uptake shifts for forest ecosystem functioning and climate change mitigation, there are still many uncertainties about the climate change impacts on the intra-annual tree growth dynamics, biomass production and carbon uptake in temperate trees.

In temperate forest ecosystems, trees grow in annual cycles during the growing season, which is determined by a period of favourable temperatures that enable trees to photosynthesize and grow (Cuny et al., 2015; Rossi et al., 2006). Although there are significant interspecific differences in the timing of the growing season as well as growth dynamics, the temporal changes in timing, rate and duration of growth (within and between seasons) are primarily driven by variation in temperatures and water availability over time (D'Orangeville et al., 2018a; Etzold et al., 2022). In most temperate zones, including Europe, temperatures have been increasing while the water balance has been decreasing (Stocker et al., 2013), causing significant changes in temporal growth patterns and forest productivity. However, whether tree productivity will increase or decrease under climate change depends on whether gains in productivity due to a longer growing season and higher temperature will be greater or smaller than productivity losses due to increased respiration and seasonal water deficits (Buermann et al., 2018; Keenan et al., 2014; Piao et al., 2008).

Climate change has already significantly shifted the growing season across European forest ecosystems and tree species (Menzel et al., 2006). Due to increasing temperatures, the growing season advances to the earlier days of spring and lasts until the later days in autumn (Menzel and Fabian, 1999), lengthening the growing season and potentially increasing productivity and seasonal carbon uptake in forest trees (Pretzsch et al., 2014; Zani et al., 2020). However, under climate change, rising temperatures are accompanied by increasing water limitation during the growing season due to increased evapotranspiration and increasing frequency and intensity of droughts (Stocker et al., 2013). The decrease in water availability reduces tree growth and forest productivity (Bose et al., 2021; Kasper et al., 2022; Montibeller et al., 2022), offsetting the productivity gains caused by longer growing seasons (Buermann et al., 2018). The net change in tree productivity and carbon uptake under climate change, therefore, depends on whether the negative effect of water availability prevails over the positive effect of higher temperatures.

Whereas the effect of higher temperatures on the earlier onset of the growing season across species has been well documented (Asse et al., 2018; Cleland et al., 2007; Delpierre et al., 2016), the information on the shifts in the growing season end is far more ambiguous with both positive and negative shifts reported depending on the geographical area and tree species (Dow et al., 2022; Menzel et al., 2006). The changes in the timing of the growing season end are, therefore, likely driven by a complex of factors and processes during the growing season, which may potentially shift the growing season ends toward earlier or later dates

(Zani et al., 2020), affecting significantly more the growing season length and the number of growing days than the shifts in growing season start (Etzold et al., 2022). However, how the variation in the growing season end due to changes in climate affects tree productivity remains poorly understood.

In addition to growing season length, tree productivity is also determined by the rate of radial stem growth that trees achieve during the growing season, which may also be altered by changing climate patterns (Delpierre et al., 2016). The radial stem growth accelerates within the first weeks after the growth resumption after winter dormancy, peaking in the period with the longest daylight around the summer solstice (Dow et al., 2022; Etzold et al., 2022). After this period with maximum growth rates, the radial growth usually declines significantly (Cuny et al., 2015). Therefore, most of the radial stem growth is realized during the early rapid growth phase, and the tree growth rates during this phase greatly determine the magnitude of biomass production during the whole growing season (Delpierre et al., 2016). However, there is still little information on how the intra-annual growth rate dynamics, growth rate maximums, and the timing of the starts and ends of the growing season change with warmer and drier climate and how these changes affect tree biomass production in temperate trees of different functional types.

To address this knowledge gap, we studied shifts in intra-annual growth dynamics, growth phenology and aboveground biomass (AGB) production caused by the heatwave in 2022 (hot year) in eight common European species of various functional types (broadleaved deciduous, needleleaf evergreen and needleleaf deciduous) in the Czech Republic. To do that, we analyzed precise growth data obtained from automatic dendrometers, which continuously measured stem radius changes throughout the hot year 2022 and the previous normal and wet year 2021. To find out how changes in growth phenology and maximum growth rates affect the AGB production, we also modelled yearly AGB production as a function of growing season length, the timing of the growing season, and growth rates achieved during a peak growth period, together with stem diameter. Specifically, we hypothesized that in response to the unusually warm weather a) the growth starts and peaks earlier but also ends earlier (Dow et al., 2022); hence the growing season does not lengthen significantly; however, b) due to the occurrence of a prolonged period of below-average precipitation before and during the growing season in the hot year, we expected fewer number of growing days in that year, causing slower growth (Etzold et al., 2022) and lower AGB production. We also predicted that c) the maximum growth rates the trees achieve during the growing season are strongly linked to yearly AGB production but due to the adverse effect of the heatwave and increased water limitation on tree growth (Teskey et al., 2015), we expect them to be lower in the hot year, leading to a decline in tree productivity. In addition, we predicted that d) the yearly AGB production increases with tree size. As trees grow larger, the amount of biomass they contain increases exponentially. Therefore, even if two trees have the same stem radial increment, a smaller tree has a lower total biomass production and a lower capacity for carbon sequestration than a larger tree. We expected to find all these changes and effects across all species but with significant inter-specific variation among them. Overall, our study aims to contribute to a better understanding of the complex interactions between climate variability and tree growth, with implications for carbon sequestration across common European forest species.

2. Methods

2.1. Study area

The study was carried out in two Central-European temperate forests located between 50.09291°–50.119329° N and 13.84185°–13.86853° E in the Křivoklátsko Protected Landscape in the western part of the Czech Republic (Fig. S1). The forests in the area are composed of a variety of broadleaved and coniferous tree species. The elevation ranges between 373 and 428 m a.s.l. The average annual air temperature is 8.5 °C. The warmest month is July (average temperature 18.3 °C), and the coldest month is January (average air temperature –1.0 °C), based on data from 1991 to 2020 obtained from the nearest weather station (Lány). The average total annual precipitation is 583 mm. The precipitation is distributed across all months, with most rainfall typically falling from July to August. The soils are cambisols on granodiorite bedrock.

