

# 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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Bosela, M., Stefancik, I., Marcis, P., Rubio-Cuadrado, A. and Lukac, M. ORCID: https://orcid.org/0000-0002-8535-6334 (2021) Thinning decreases above-ground biomass increment in central European beech forests but does not change individual tree resistance to climate events. Agricultural and Forest Meteorology, 306. 108441. ISSN 0168-1923 doi: https://doi.org/10.1016/j.agrformet.2021.108441 Available at https://centaur.reading.ac.uk/98594/

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To link to this article DOI: http://dx.doi.org/10.1016/j.agrformet.2021.108441

Publisher: Elsevier

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- 2 beech forests but does not change individual tree resistance to climate events
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#### 15 Abstract

16 European beech plays a prominent role in the adaptation of European forests to and mitigation of 17 climate change. Forest management may increase the mitigation potential of beech forests by 18 accelerating carbon accumulation in tree biomass, but little is known about the interaction between 19 the rate of biomass expansion in beech and its sensitivity to climate variation or its resistance to 20 extreme drought episodes. A 60-year thinning experiment in beech forests in Central Europe was 21 used to generate tree-ring width series describing past radial growth of dominant, co-dominant and 22 sub-dominant beech trees. Randomisation applied to daily climate data was used to find the period 23 of the year during which climate best explains beech growth. Results show that carbon uptake by 24 above-ground biomass is higher in unmanaged stands and that thinning does not affect beech 25 growth sensitivity to climate. Further, this study shows that average daily temperature amplitude 26 and precipitation in March-July are the best predictors of radial growth in beech at lower-elevation 27 sites. In a key finding, this research shows that site quality and thinning intensity increase tree size, 28 which in turn lowers their resistance to drought. Using forest management to increase the 29 productivity of European beech may thus increase its vulnerability to climate change.

30

31 Keywords: climate-smart-forestry, carbon uptake, drought, Fagus sylvatica, thinning, tree ring

32

#### 34 1 Introduction

Globally, forests represent a significant store of carbon and contribute to the removal of excess 35 36 greenhouse gasses from the atmosphere, mitigating the impacts of climate change in the process 37 (IPCC, 2018). At the same time, global climate change alters the growth of forest ecosystems both 38 positively and negatively (McDowell et al., 2020). The impact of ongoing climate change on the 39 world's forests is very likely to determine their future contribution to mitigation efforts. Radial 40 expansion of tree trunks is one of the main processes of semi-permanent removal of carbon dioxide 41 from the atmosphere (Babst et al., 2014), in seasonal forests it is documented by the appearance of 42 annual growth rings (Zweifel et al., 2006). The activity of cambium, plant tissue responsible for the 43 production of durable wood, is tightly regulated by variation of resource availability within each 44 annual cycle (Jacoby and D'Arrigo, 1997).

45 Tree growth is however a long-term process, often taking place across many decades or centuries. 46 Analyses of ring width have thus been used to document past changes in environmental conditions 47 or the levels of competition between trees in a forest ecosystem, which together impact resource 48 availability. Climate change has already been documented by looking at tree ring width series. Long-49 term changes in tree growth were shown (Tei et al., 2017), speeding up or slowing down tree growth 50 by shifting the new conditions closer or further away from the climatic optimum of the species 51 (McCullough et al., 2017). European beech (Fagus sylvatica L.) is one of the most important tree 52 species in Europe, both commercially and ecologically. Its current distribution range extends from 53 southern Scandinavia to the south of Italy, and from Spain in the west to northeast Turkey in the east 54 (de Rigo et al., 2016). Beech requires a growing season of at least 140 days, annual average 55 temperature between 2 and 15°C, and annual precipitation in a range of 500–1800 mm. This tree 56 species is considered relatively resistant to ongoing climate change but some populations at the 57 trailing edge of its distribution may no longer be viable (Hlásny et al., 2014), partly as a result of its 58 sensitivity to climate variation (Kolář et al., 2017).

59 In 2019, 54% of the global forest area had management plans and approximately 3% of world's 60 forests were intensively managed plantations (FAO, 2019). The total volume of annual roundwood 61 removed from the world's forests reached approximately 3.8 billion cubic meters in 2017 (FAO, 62 2019). In Europe, the fellings-to-increment ratio has been relatively stable for some time and remains 63 under 80 % across the continent, Europe's forests are thus slowly accumulating carbon in tree 64 biomass (FOREST EUROPE, 2015). If forest management can increase tree productivity, it could have 65 a large potential to increase climate mitigation by forests. To achieve that, management should focus 66 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 67 68 significant factors affecting carbon exchange in managed forests (Noormets et al., 2015). Harvesting 69 and species conversions over the past centuries of intensive forest management had accumulated a 70 debt of about 3.1 gigatons of carbon (Naudts et al., 2016).

