Thinning decreases above-ground biomass increment in central European beech forests but does not change individual tree resistance to climate events

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A B S T R A C T

European beech plays a prominent role in the adaptation of European forests to and mitigation of climate change. Forest management may increase the mitigation potential of beech forests by accelerating carbon accumulation in tree biomass, but little is known about the interaction between the rate of biomass expansion in beech and its sensitivity to climate variation or its resistance to extreme drought episodes. A 60-year thinning experiment in beech forests in Central Europe was used to generate tree-ring width series describing past radial growth of dominant, co-dominant and sub-dominant beech trees. Randomisation applied to daily climate data was used to find the period of the year during which climate best explains beech growth. Results show that carbon uptake by above-ground biomass is higher in unmanaged stands and that thinning does not affect beech growth sensitivity to climate. Further, this study shows that average daily temperature amplitude and precipitation in March-July are the best predictors of radial growth in beech at lower-elevation sites. In a key finding, this research shows that site quality and thinning intensity increase tree size, which in turn lowers their resistance to drought. Using forest management to increase the productivity of European beech may thus increase its vulnerability to climate change.

1. Introduction

Globally, forests represent a significant store of carbon and contribute to the removal of excess greenhouse gasses from the atmosphere, mitigating the impacts of climate change in the process (IPCC, 2018). At the same time, global climate change alters the growth of forest ecosystems both positively and negatively (McDowell et al., 2020). The impact of ongoing climate change on the world's forests is very likely to determine their future contribution to mitigation efforts. Radial expansion of tree trunks is one of the main processes of semi-permanent removal of carbon dioxide from the atmosphere (Babst et al., 2014), in seasonal forests it is documented by the appearance of annual growth rings (Zweifel et al., 2006). The activity of cambium, plant tissue responsible for the production of durable wood, is tightly regulated by variation of resource availability within each annual cycle

(Jacoby and D'Arrigo, 1997).

Tree growth is however a long-term process, often taking place across many decades or centuries. Analyses of ring width have thus been used to document past changes in environmental conditions or the levels of competition between trees in a forest ecosystem, which together impact resource availability. Climate change has already been documented by looking at tree ring width series. Long-term changes in tree growth were shown (Tei et al., 2017), speeding up or slowing down tree growth by shifting the new conditions closer or further away from the climatic optimum of the species (McCullough et al., 2017). European beech (*Fagus sylvatica* L.) is one of the most important tree species in Europe, both commercially and ecologically. Its current distribution range extends from southern Scandinavia to the south of Italy, and from Spain in the west to northeast Turkey in the east (de Rigo et al., 2016). Beech requires a growing season of at least 140 days, annual average

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temperature between 2 and 15 °C, and annual precipitation in a range of 500–1800 mm. This tree species is considered relatively resistant to ongoing climate change but some populations at the trailing edge of its distribution may no longer be viable (Hlásny et al., 2014), partly as a result of its sensitivity to climate variation (Kolář et al., 2017).

In 2019, 54% of the global forest area had management plans and approximately 3% of world's forests were intensively managed plantations (FAO, 2019). The total volume of annual roundwood removed from the world's forests reached approximately 3.8 billion cubic meters in 2017 (FAO, 2019). In Europe, the fellings-to-increment ratio has been relatively stable for some time and remains under 80 % across the continent, Europe's forests are thus slowly accumulating carbon in tree biomass (FOREST EUROPE, 2015). If forest management can increase tree productivity, it could have a large potential to increase climate mitigation by forests. To achieve that, management should focus on increasing annual productivity and prolonging the residence time of carbon in tree biomass. At the same time, forest ecosystem disturbance due to harvest operations is amongst the most significant factors affecting carbon exchange in managed forests (Noormets et al., 2015). Harvesting and species conversions over the past centuries of intensive forest management had accumulated a debt of about 3.1 gigatons of carbon (Naudts et al., 2016).

However, little is known whether and to what extent forest management modifies the response of trees to climate variation. Existing evidence is contradictory, showing negative (Mausolf et al., 2018), inconclusive (Pérez-de-Lis et al., 2011), and positive (Bottero et al., 2017; Manrique-Alba et al., 2020) effects of silvicultural interventions on the climate sensitivity of forests. Studies reporting negative effects of thinning on productivity suggest that harvest enlarges crown size, increasing water demand and leading to higher vulnerability to drought (Mausolf et al., 2018). On the other hand, the density reduction by thinning may attenuate competition for soil resources and thus enhance tree resistance to drought (Andrews et al., 2020; Bottero et al., 2017). In fact, thinning has recently been shown to increase the resistance of beech trees to extreme weather events (Manrique-Alba et al., 2020).

Trees are long-living organisms, this study thus makes use of a 60 year long thinning experiment and reports on the analysis of 179 tree ring series generated by coring dominant, co-dominant and sub-dominant beech trees and spanning at least 7 decades. The main contribution of this work is to describe the relationship between the productivity and climate sensitivity of a temperate tree species. Stands of European beech were subjected to contrasting thinning regimes to allocate site productivity to contrasting tree size classes and the following hypotheses were tested: (H1) thinning of canopy trees decreases vulnerability to heat and drought stress and (H2) beech stands growing at lower elevations are more sensitive to this type of stress. Further, this study evaluates the hypothesis that (H3) observed climate change has already caused a decrease of radial increment of beech in Central Europe.