2.2. Study design and tree measurements

To measure tree growth, intra-annual growth dynamics, and growth phenology, we installed automatic point dendrometers D1 (TOMST, Prague, Czech Republic) on 82 trees in 2020. The trees were selected within 23 permanent circular plots (1000 m² each) located in 6 transects (3 to 5 plots in each transect), with a minimum distance between the transects of 500 m and a minimum distance between plots in the transect of 100 m (Fig. S1). In each plot, we selected four healthy trees of different species with a crown in the main canopy to install the dendrometers. In plots with fewer than four species in the main canopy, we replicated the dendrometer installation on the most dominant species to keep the number of dendrometers per plot constant. The selected species represented a common European temperate species (most of them are also common in boreal forests) of a variety of functional types (Leuschner and Meier, 2018): evergreen conifers Norway spruce (*Picea abies* L.; 21 trees) and Scots pine (*Pinus sylvestris* L.; 5 trees), a deciduous conifer European larch (*Larix decidua* Mill.; 11 trees), and deciduous broadleaved species European beech (*Fagus sylvatica* L.; 17 trees), pedunculate oak (*Quercus robur* L.; 13 trees), birch (*Betula pendula* Roth.; 5 trees), linden (*Tilia cordata* Mill.; 5 trees), and European white elm (*Ulmus laevis* Pall.; 5 trees).

The dendrometers were installed on the north-facing undamaged part of the stem at the height of 1.3 m above the ground. Bark was removed from the stem at the measurement area. Since the moment of the installation (during 2020), the dendrometers have been automatically measuring stem radius changes with a resolution of 1 μm every 15 min, storing measured data in an internal datalogger. The dendrometers were regularly checked for possible malfunctions, and data were downloaded after the end of the growing season. The last data download was done in November 2022. For this study, we used data from two complete growing seasons, 2021 and 2022. We also measured stem diameter of the trees 1.3 m above the ground (DBH) before the growing season in 2021. Because 2021 was climatically within long term average, while 2022 was unusually warm and significantly drier

Table 1

Mean temperatures and precipitation in the normal year 2021, the hot year 2022 and the long-term (1991–2020) averages (Normal). GS stands for the main growing season during which most of the observed radial stem growth was realized (May–August); pre-GS refers to two months, March and April, which preceded the onset of radial growth. Winter refers to the main winter period (January and February) before the growing period.

Period	Mean temperatures (°C)				Precipitation (mm)	
	Year	GS	pre-GS	Winter	Year	GS
2021	8.3	15.9	4.6	–0.45	657	337
2022	9.6	17.3	5.1	2.55	558	209
Normal	8.5	16.0	6.2	–0.35	583	215

(Table 1), the difference between the two weather patterns represented the shift predicted for Central Europe under climate change (Christensen and Christensen, 2007). Therefore, we could explore how the expected climate shifts affect the start and end of the growing season as well as tree intra-seasonal growth dynamics and yearly tree growth and productivity of central European temperate trees under climate change.

2.3. Climate data

Data on temperatures, precipitation and vapour pressure deficit (VPD) for the years 2021 and 2022, as well as long-term (1991–2020) averages, were obtained from the official weather station Lány (of the Czech Hydrometeorological Institute), located approximately 3 km from the study sites. In the year 2021 (normal year) temperature was similar to the long-term average, and the precipitation was slightly above the average (Table 1). The above-average rainfall in 2021 mainly fell from January to August, i.e., during the main growing season (May–August) while in later months, the precipitation was lower than average (Fig. S2, Table 1). The year 2022 (hot year) was significantly warmer than the long-term average, with a particularly warm winter and main growing season (Table 1). The total yearly precipitation was only slightly lower than the average one, but it was distributed irregularly over the year (Fig. S2). Before and during the growing season of 2022, there was a period with below-average precipitation spanning from late 2021 until July 2022 (except for June; Fig. S2). VPD was higher in the hot year 2022 and lower in the normal year 2021 in most months compared to long-term averages (Fig. S3).

2.4. Data processing

Raw measurements of stem radius changes (Rad_{stem}) downloaded from dendrometers were checked and fixed from erroneous measurements and artefacts (e.g., jumps resulting from dendrometer adjustments) and then aggregated into daily means using “PLOTer” R package, which was developed for this purpose (Plichta and Matula, in prep.). Daily stem radius changes were then calculated from Rad_{stem} as moving average with a 14-day window rolling in one-day intervals and smoothed by generalized additive model (GAM) using cubic regression spline ($s(\text{bs}=\text{'cs'})$) and basis dimensions (k) set to 25. We then used thresholds corresponding to 5 % of maximum Rad_{stem} daily rates to determine the date of the beginning and end of secondary stem growth (GS_{start} and GS_{end} , respectively) (Fig. S4). The length of the growing season ($\text{GS}_{\text{length}}$) was calculated as the difference (in days) between GS_{end} and GS_{start} . Also, cumulated daily growth (GRO) was calculated from the Rad_{stem} data using the zero growth concept (Zweifel, 2016). The daily growth rates were then calculated as:

$$\text{GRO}_{\text{rate}} = \text{GRO}_{\text{day}} - \text{GRO}_{\text{day}-1}$$

In which GRO_{rate} denotes daily growth rate, GRO_{day} and $\text{GRO}_{\text{day}-1}$ represent GRO reached in a given day and GRO reached in a previous day, respectively.

Using GRO_{rate} , we calculated the number of growing days (NGD) as the sum of days in the growing season with $\text{GRO}_{\text{rate}} > 0$ and the maximum daily growth rate (GRO_{max}) and its timing for each tree and year.

To calculate yearly AGB production, we first calculated DBH yearly increment as $2 \times$ yearly stem radius increment, which we obtained from the dendrometer data. The DBH yearly increments were then summed with measured DBHs to obtain DBH values the trees reached after each growing season. Using DBH yearly values, species identity, species-specific wood density and geographical coordinates of the plots, we calculated aboveground biomass (AGB) for each tree at the start of the measurements (2020) and for two consecutive years using the R package “allodB” (Gonzalez-Akre et al., 2022). The yearly AGB increment (AGBI) was then calculated as follows:

$$AGBI = AGB_{year} - AGB_{year-1}$$

In which AGBI denotes a total yearly increase in AGB, AGB_{day} and AGB_{day-1} represent total AGB reached in a given year and total AGB reached in a previous year, respectively.

2.5. Statistical analyses

To quantify inter-annual differences in growth phenology and productivity across species, we modelled each of the calculated variables (radius growth, AGBI, GS_{end} and GS_{start} , GS_{length} , NGD, GRO_{max} , and the day of GRO_{max}) as a function of the year (factor) using linear mixed-effect models. Plot identity (plotid) and species identity (speciesid) were used as random effects in the models. To detect the effect of species identity in addition to the effect of year, we used the same models but with speciesid and its interaction with year as fixed-effects terms. If the interaction was significant ($P < 0.05$), we ran the models separately for each species.

To explore how growth phenology, maximum growth rates and growth size affect AGB yearly productivity across all years and species, we created three models:

$$\begin{aligned} AGBI_{ijp} = & \beta_0 + \beta_1 Si + \beta_2 Phenol + \beta_3 GRO_{max} + \beta_4 DBH \\ & + \beta_5 (Phenol \times DBH) + \beta_6 (Si \times DBH) + b_{pj} + \varepsilon_{ijp} \end{aligned}$$

where β_0 is the intercept, $\beta_1 Si$ means the fixed effect of species i, $\beta_2 Phenol$ represents the fixed effect of either NGD (model 1), GS_{length} (model 2) or GS_{end} and GS_{start} (model 3), $\beta_3 GRO_{max}$ denotes the fixed effect of GRO_{max} , $\beta_4 DBH$ represents the fixed effect of DBH, $\beta_5 (Phenol \times DBH)$ and $\beta_6 (Si \times DBH)$ denote the interaction terms between phenology and DBH and between species and DBH, respectively. The term b_{pj} means the random effect of tree identity nested in the plotid j and ε_{ijp} is the residual error term. The variables AGBI and GRO_{max} were log10-transformed to linearise and normalize them. To check for multicollinearity, we calculated variation inflation factors (VIF), which confirmed no significant correlations among the variables in the models ($VIF < 1.5$). We then performed stepwise elimination to remove statistically insignificant variables with $P > 0.05$. The reduced models were then compared to the previous best model using Akaike information criterion (AIC). For the final (reduced) models, we calculated marginal R^2 (Nakagawa et al., 2017) to find out how much variation in AGBI was explained by the fixed-effect variables in the model. The final models (with different growth phenology variables) were then compared using AICs and R^2 s. To quantify the effects of each explanatory variable in the final models, we calculated its marginal effect while holding the other variables in the model constant.

To find out how species-specific changes in growth dynamics and growth phenology are related to changes in tree productivity, we ran linear models with either the relative or absolute inter-annual change in AGBI as a response variable and AGBI in the normal year (i.e. in the year with the highest productivity) and changes in NGD, GS_{start} and GS_{end} as explanatory variables. Because *Fagus* was a significant outlier in the model with AGB productivity in the normal year, it was excluded from the analyses. *Pinus* was, for the same reason, excluded from the models with GS_{end} and GS_{start} .

All the analyses were carried out using R software (R Core Team, 2022). The mixed-effect models were done using "lme4" package (Bates et al., 2015).

3. Results

3.1. Inter-annual changes in aboveground biomass production

AGBI in the hot year 2022 was, on average, lower by 36 % than in the normal year 2021 (mean AGBI 2021 = 21.0 ± 2.66 kg, mean AGBI 2022 = 13.4 ± 2.70 kg, $P < 0.001$), but the inter-annual change in AGBI varied significantly among species (interaction year \times species, $P =$

0.006). The largest declines in AGBI were found in *Ulmus* (75 %), *Betula* (61 %), *Picea* (52 %), *Larix* (49 %) and *Quercus* (37 %) ($P < 0.001$), whereas there were only insignificant declines in *Fagus* and *Tilia* ($P \geq 0.1617$; Fig. 1). *Pinus* was the only species whose AGBI slightly increased in the hot year (Fig. 1), although the change was not significant ($P = 0.580$). A similar pattern of inter-annual decline in the hot year was also found for radial growth (Fig. S5).

3.2. Changes in growth phenology and dynamics

Across the species, GRO_{max} occurred 22 days earlier in the hot year compared to the normal year ($P \leq 0.001$). GRO_{max} was recorded on DOY 160 in the hot year, 11 days before the summer solstice, while in the normal year, it was recorded on DOY 182, 11 days after the summer solstice. The earlier growth rate peak in the hot year was followed by a quick drop in growth (in July), whereas the later-achieved growth rate peak in the normal year was sustained for a longer time, declining approximately one month later (Fig. 2). Within species, the growth peaked significantly sooner in the hot year in all species ($P \leq 0.026$) except for *Larix* and *Tilia* (Fig. S6). The earlier peak of growth was negatively related to AGBI ($P = 0.005$; Fig. 3), and this relationship did not differ among species ($P > 0.204$).

In the normal year, the growing season started, on average, on DOY 131 (± 4.0 ; May 11) and ended on DOY 237 (± 2.5 ; August 25), whereas, in the hot year, growth started on average on DOY 126 (± 4.1 ; May 6) and ended on DOY 205 (± 2.6 ; July 24). This means that, in the hot year, GS_{start} occurred on average 5 days earlier, and GS_{end} occurred almost 25 days earlier compared to the normal year. The inter-annual shifts in GS_{start} did not vary significantly among species (interaction growth start \times species $P = 0.180$). In contrast, the interannual shift in GS_{end} varied among species (interaction growth end \times species $P < 0.001$; Fig. 4). It was smallest in *Fagus* and *Tilia* (around 20 days), while it was largest in *Picea* and *Pinus*, which both ended their growth >40 days earlier in the hot year in comparison with the normal year (Fig. 4).

The growing season in the hot year was shorter by 21.1 (± 1.6) days on average, lasting 125.5 (± 4.51) days, while in the normal year, it lasted 146.5 (± 4.49) days, but there was significant variation among species in this respect (Fig. S7). A shorter growing season in the hot year was found for *Betula*, *Fagus*, *Larix*, *Picea*, *Quercus* and *Ulmus* ($P \leq 0.005$) but not for *Pinus* and *Tilia* ($P \geq 0.088$).

NGD in the hot year was 103 (± 5.1), whereas it was 123 (± 5.2) in the normal year, i.e. 20 days more ($P < 0.001$). The inter-annual difference in NGD varied significantly among species (interaction NGD \times species $P = 0.004$; Fig. 5). The decline in NGD in the hot year was significant ($P \leq 0.032$) in all species except for *Fagus*, *Quercus* and *Tilia* ($P \geq 0.064$), being largest in *Betula*, *Picea* and *Ulmus* (>30 days, Fig. 5). NGD decreased with later GS_{start} (standardized coefficient = -11.8 ± 1.31 , $P < 0.001$) and increased with later GS_{end} (standardized coefficient = 17.8 ± 1.08 , $P < 0.001$). GS_{start} and GS_{end} together explained 69 % of the variation in NGD (marginal $R^2 = 0.69$) but when tested separately GS_{start} had explained significantly less variation in NGD (marginal $R^2 = 0.18$) than GS_{end} (marginal $R^2 = 0.45$). GS_{end} therefore influenced NGD significantly more than GS_{start} . Trees grew on average 83.3 (± 1.30) % of the days of the growing season, and this ratio did not vary significantly either with year or species ($P \geq 0.119$).