2. Material and methods

2.1. Experimental design

This study makes use of an experiment originally set up in the 1960s in Slovakia to study the effects of thinning regimes on beech stand productivity on 10 locations (Fig. 1). At each site, experimental stands were selected using the following criteria: (i) they were established by natural regeneration only, and (ii) no thinning was applied in these forests before the start of the experiment. Four out of the original 10 experimental sites were chosen for this study, describing the range of environmental conditions representative of the current distribution of beech in the country. Two of the sites were dominated by beech, while the other two were representative of mixed-species stands (Fig. 2). The forest stand on the Motycky site is composed of beech, silver fir (*Abies alba* Mill.), mountain maple (*Acer pseudoplatanus* L.), and Norway spruce (*Picea abies* (L.) H. Karst.). Beech, douglas fir (*Pseudotsuga mensiesii* Mirb.), silver fir and Norway spruce create the mixed stand on St Hory site. The proportion of beech on individual plots and censuses ranges from 22% to 100%.

Each of the sites features between 3 and 5 square plots 0.25 ha in size and subjected to different thinning regimes, as well as a control plot (C) where the stand is left to natural development. Tree diameter at breast-height (DBH) of all living, dead and harvested trees was measured every
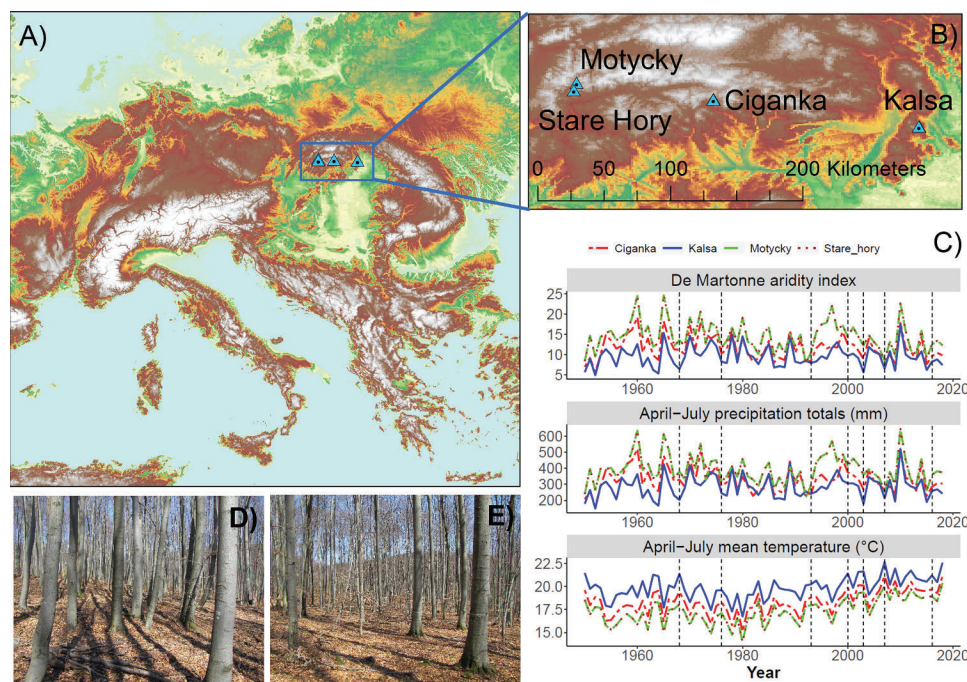

Fig. 1. **(A)** Geographical location of the experimental sites against the orography of Europe, **(B)** position of experimental sites in the Western Carpathian Mountains, **(C)** mean annual temperature, total precipitation and De Martonne aridity index at each experimental site, climatically extreme years highlighted by vertical dashed lines (1968, 1976, 1993, 2000, 2003, 2007, 2016), **(D)** illustration of a control (no management) and **(E)** thinned stands at the Kalsa location.
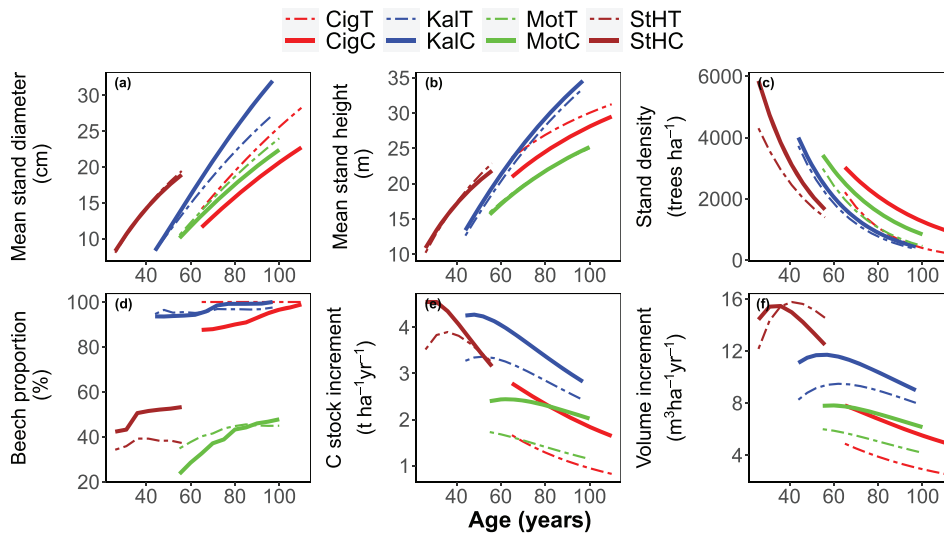
Fig. 2. Stand characteristics describing the long-term experimental plots used in this study; (a) mean stand diameter (quadratic mean), (b) mean stand height (mean tree height weighted by basal area), (c) stand density, (d) proportion of beech in the stand (% of stand volume), (e) carbon (C) stock increment (biomass conversion factors applied to stem volume) and(f) merchantable volume increment (tree stems at least 7 cm in diameter at thinner end). Four sites were studied: Ciganka (Cig), Kalsa (Kal), Motycky (Mot) and Stare Hory (StH), with two thinning regimes applied at each site: no management control (C) and thinning from above (T).