GRO_{max} was higher in the normal year ($40.8 \pm 2.71 \mu\text{m day}^{-1}$) than in the hot year ($33.2 \pm 2.77 \mu\text{m day}^{-1}$, $P = 0.001$). At the species level, GRO_{max} was significantly higher in the normal year in *Larix*, *Picea* and *Ulmus* ($P < 0.015$) and insignificantly higher in *Betula* and *Quercus* ($P > 0.068$; Fig. 5).

3.3. Effects of growth dynamics on tree productivity

The model with NGD together with GRO_{max} and DBH (as explanatory variables) fitted best the variation in AGBI across the species and years (marginal $R^2 = 0.88$, $P < 0.001$, AIC = 167.8). The effects of all the

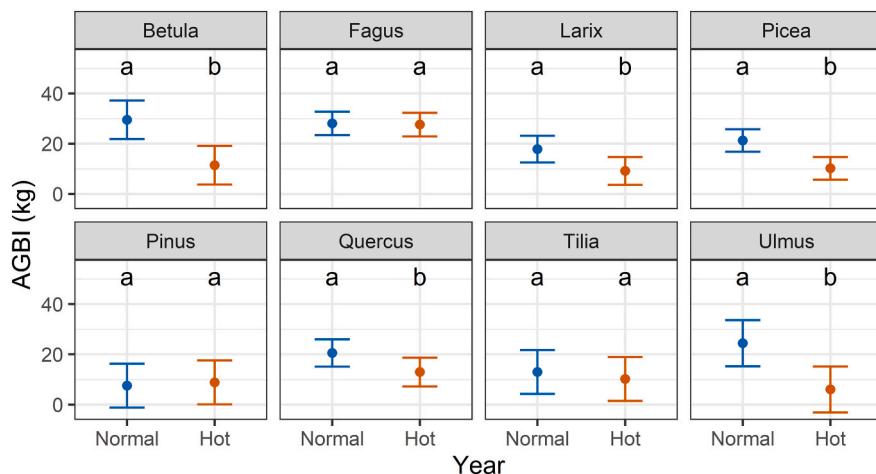


Fig. 1. Mean yearly aboveground biomass yearly increment (AGBI) of individual trees in the normal year 2021 and the hot year 2022. Points represent means; error bars denote the standard error of the mean. Different letters within each plot mean significant inter-annual differences ($P < 0.05$). For each species, the differences between years were tested using linear mixed effect model with plot identity as random effect. $n = 82$ trees of 8 species (details in Methods).

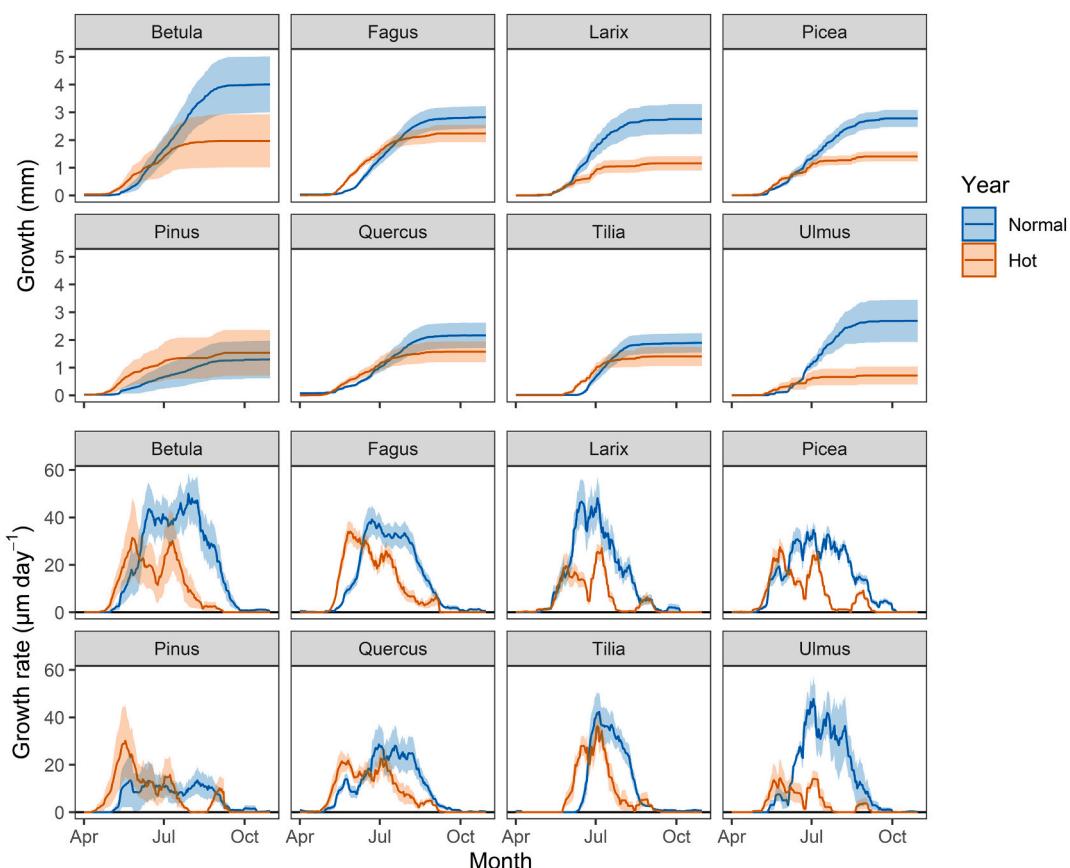


Fig. 2. Stem radial growth (Growth) and daily growth rate (Growth rate) dynamics during hot and normal years in the studied species. Lines connect daily mean values, the shaded areas around the standard error of the mean.

explanatory variables in the model were positive (Fig. 6). While holding the other variables constant, AGBI increased with NGD at the rate of 0.15 kg AGB per each extra growing day. Trees with the lowest NGD (56) had approximately 6.9 kg of AGBI, while trees with the highest NGD (160) had around 22.8 kg of AGBI, i.e. more than three times more (Fig. 6). GRO_{max} had an even larger positive effect on AGBI than NGD (Fig. 6). Trees with lowest GRO_{max} produced <1 kg of AGBI, whereas trees with highest GRO_{max} produced around 54 kg of AGBI. DBH also greatly affected AGBI (Fig. 6), with trees with 10 cm in DBH having

around 6 kg AGBI, whereas the biggest trees (100 cm in DBH) had around 120 kg of AGBI.

Timing of the onset and end of the growing season also significantly influenced AGBI ($P < 0.001$). The model with GRO_{start} and GRO_{end} (together with DBH and GRO_{max}) also explained a large proportion of variation in AGBI (marginal $R^2 = 0.87$, $P < 0.001$), but it was worse than the model with NGD ($\Delta AIC = 14$). The earlier GRO_{start}, which ranged from the half of April to the beginning of June, was associated with greater AGBI ($P = 0.047$), increasing 0.1 kg per each day of the earlier onset of

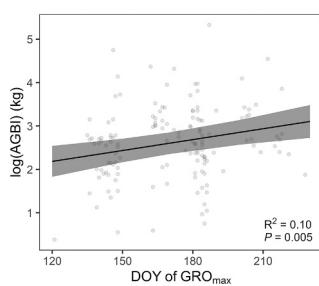


Fig. 3. The relationship between yearly AGB (AGBI) increment and DOY of the maximum daily growth (GRO_{max}). Points represent observations; the line and grey zone represent fitted linear mixed-effects model and 95 % confidence intervals, respectively.

growth. The later GRO_{end} , which ranged from the end of July to the beginning of September, led to greater AGBI ($P < 0.001$), increasing 0.13 kg per each day of the later end. The longer GS_{length} led to greater AGBI ($P < 0.001$; Fig. 6), but the model with it had a much worse performance than the other models ($\Delta AIC = 75$ from the best model). The fixed effect of species identity and the interaction effects were not

significant ($P \geq 0.065$) and were removed from all the models.

3.4. Species-specific changes in AGB production

The species with greater production of AGB in the normal year were associated with a greater decline in AGB production in the hot year (Figs. 7A, S8). The only exception was *Fagus*, which was one of the species with the highest AGBI in the normal year, but its AGBI did not decline significantly in the hot year. For the other species, the negative relationship between mean AGBI in the normal year and mean AGBI change in the hot year was strong in terms of both absolute ($R^2 = 0.89$, $P < 0.001$) and relative ($R^2 = 0.77$, $P < 0.001$) values (Figs. 7, S8). The mean decline in AGBI in the hot year was also strongly related to a mean decrease in NGD ($R^2 = 0.69$, $P = 0.012$) and earlier GS_{end} ($R^2 = 0.82$, $P = 0.003$), except for *Pinus* (Fig. 7B and D, respectively). The earlier GS_{start} in the hot year helped to buffer the decline in AGBI (Fig. 7C), but due to large variation, its effect was not statistically significant despite relatively high R^2 ($R^2 = 0.34$; $P = 0.100$). The species-specific change in GRO_{max} did not correlate significantly with the species-specific change in AGBI ($P = 0.287$).

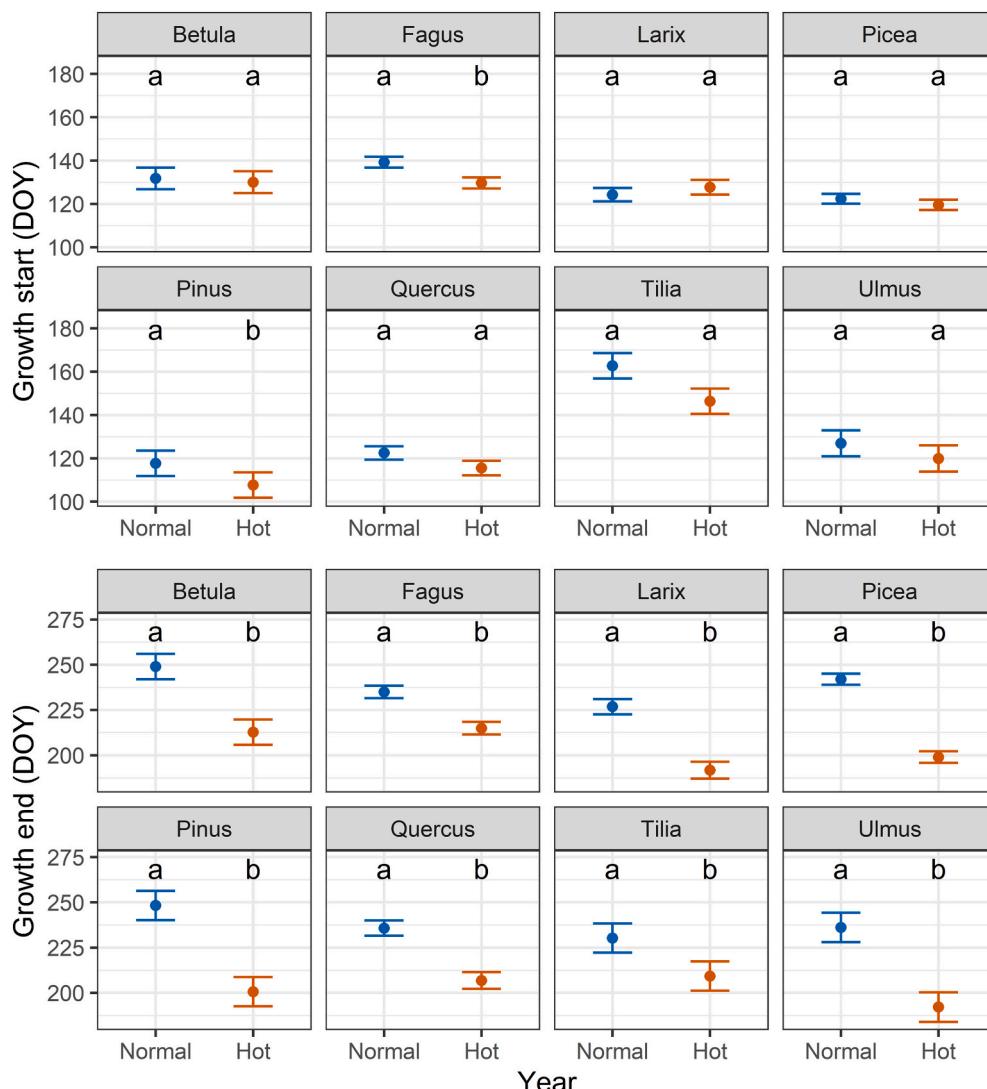


Fig. 4. Mean DOY of growing season start and end in the normal year 2021 and the hot year 2022. Points represent means and error bars denote the standard error of the mean obtained from linear mixed-effects models. Different letters within each plot mean significant inter-annual differences ($P < 0.05$). For each species, the differences between years were tested using linear mixed effect model with plot identity as random effect. $n = 82$ trees of 8 species (details in Methods).