5 years in each plot from the establishment of the experiment. Tree height was measured in a subset of trees covering the plot DBH distribution to allow for the construction of stand-specific height-diameter models (H-D). As part of the dendrochronological sampling in this study, at each site we sampled trees only in plots where free-crown thinning was applied (T – thinning from above) and in the control plots with no intervention (C – unmanaged, Bosela et al., 2016). The thinning interval was 10 years, while the intensity of each intervention was driven by the needs of an individual forest stand and its age, ranging from the removal of 34% of trees in young to 1% in mature stages (Fig. 3 and Fig. S1 in Supplementary Material).

2.2. Stand characteristics

To estimate tree height where this was not measured, an H-D exponential regression model *height = Asym * EXP(-Slope/DBH)* was developed based on a sample of 36,959 heights measured over the study period. The model was fitted separately for each plot and every 5-year inventory cycle to maximize the precision of tree height estimates.

National tree-level models (Gschwantner et al., 2019; Petráš and Pajtík, 1991) were used to estimate (i) tree merchantable volume (stem and branch volume with thinner end diameter more than 7 cm) and (ii) total above-ground tree volume of woody components (stem and all branches). Biomass expansion factors were used to convert tree volume to dry biomass (Eggleston et al., 2006). Individual tree mortality and harvest volume were recorded at each inventory and were used to calculate carbon loss during the 5-yr inventory cycle.

An exponential equation was used to predict stand height, diameter growth, carbon stock, and merchantable volume from age in plot *j*:

$$Y_j = a^* EXP\left(-b / X_j\right) \tag{1}$$

Where Y is the dependent variable (stand height, diameter, carbon stock, or merchantable volume), a and b are the regression parameters to be estimated and X is the independent variable (age). A negative exponential function was used: $Y_j = a * EXP(-b*X_j)$ to estimate stand density in plot *j*.

Derivative of equation (1) was then used to calculate the increment (Y_R) of carbon stock and merchantable volume:
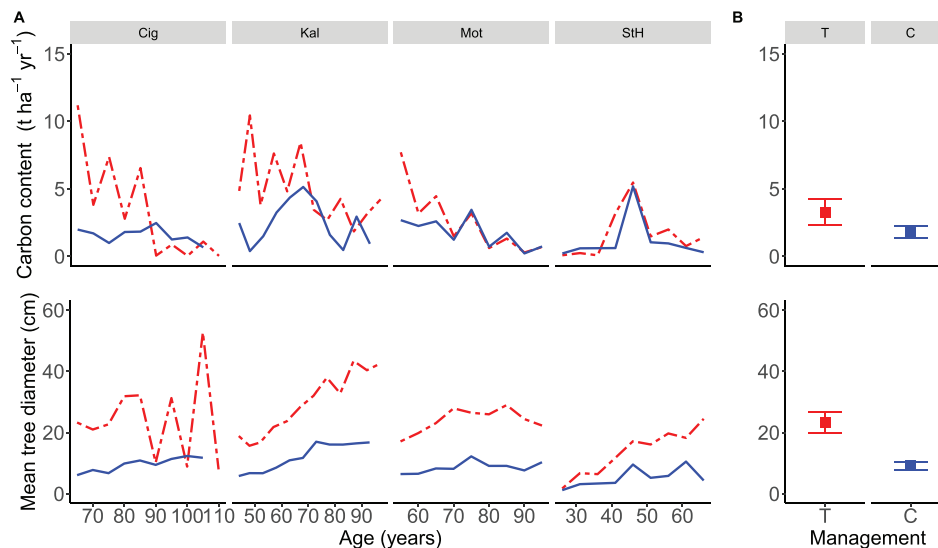

Fig. 3. Carbon content (upper) and mean tree diameter (lower) of all trees removed by harvesting in the thinned (T) and natural selection in the unmanaged control (C) plots over 5-year measurement intervals at **(A)** four experimental sites: Ciganka (Cig), Kalsa (Kal), Motycky (Mot) and Stare Hory (StH). Pane **(B)** shows mean carbon content and tree diameter of removed trees across all sites ± 95% confidence intervals.

$$Y_{Rj} = a^* \left(\text{EXP} \left(-b/X_j \right)^* \left(b \big/ X_j^2 \right) \right) \tag{2}$$

The correlation coefficients between the dependent and the explanatory variables for all these models ranged between 0.70 and 0.99.