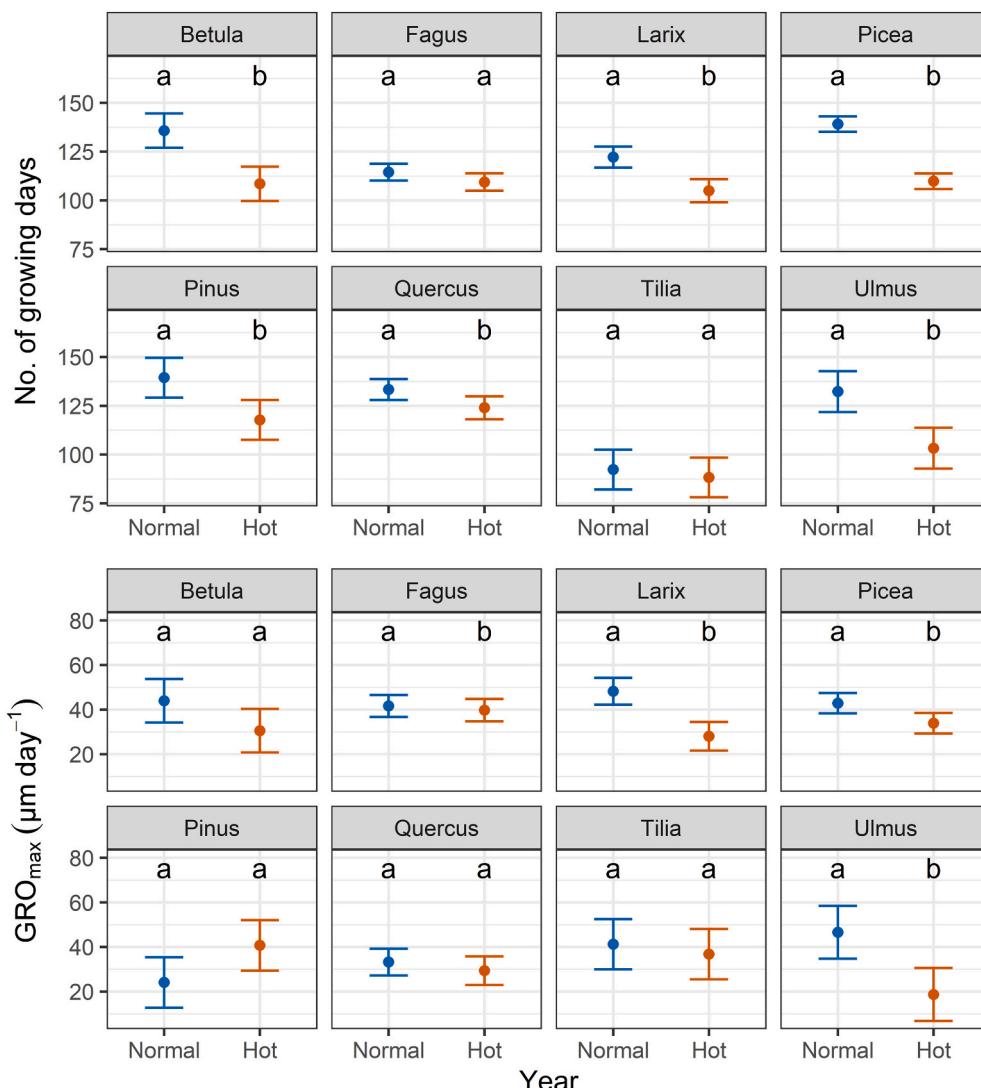


Fig. 5. Mean number of growing days (GRO > 0) and mean maximum daily growth rate (GRO_{max}) in the normal year 2021 and the hot year 2022. Points represent means and error bars denote the standard error of the mean obtained from linear mixed-effects models. Different letters within each plot mean significant inter-annual differences ($P < 0.05$). For each species, the differences between years were tested using linear mixed effect model with plot identity as random effect. $n = 82$ trees of 8 species (details in Methods).

4. Discussion

Our study revealed that the unusually warm and drier weather in 2022 (i.e. hot year) significantly shifted growth phenology and dynamics and led to a decline in radial stem growth and productivity in the majority of the tree species of our study. As expected, most species started to grow significantly earlier in the hot year than in the previous normal year (by 5 days on average). However, in the hot year, the earlier onset of growth was followed by an even earlier end of growth (by 20 days on average), causing a significant shortening of the growing season and a decline in the number of growing days, which, in turn, led to a decrease in yearly AGB production. Because such changes in growth phenology, dynamics and productivity were found in several common tree species (although not all) of varying functional types, it is evident that climate change is likely to cause significant changes in the yearly growing cycles of many temperate European tree species, limiting their productivity and carbon sequestration in the future.

4.1. Changes in tree growth dynamics and productivity

Generally, our results showed that the shorter growing season, either due to later onset of growth or earlier growing season end, decreases tree productivity, which is in line with previous findings that a shorter growing season is associated with lower biomass growth and carbon

uptake (Gao et al., 2022; Liu et al., 2022; Richardson et al., 2010). Although the intra-annual maximum growth rate and tree size proved to have larger effects on yearly AGB yield (Fig. 6), the impact of the shorter growing season and lower number of growing days on tree productivity is still substantial. Considering the observed rate in AGB production of 0.15 kg per each growing day and the average tree density of 677 trees ha^{-1} in the studied forests (Matula, unpublished data), the increase or decrease of the length of growing season by just one growing day may cause increase or decrease, respectively, in AGB production of approximately 100 kg ha^{-1} . Such change in AGB production equals the difference of about 50 kg ha^{-1} (calculated as AGB * 0.5) in yearly carbon sequestration just in the aboveground tree tissues. Therefore, the observed average decrease of 20 growing days in the hot year means a decline in carbon uptake of 1 t ha^{-1} per year. Surprisingly, the significant effects of growth phenology on tree productivity did not vary among species, which comprised a variety of functional types (broad-leaved deciduous, evergreen and deciduous needleleaf). Because evergreen needleleaf species *Picea* (although not Pine) was among the species with the largest growth phenology shifts and declines in productivity, our results do support the finding of Richardson et al. (2010) that the productivity of evergreen needleleaf forests is less sensitive to phenology than the productivity of deciduous broadleaf forests.