2.3. Tree ring sampling and climate data

In 2018, fifteen to forty-two dominant, co-dominant and sub-dominant trees were selected in the C and T plots at each of the four sites selected for this research (Table 1). One core was taken from each selected tree using Pressler increment borer (Bosela et al., 2014), perpendicular to the slope of the site, generating a total of 179 tree-ring-width (TRW) series. Core samples were air-dried and sanded to increase the visibility of annual tree rings; their widths were established at 0.001 mm resolution using the LINTAB (RINNTECH. Ltd.) measuring system. Cubic smoothing spline of 50% frequency response at 30-year cut-off was then applied to each TRW series to remove age-related growth trends and the variability related to factors other than climate (Fritts, 2001). The procedure of detrending is used to reduce the noise in tree ring variability related to factors other than those being tested. Individual tree ring-width indices (RWI) were calculated by dividing the actual and the spline-corrected TRW. Finally, mean plot chronology of RWI series was computed using bi-weight robust mean.

Since instrumental data were not available for all sites and the entire period assessed here, daily climate data were obtained from E-OBS gridded database at $0.1 \times 0.1°$ resolution (Cornes et al., 2018), selecting the points closest to each experiment site. Climate data were not manipulated to preserve the original interannual pattern of mean daily temperature, maximum, and minimum daily temperature and daily precipitation which were used in this study. We standardised all tree-ring series to remove site effects on tree growth while preserving interannual patterns within each dataset, allowing us to use original E-OBS data. Thus, even if these were possible biases in climate data due to the shift in coordinates between the site and E-OBS grid point it did not affect our results. Daily observation data were available only for Kalsa (1960-2009), we compared daily temperature and precipitation between E-OBS and observation data using Pearson's correlation and linear regression (Fig. S2). We found a very good fit between E-OBS and observed temperature, but higher intensity precipitation events are underestimated in E-OBS.

2.4. Finding best climate variables to explain tree growth

The effect of climate variability on radial growth of beech was explored in the "climwin" R package (van de Pol et al., 2016), where the "slidingwin" and "randwin" functions were applied to find the window (time period of the year) that best explained high-frequency variation of tree ring width. All possible windows from the beginning of July of the preceding year to the end of December of the current year were tested. Time windows were 1 to 549 days long and were constructed at a daily resolution to avoid the arbitrary nature of monthly climate data. Linear and quadratic relationships between the climate in the constructed time windows and radial growth were tested. Aggregate statistics describing a climate variable in its optimum time window were tested, the mean was found to be the best predictor and was thus used in further analyses.

Best models were selected on the basis of ΔAICc (Akaike Information Criterion with a correction for small sample sizes) and the random-isation function "randwin" was then used to calculate the likelihood of obtaining AIC-determined model by chance. Ten replications were run and an alternative P_C statistic for $P_{\Delta AICc}$ (the likelihood that a climatic signal is real) was calculated (van de Pol et al., 2016).

2.5. Statistical analyses

Quadratic regression was used to test the relationships between the climate and RWI, followed by an application of Generalized Additive Models (GAM) to investigate the interactive effects of climate and thinning regimes on the formation of radial growth (RWI) as a linear combination. The sensitivity of radial growth to climate variation was expressed as a long-term correlation between the two. A commonly used resilience index is calculated as the ratio between the ring width in the year of extreme weather and the mean of three preceding years (Lloret et al., 2011). However, this index is strongly affected by the detrending methodology applied to the TRW series, and the arbitrary choice of the period length used to calculate the mean growth during pre-stress years - and thus the potential occurrence of climate extremes during the three years preceding the target year (Schwarz et al., 2020). In this study, the resistance index was therefore defined as the ratio between the ring width in the year of an extreme weather event to the normal growth defined by the spline fit (Section 2.3) and was calculated for the two years with the greatest growth decline (2000 and 2003). At each site, linear mixed models were used to test the interactive effects of site and thinning regimes (fixed effects) on tree resistance. In this analysis, year was used as a random component to remove the effect of temporal autocorrelation.

3. Results

3.1. Biomass growth and carbon storage of beech forests

Long-term measurements carried out every five years since the 1960s show that the annual standing volume increment is about 36% larger in unmanaged than in thinned beech forest stands (range from +1 to +94%, Fig. 2) with the largest differences on the Ciganka site. Assuming the wood density does not change due to thinning (Candel-Pérez et al., 2018), this translates to an increase of carbon uptake by about a third in the unmanaged forests. Stand density follows a decreasing exponential age-related decay curve, with the highest tree density always found in the unmanaged stands. Among the sites explored in this study, beech is the most productive at the warmest low-elevation site (Kal - Kalsa) and in the youngest beech forest located in the cold mountain site well supplied with rainwater (StH - St_Hory, Fig. 1C and Fig.2).

The amount of carbon in trees that have died and/or been removed during thinning interventions is typically higher in the thinned than in the control plots (Fig. 3). The carbon removals range from 1% to 34% and its proportion from the total decreases with stand age. Carbon removal from the live biomass pool in the unmanaged stands is mostly that of suppressed trees (natural selection). This is indicated by the significantly smaller mean tree diameter of dead trees in control plots, whereas in the thinned stands it is the canopy trees that are harvested

Table 1

Key characteristics of experimental sites considered in this study. Number of cored trees in the control (C) and thinning (T) treatments was determined according to stand heterogeneity.

Site (abbrev.)	Species	No of cores (T+C)	Lon (°)	Lat (°)	Age (yr)	Altitude (m.a.s.l.)	Est.[1] (yr)	Aspect	Slope (°)	Soil
Motycky (Mot)	Mixed	15 + 15	19.16	48.87	100	883	1971	N-W	30	Rendsic leptosol / Calcaric cambisol
St Hory (StH)	Mixed	40 + 42	19.13	48.82	56	670	1972	W	35	Cambisol
Ciganka (Cig)	Beech	15 + 15	20.09	48.76	110	560	1966	N-W	20	Haplic Cambisol (Dystric)
Kalsa (Kal)	Beech	18 + 19	21.48	48.58	97	520	1960	E	15	Stagni-Eutric Cambisol

Note: [1] – year of establishment of experimental plots and initiation of the thinning regimes

and represent carbon loss (thinning from above).

3.2. Long-term climate sensitivity of beech forests

The period of the year when the selected climate variable best explains the radial growth of beech trees was shown to differ between the sites, but also between stand management approaches (Table 2). Beech trees at two sites were found to be strongly climate-sensitive (Kalsa and Stare Hory), while the randomisation exercise indicates that the climate signal is statistically significant only at the warmest site Kalsa (Supplementary Fig. S6-S37). Here, the period best-predicting radial growth was that from the beginning of May to mid-July. On the other hand, the shortest time window indicated for the locality of Stare Hory is just one day, model randomisation thus does not support the presence of radial growth climate sensitivity at this site.

3.3. Effect of thinning and productivity on the growth-climate sensitivity

The analysis presented in this study does not support H1, suggesting that the reduction of stand density as a result of planned thinning does not impact long-term climate sensitivity in beech (Fig. 4). RWIs, as driven by temperature and precipitation variation, were not significantly different between the two management alternatives (p > 0.05, Table S1). Daily temperature amplitude and average daily precipitation were found to be the best predictors of RWI within a given year. Fig. 4 shows the relationships between these variables, focusing on time windows identified as the most important by the model comparisons (Table 2). The Kalsa site is interesting as it is sensitive to climate variation, possibly due to being at the trailing edge of beech distribution (the warmest and the driest site, Fig. 1c). At this site, increasing daily amplitude causes a continuous decline of RWI (Fig. 4a), confirming hypothesis H2.

3.4. Growth trends and responses to climate extremes

High temporal synchrony of radial growth reductions across the sites clearly shows that the identified trends are driven by large-scale weather patterns (Fig. S3). However, Ciganka - the oldest stand typical for its lowest radial increment in this experiment - did not share this pattern. Probably, factors other than the annual variation of weather may be affecting climate sensitivity of radial growth. Compared to the long-term average, TRW of beech stands across all sites have decreased in the 2000s and 2010s. Radial growth rate of trees in the youngest stand located at high elevation (Stare Hory, 670 m a.s.l.) significantly decreased between 2000 and 2019 (Mann-Kendal trend test p-value = 0.039 (thinned) and 0.003 (control)). Similarly, radial expansion of beech trees at the most productive site (Kalsa) decreased during the drought years 2000 and 2003 by about 40%, compared to previous years, and did not recover since (Fig. S3). In general, the extreme 2000 and 2003 summer droughts reduced radial growth by 15–43% (or by 28% and 32% for control and thinned variants, respectively). These

finding support acceptance of hypothesis H3. Comparison between marginal and conditional r-squared values shows that growth responses to extreme weather events differ between 2000 and 2003 and that the resistance to extreme heat and drought events strongly depends on tree size and is site-specific (Table 3; Fig. 5b). Interestingly, the larger a tree is (compared to the mean of its cohort), the smaller its resistance to drought. Again, the Ciganka site stands out in comparison to the others, the resistance index is strongly influenced by stand management at this site only (Fig. 5a), partially supporting hypothesis H1. However, thinning did not lead to changes in resistance at the other sites, a fact which diminished our ability to draw general conclusions. Moreover, beech trees found at the Ciganka site were taller on the thinned plot than on the control, despite being the same age, suggesting site productivity may affect resistance.

3.5. Interactive effect of temperature and precipitation on radial growth

A very strong interactive effect between daily temperature amplitude and daily precipitation on radial growth was found at the climate-sensitive site "Kal" (Table S1). These two factors explained 72% of the total high-frequency variance of radial growth in both management treatments at this site. The interaction suggests that the effect of daily temperature amplitude becomes stronger at low levels of precipitation (Fig. S4).

4. Discussion

An analysis of data from a long-term thinning experiment, in combination with advanced dendrochronological coring, shows that the effect of thinning on climate sensitivity of beech trees is negligible (H1), and that beech stands growing at lower elevations are more sensitive to heat and drought stress (H2). In addition, data from the four sampled sites indicate that an overall decrease of beech radial growth is already detectable (H3).