However, it is worth to note that the presented declines in biomass production in the hot year might be slightly overestimated because, in

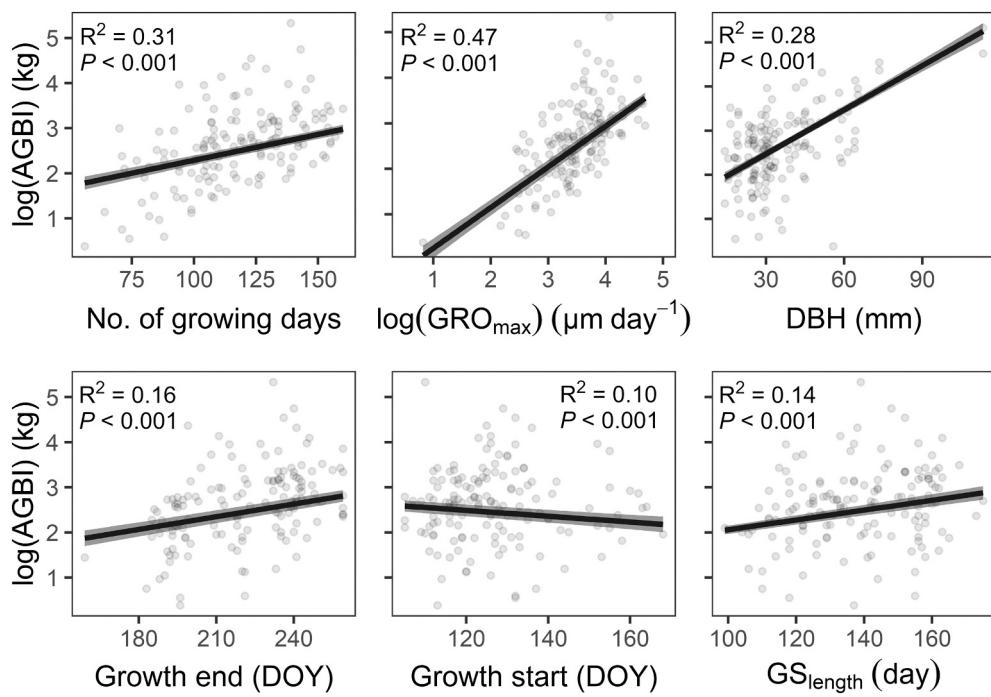


Fig. 6. The effects of growth phenology variables, maximum daily growth rate (GRO_{max}) and DBH on yearly AGB production (AGB). The lines are partial effects from full linear mixed-effects models in which all but the presented variables in each subplot were set to mean values. AGB and GRO_{max} were log10-transformed to linearize and normalize residuals.

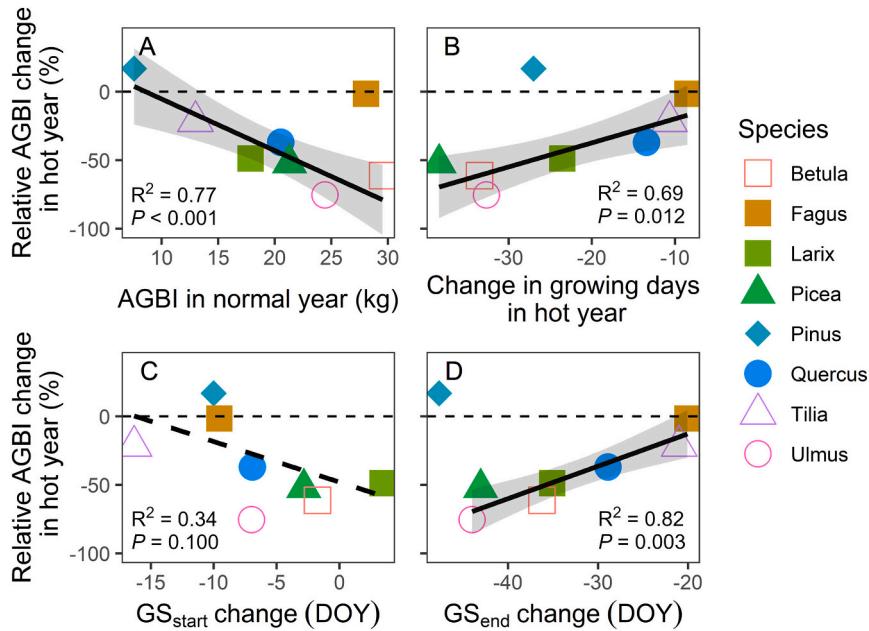


Fig. 7. The relationships between mean change in AGB production on a species level in the hot year and a) AGB increment (AGBI) in the normal year, b) change in NGD in the hot year and the change in c) growing season start (GS_{start}) and d) growing season end (GS_{end}). Points represent species means, black lines represent fitted linear models; the solid black lines with marked confidence intervals (grey) represent models with $P < 0.05$, and the dashed line without confidence intervals models with $P > 0.05$. Fagus, as a significant outlier, was excluded from the model presented in a) while Pinus was, for the same reason, excluded from the models shown in c) and d).

our biomass calculations, we did not account for the possible changes in wood density due to variation in biomass allocation into the secondary wall after the growth cessation (Cuny et al., 2015). The increase in wood density could partially compensate for the lower radial growth in the hot year (Bouriaud et al., 2015; Pretzsch et al., 2018), which we did not capture in our study.

4.2. Shifts in growth phenology

As expected, tree growth started and peaked earlier in the hot year. However, the earlier peak of radial growth was unexpectedly followed

by a rapid decline in growth and an earlier end of the growing season. This result corroborates similar findings of previous studies from temperate forests in Europe (Etzold et al., 2022) and North America (Dow et al., 2022), who also found that the warmer climate leads to an earlier start and earlier end of growth. Therefore, it is evident that the rise in temperatures predicted for temperate zones of Europe and North America under climate change (Christensen and Christensen, 2007) will shift the whole annual growing cycle toward earlier days but is likely not lead to a longer growing season and more growing days. And, because the growing season shortening in our study proved to cause a significant decline in tree productivity, it is also likely that the changes in growth

phenology might lead to a significant decline in productivity and carbon sequestration in many temperate forest ecosystems. The findings of our and the other studies contrast with a study by Keenan et al. (2014), who predicted an extension of the growing season and increased carbon uptake in temperate forests in the US due to climate change.