4.1. Long-term trends of growth-climate sensitivity

In Slovakia, there is evidence of beech radial growth already being affected by drought defined as a combination of higher temperature and less precipitation. This effect is prominent at warmer sites, but not as pronounced at upper-elevation sites with colder mountain conditions (600 – 800 m a.s.l.). At Kalsa, the warmest and the driest site observed here, the strongest driver of annual growth variation was the amount of precipitation in the period from the beginning of May until half July, squarely in line with a recent finding from Central Europe (Kolář et al., 2017). Here, beech bud burst usually starts during the second half of April (Vitasse and Basler, 2013), while radial growth peaks in the second half of June and terminates around mid-August (Bošel'a et al., 2013). The sensitivity of radial growth to summer precipitation ties in with the period of maximum growth and has recently been shown to increase at a multi-decadal scale (Kolář et al., 2017). In this study, an expected

Table 2
Identification of optimum time windows predicting beech tree radial growth based on precipitation (Prec), diurnal temperature amplitude (T ampl), mean daily (T day), and maximum daily temperature (T max). ΔAICc is defined as AICc of a full model minus AICc of a baseline model with no climate data (van de Pol et al., 2016). Start and End indicate the beginning and end of the optimum period in each plot (Julian days).

| Plot	Prec				T ampl				T day				T max			
	r-sq	ΔAICc	Start	End	r-sq	ΔAICc	Start	End	r-sq	ΔAICc	Start	End	r-sq	ΔAICc	Start	End
CigT	0.24	-14.35	299	302	0.26	-16	87	88	0.2	-10.37	219	221	0.18	-8.72	216	225
CigC	0.19	-9.89	68	69	0.23	-13.08	29	33	0.18	-8.69	329	329	0.2	-10.44	12	12
kalT	0.36	-25.64	198	283	0.41	-30.87	219	282	0.31	-20.17	195	277	0.39	-28.68	194	277
kalC	0.41	-30.64	198	283	0.47	-38.1	198	282	0.36	-25.94	196	277	0.45	-35.8	195	277
MotT	0.19	-9.27	92	92	0.27	-16.23	139	141	0.19	-9.94	65	67	0.21	-11.49	158	158
MotC	0.21	-10.99	270	284	0.21	-11.26	139	142	0.17	-7.84	11	37	0.27	-16.48	317	320
StHT	0.42	-22.19	250	283	0.31	-13.41	201	300	0.26	-9.81	199	200	0.24	-8.52	154	158
StHC	0.45	-26.07	250	284	0.41	-22.73	196	351	0.26	-11.03	302	303	0.27	-11.48	302	303
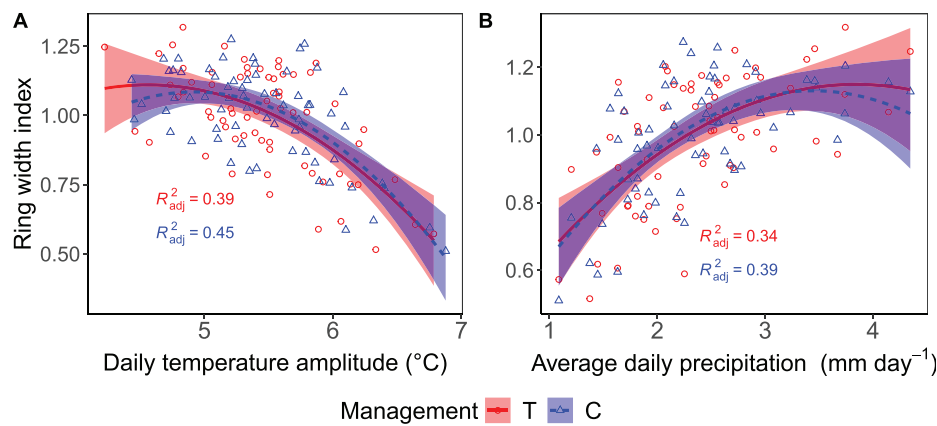
Fig. 4. Annual diameter growth (RWI) of European beech on Kalsa (Kal) site, as affected by average **(A)** daily temperature amplitude (daily max – min) and **(B)** daily precipitation for periods identified as best predictors of RWI. Stands were subjected to two thinning regimes (thinned (T) and unmanaged control (C)). The entire study period of 1950-2017 was used to calculate the relationships.

Table 3
Influence of site and management (fixed effects) on the resistance index in 2000 and 2003, the two years with the strongest drought-related growth reduction. Year was treated as a random effect and the standard deviation of the intercept was estimated.

	Estimate	Std.Error	DF	t-value	p-value
Fixed effects:					
Intercept	0.7001724	0.04168079	365	16.798441	<0.001
management (O)	0.1690689	0.05109186	365	3.309116	0.001
site (Kal)	-0.0647245	0.04891673	365	-1.323157	0.1866
site (Mot)	0.1208253	0.04832806	365	2.500107	0.0129
site (StH)	0.0234188	0.04236313	365	0.552812	0.5807
management (O): site (Kal)	-0.1534489	0.06876371	365	-2.23154	0.0263
management (O): site (Mot)	-0.1595838	0.06834619	365	-2.334934	0.0201
management (O): site (StH)	-0.1455626	0.05971568	365	-2.437594	0.0153
Random Effects:	(Intercept)	Residual			
StdDev:	0.029397	0.1978779			
R² marginal	0.11				
R² conditional	0.13				

Fig. 5. **(A)** Effects of European beech stand management in thinned (T) and control (C) plots on radial growth resistance to the 2000 and 2003 extreme droughts on individual sites (Ciganka (Cig), Kalsa (Kal), Motycky (Mot) and Stare Hory (StH)). Values represent mean for each site ± 95% confidence interval, p-values were estimated by post-hoc pairwise comparisons. **(B)** Relationship between tree productivity (average radial growth in three years preceding the most severe drought of 2000) and the resistance index (calculated as the ratio between the ring width in the year of extreme weather event to the normal growth defined by spline fit set with time period = 30 years and smoothing parameter = 0.5).

positive response of growth to annual temperature variation at the higher-elevation sites was however not seen. Only a weak negative effect of daily temperature amplitude on beech growth was detected in forests growing at upper elevations in a colder environment, suggesting that today they are less climate-sensitive than those growing in warmer locations. Moreover, the growth-climate relationship at the most climate sensitive and the most productive site did not change between the two analysed periods (1951-1983 and 1984-2017; Fig. S5), corresponding with the principles of James Hutton's theory of uniformitarianism as applied to dendroclimatology (Fritts, 1976). The uniformitarianism theory posits that the growth-climate sensitivity does not change over time and forms a crucial condition for tree-ring-based reconstructions of climate variation to the past. However, evidence of the variation in growth-climate relationships is widespread in tree-ring studies (Wilmking et al., 2020).

4.2. Thinning and growth sensitivity to climate

No evidence confirming the hypothesis that thinning from above makes the remaining canopy trees more or less vulnerable to climate variation was found in this study. The hypothesis tests the assumption that by removing direct competition for light, water and nutrients, the target trees that remain in the stand will enhance their fitness and thus
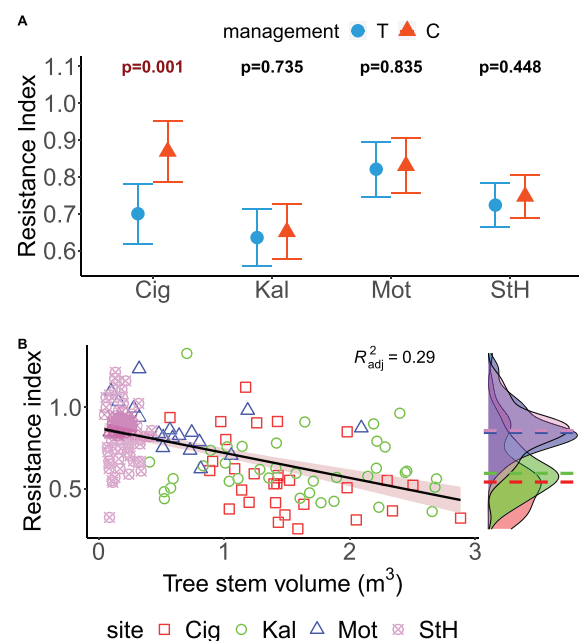
reduce vulnerability to adverse climate conditions (Andrews et al., 2020; Bottero et al., 2017). Similarly, and in contrast to a recent finding from beech ecosystems elsewhere (Mausolf et al., 2018), this research shows that leaving the stand to natural development and self-thinning increases climate resilience in beech. Clearly, forest stand dynamics have a role in attenuating climate sensitivity of closed-canopy beech forests typical for intense competition. The suppressed trees that are usually harvested during *thinning from below* interventions are considered to be less climate-sensitive (Bosela et al., 2016). Removing these trees thus may increase the mean climate variation sensitivity of the

remaining beech stand. *Thinning from above*, as applied in this study, leaves the supressed trees in situ and subjects them to natural mortality very much akin to the self-thinning of unmanaged forests. The type of thinning applied to the plots used in this study may thus partly explain the finding that the climate sensitivity of canopy trees was not significantly affected by the thinning regime. Indeed, the effects of silviculture (density regulation) depend on multiple factors and are known to range from negative (Mausolf et al., 2018), through no effect (this study), to positive (Bottero et al., 2017; Manrique-Alba et al., 2020). Species mixture can also reduce vulnerability of beech to drought compared to monospecific stands (Mölder and Leuschner, 2014). Beech trees growing in a mixture often have larger crowns and higher crown plasticity compared to trees in pure stands (Pretzsch et al., 2016). However, the effect of species mixture depends on various factors including, for example, soil type and quality (Mölder and Leuschner, 2014). In our study, a combined effect of site and species mixture is likely but their individual contribution to explaining climate sensitivity and responses to extreme weather events cannot be unequivocally quantified. Nevertheless, growing species in a mixture can significantly increase productivity and in turn the risk of embolism, as found in our study. For example, the mixed forest stand at the St Hory site grew faster and reached higher productivity than monospecific stands. Beech trees at this site also had lower resistance during 2000 and 2003 droughts. Overall, the influence of elevation and site quality on beech vulnerability to drought seems stronger than that of species mixture.

4.3. Growth reactions to extreme weather events

This study shows that the resistance of beech trees to extreme weather events is strongly negatively affected by tree size and site quality. Fast-growing, taller, and larger trees typically have greater xylem vessel diameter, leading to a higher probability of embolism under extreme conditions (Micco et al., 2019; Olson and Rosell, 2013; Rosell et al., 2017). Faster-growing trees rely on higher hydraulic conductivity to support growth, which trades-off as a higher risk of cavitation and vulnerability to drought (Rosell et al., 2017). The faster growth rate of the youngest forest stands in this study (StH) may therefore explain their lower resistance, compared to the nearby older forest stand (Mot). Documented age-related changes in tree sensitivity to climate variation do not paint a consistent picture (Esper et al., 2008a; Zang et al., 2014), suggesting the possibility of different extreme weather coping strategies evolved by different species (Micco et al., 2019; Rennenberg et al., 2006).