The reason for such shifts in the timing of the growing season and growth dynamics is probably due to increased carbon sink limitation. Zani et al. (2020) demonstrated that the earlier onset of growth due to higher temperatures increases photosynthetic activity and, thus, carbon production and growth early in the growing season. However, the increased early carbon production leads to earlier carbon sink saturation and, in turn, to an earlier end of the growing season (Zani et al., 2020). The carbon sink saturation means that the growth potential of a tree is reached within given environmental conditions (i.e. within nutrient and water availability limitations). The growth of the trees in our study was much smaller in the hot year, despite the earlier onset of growth, which indicates that the other limitations prevailed. Given that soil nutrients did not change over the two study years, it was most likely increased water limitation, which affected the trees in our study in the hot year. Water deficit often accompanies heatwaves and exacerbates the adverse effects of heat stress on tree growth (Teskey et al., 2015). The hot year 2022 was indeed not only warmer but also drier (although not extremely) during most of the vegetation season due to lower-than-average rainfall before and during the growing season (Table 1; Figs. S1, S2). And, because increased water deficit reduces tree growth by impeding the cambial proliferation activity and subsequent wood cells formation and expansion (Balducci et al., 2013; Körner, 2015; Tardieu et al., 2011), the decline in tree productivity and earlier end of growth in the hot year was likely exacerbated by lower water availability (Olivar et al., 2022) and greater VPD (Tumajer et al., 2022) during the growing season, leading to a decrease in growth rates and the number of growing days. Moreover, we believe that the increased water limitation may also have exacerbated the effect of the heatwave on the earlier growing season end by further advancing the carbon sink saturation. The earlier onset of growth and higher spring temperatures in the hot year probably led to greater carbon production in trees early in the growing season (Zani et al., 2020). However, the produced carbon could accumulate faster because of slower carbon use by growth, which was suppressed by increased water limitation, leading to earlier carbon saturation. Therefore, we speculate that in areas and/or during growing seasons with higher water availability (e.g. areas with high soil water level, warm but rainy years or areas), the shifts in growth phenology due to warmer climate may not be as negative as we observed in our study and that the effect on productivity may be unaltered or even positive as observed in previous studies (D'Orangeville, Houle, et al., 2018; Dow et al., 2022; Gao et al., 2022).

As predicted, the maximum daily growth rates achieved during the growing season greatly influenced yearly AGB production, with only small changes in it leading to substantial changes in tree productivity (Fig. 6). This finding agrees with Delpierre et al. (2016), who showed a large effect of growth intensity during the first rapid growing phase on aboveground wood production. The likely reason is that most of the tree growth is realized in a relatively short period of fast growth; therefore, the faster the growth rate trees can achieve during this period, the more biomass they produce in the whole growing season. The enormous influence of the maximum daily growth rate over total tree growth and productivity points to the crucial role of the timing of drought on tree growth (D'Orangeville et al., 2018b; Foster et al., 2014). For example, Salomón et al. (2022), who used automatic dendrometers to quantify the effects of the 2018 heatwave and megadrought (Moravec et al., 2021) on tree growth across Europe, did not find consistent growth reduction such as we did in our study in the hot year 2022. The likely reason for this discrepancy is the different timing of the drought. The drought in 2018 occurred later in the summer (starting in late July; Salomón et al., 2022), whereas the drier conditions in the hot year 2022 happened before and during most of the months of the growing season (May–July; Figs. S2,

S3), affecting tree growth despite being less intense than in 2018.

4.3. Species-specific sensitivity to warming climate

The rates of temporal changes in growing season length and the number of growing days was not constant across species, varying on a large gradient from species with insignificant changes to species with growing seasons shortened by 40 days and growing days reduced by >30 days in the hot year (Fig. 5). Surprisingly, the rates of growing season shortening and the decrease in the number of growing days were strongly correlated with the decline in AGB yield (except for Pine; Fig. 7). This finding implicates that species, which are more sensitive to climate fluctuation in terms of their growth phenology and dynamics, are also more likely to have their growth reduced under climate change. We also found out that, in most species, the negative impact of the hot year on tree productivity strongly increased with tree species productivity in the normal year (Fig. 6, S8). Because the fastest-growing and the most productive tree species were also the ones with the most shifted phenology, it is evident that the sensitivity to climate change increases with tree productivity. This pattern also implies that the tree species with greater growth are likely to have their carbon uptake reduced significantly more than slower-growing, less productive species.

Fagus (European beech) was the only species that was among the most productive tree species, but its productivity was not significantly affected by the hot year. This was surprising because it is known to be less tolerant to drought than, for example, *Quercus* (Kasper et al., 2022), whose growth declined significantly in the hot year. However, the sensitivity of European beech to drought has been shown to vary considerably within the species, with populations from climatically drier areas being more drought-tolerant than those from wetter areas (Leuschner, 2020; Sánchez-Gómez et al., 2013; Schmied et al., 2023). And, because our study sites are located in one of the driest areas of the European beech distribution in Central Europe (Weigel et al., 2023), the local beech populations in our study may be better adapted to drought than in other areas. Another reason may be that it is less sensitive to climate variation in terms of growth phenology because it was the species with the smallest decline in the number of growing days and the smallest shift in the growing season end in the hot year (Fig. 7). This pattern indicates the influence of growth phenology shifts on tree productivity and carbon uptake.

5. Conclusions

The climate in temperate zones of Europe becomes increasingly warmer and drier (Stocker et al., 2013), affecting forest productivity and carbon uptake (Buermann et al., 2018; Keenan et al., 2014). Using high-precision growth data from automatic dendrometers, we quantified the impacts of the heatwave in 2022 on growth phenology, dynamics and AGB production in eight common temperate species in two forests in the Czech Republic. The growth not only started and peaked earlier but also ended significantly earlier in the hot year 2022 than in the normal and wet year 2021, resulting in a significantly shorter growing season and fewer growing days. These shifts also led to a decline in growth and productivity. These findings indicate significant future shifts in annual growing cycles and a decline in carbon uptake under climate change, at least in drier areas of Central Europe, to which our sites climatically belong. However, our study also shows that the climate-induced shifts in growth phenology and productivity disproportionately affect the most productive species, significantly limiting their high carbon sequestration potential. Because such species are crucial not only for carbon uptake but also for timber production, such changes in tree productivity due to climate change are likely to have significant negative economic impacts on the forestry industry in addition to reducing the climate-change mitigation potential of temperate forests.

CRediT authorship contribution statement

Matula Radim: Conceptualization, funding acquisition, methodology, visualization, writing.

Knížová Soňa: Methodology, editing.

Vítámvás Jan: Data collection, methodology, editing.

Šrámek Martin: Data collection, methodology, editing

Kníž Tomáš: Data collection, methodology, editing

Ulbrichová Iva: Data collection, methodology, editing

Svoboda Miroslav: Data collection, methodology, editing

Plichta Roman: Data analysis, methodology, writing, editing

Declaration of competing interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Radim Matula reports financial support was provided by Technology Agency of the Czech Republic.

Data availability

Data will be made available on request.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.scitotenv.2023.166906>.

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