The tenet underlying forest thinning dictates that removal of canopy trees improves resource availability for the remaining stand and stimulates its growth rate. This study shows that in some conditions, faster growth comes at the expense of higher vulnerability to extreme weather events (the Ciganka site, Fig. 5). This effect was not observed at the other three sites, alluding to an interaction between stand management and site conditions, as suggested by Lévesque et al. (2015). However, contrasting results and interpretations limit the understanding of the general mechanism (D'Amato et al., 2013; Esper et al., 2008b; Martínez-Vilalta et al., 2012a; Metz et al., 2016; Pretzsch et al., 2013; Thurm et al., 2016), the type of tree species mixture has also been indicated to affect drought response (Martínez-Vilalta et al., 2012b). Beech trees have been shown to produce more wood when growing in a mixture (Bosela et al., 2015; Metz et al., 2016; Pretzsch et al., 2013), which in connection with the findings of this study implies lower resistance to extreme climate of beech trees growing in mixed forests. A comparison between pure and mixed beech forests in our study does not provide evidence of growth facilitation, possibly due masking by factors.

4.4. Effect of thinning on carbon uptake in beech forests

Van Deusen (2010) has shown that unmanaged forest stands store more carbon in living trees than their managed counterparts and this study confirms that finding. Here, thinning has resulted in a slower accumulation of carbon in living biomass (Fig. 2e), but the total timber production over the rotation period does not differ significantly between the thinning regimes, as recently indicated by Bosela et al. (2016). The discrepancy can be explained by the off-take of tree stems during regular thinning interventions. If added to the carbon stored in the remaining forest, the total usually exceeds carbon storage of unmanaged forests (Van Deusen, 2010), but its climate mitigation impact is driven by the half-life of resulting wood products (Profft et al., 2009).

4.5. Limitations and future work

The balance of carbon that ends up in long-lasting wood products against that which joins stable soil organic matter pools is currently unknown. Thus, the overall impact of thinning on carbon storage and its contribution to climate change cannot be easily estimated. Further, the issue of the broad distribution of European beech must be considered when selecting sample sites. We were not able to take this into account, covering only a limited range of climatic conditions affecting beech across Europe. As a result, we can draw conclusions specific to these conditions only. Future research should include various species mixture types, a range of soil conditions, latitude, longitude and elevation gradients, and different thinning alternatives.

Our database covers a 60-yr experiment with repeated measurements conducted every 5 years and supplemented by 179 tree-ring samples, allowing us to study the long-term development of tree populations (Nehrbass-Ahles et al., 2014). Tree-ring samples allow scaling to 1-yr resolution and so investigating drivers of inter-annual variance of radial increments of trees in the population under study. However, such experimental plots are difficult to sustain in the long-term due to budgetary constraints, our study thus makes use of only eight plots on four localities across the country. Clearly, the sites cover a relatively large variation in site conditions and lack replication within each site, limiting our ability to draw conclusions and make broader generalisations.

A widely used resistance index calculation approach defines the index as the ratio between the ring width in the year of extreme climate event to the average of TRW in three years preceding the target year (Bose et al., 2020; Gazol et al., 2016; Lloret et al., 2011). Using this approach, however, some issues arise (Schwarz et al., 2020). First, the question of the definition of an extreme climate event (Zang et al., 2020): here we used a combination of climate data (summer temperature and precipitation, de Martone aridity index), tree-ring data itself and a literature search to identify years with high climatic stress. An important additional point is that there is no standard definition of drought in ecological studies (Slette et al., 2019). Second, the standard index may be as much influenced by the stress experienced in the year of stress as by the vagaries of the growing conditions in the preceding years. To reduce this shortcoming, we first used the spline fit to define a "normal" growth and then calculated the resistance index as the ratio between the annual ring width and the spline fit. Even this approach is not fully free from potential misinterpretation, the signal of the spline fit is driven by the selection of the reference period and the smoothing parameters to set up the function. The trade-off between filtering out inter-annual fluctuations to derive the spline trend while preserving the long-term environmental change signal remains unresolved and may form a potentially interesting future research.

Using gridded daily data from global databases such as E-OBS may lead to misrepresentation of growth-climate relationships. Overall, using this data for ecological studies is appropriate, especially when instrumental data are not available for the site or they do not cover the study period (Jevšenak, 2019; Nechita et al., 2019). Interpolation of E-OBS to a specific location to improve accuracy may be advisable, however in this study we did not interpolate E-OBS daily data but used the original data form the nearest E-OBS grid point. The inability of describing the weather for the exact location of each site was balanced

by the fact that the interpolation did not remove interannual variation from the weather record.

5. Conclusions

This study shows that more carbon is stored *in-situ* in tree biomass of unmanaged beech stands when compared to those under a thinning regime. Dominant and co-dominant trees in the canopy layer supported by thinning are the most productive, but also the most climate-sensitive and the most vulnerable to extreme weather events. Observed climate change may already have reduced the radial growth of sampled trees, possibly aggregating impacts of past extreme weather events. In conclusion, light thinning regimes might be preferable to more intensive interventions at sites with a higher incidence of heat and drought events, highlighting the attractiveness of close-to-nature forestry practice.

Declaration of Competing Interest

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

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Supplementary materials

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.agrformet.2021.108441.

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