71 However, little is known whether and to what extent forest management modifies the response of 72 trees to climate variation. Existing evidence is contradictory, showing negative (Mausolf et al., 2018), 73 inconclusive (Pérez-de-Lis et al., 2011), and positive (Bottero et al., 2017; Manrique-Alba et al., 2020) 74 effects of silvicultural interventions on the climate sensitivity of forests. Studies reporting negative 75 effects of thinning on productivity suggest that harvest enlarges crown size, increasing water demand 76 and leading to higher vulnerability to drought (Mausolf et al., 2018). On the other hand, the density 77 reduction by thinning may attenuate competition for soil resources and thus enhance tree resistance 78 to drought (Andrews et al., 2020; Bottero et al., 2017). In fact, thinning has recently been shown to 79 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 subdominant 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.

90

#### 91 2 Material and Methods

#### 92 2.1 Experimental design

93 This study makes use of an experiment originally set up in the 1960s in Slovakia to study the effects 94 of thinning regimes on beech stand productivity on 10 locations (Fig. 1). At each site, experimental 95 stands were selected using the following criteria: (i) they were established by natural regeneration 96 only, and (ii) no thinning was applied in these forests before the start of the experiment. Four out of 97 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 98 99 dominated by beech, while the other two were representative of mixed-species stands (Fig. 2). The 100 forest stand on the Motycky site is composed of beech, silver fir (Abies alba Mill.), mountain maple 101 (Acer pseudoplatanus L.), and Norway spruce (Picea abies (L.) H. Karst.). Beech, douglas fir 102 (Pseudotsuga mensiesii Mirb.), silver fir and Norway spruce create the mixed stand on St Hory site.

103 The proportion of beech on individual plots and censuses ranges from 22% to 100%.

**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. <sup>1</sup> (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 Cambiso	18+19 21.48 48.58 97 520 1960 E 15	520 19	)7	48.58	21.48	18+19	Beech	Kalsa (Kal)
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106 Note: <sup>1</sup> – year of establishment of experimental plots and initiation of the thinning regimes

108	Each of the sites features between 3 and 5 square plots 0.25 ha in size and subjected to different
109	thinning regimes, as well as a control plot (C) where the stand is left to natural development. Tree
110	diameter at breast-height (DBH) of all living, dead and harvested trees was measured every 5 years in
111	each plot from the establishment of the experiment. Tree height was measured in a subset of trees
112	covering the plot DBH distribution to allow for the construction of stand-specific height-diameter
113	models (H-D). As part of the dendrochronological sampling in this study, at each site we sampled
114	trees only in plots where free-crown thinning was applied (T – thinning from above) and in the
115	control plots with no intervention (C – unmanaged, Bosela et al., 2016). The thinning interval was 10
116	years, while the intensity of each intervention was driven by the needs of an individual forest stand
117	and its age, ranging from the removal of 34% of trees in young to 1% in mature stages (Fig. 3 and Fig.
118	S1 in Supplementary Material).



120

Figure 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.

#### 127 2.2 Stand characteristics

- 128 To estimate tree height where this was not measured, an H-D exponential regression model height =
- 129 Asym \* EXP(-Slope/DBH) was developed based on a sample of 36,959 heights measured over the
- 130 study period. The model was fitted separately for each plot and every 5-year inventory cycle to
- 131 maximize the precision of tree height estimates. National tree-level models (Gschwantner et al.,
- 132 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
- 134 woody components (stem and all branches). Biomass expansion factors were used to convert tree

135 volume to dry biomass (Eggleston et al., 2006). Individual tree mortality and harvest volume were 136 recorded at each inventory and were used to calculate carbon loss during the 5-yr inventory cycle. 137 An exponential equation was used to predict stand height, diameter growth, carbon stock, and 138 merchantable volume from age in plot *j*: 139  $Y_j = a * EXP(-b/X_j)$ (1) 140 Where  $\gamma$  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 141 142 negative exponential function was used:  $Y_i = a * EXP(-b*X_i)$  to estimate stand density in plot *j*. 143 Derivative of equation (1) was then used to calculate the increment ( $Y_{R}$ ) of carbon stock and 144 merchantable volume:  $Y_{Rj} = a * (EXP(-b/X_j) * (b/X_j^2))$ 145 (2)

146 The correlation coefficients between the dependent and the explanatory variables for all these

147 models ranged between 0.70 and 0.99.

#### 148 2.3 Tree ring sampling and climate data

149 In 2018, fifteen to forty-two dominant, co-dominant and sub-dominant trees were selected in the C 150 and T plots at each of the four sites selected for this research (Table 1). One core was taken from 151 each selected tree using Pressler increment borer (Bosela et al., 2014), perpendicular to the slope of 152 the site, generating a total of 179 tree-ring-width (TRW) series. Core samples were air-dried and 153 sanded to increase the visibility of annual tree rings; their widths were established at 0.001 mm 154 resolution using the LINTAB (RINNTECH. Ltd.) measuring system. Cubic smoothing spline of 50% 155 frequency response at 30-year cut-off was then applied to each TRW series to remove age-related 156 growth trends and the variability related to factors other than climate (Fritts, 2001). The procedure 157 of detrending is used to reduce the noise in tree ring variability related to factors other than those 158 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-weightrobust mean.

161 Since instrumental data were not available for all sites and the entire period assessed here, daily 162 climate data were obtained from E-OBS gridded database at 0.1 x 0.1° resolution (Cornes et al., 163 2018), selecting the points closest to each experiment site. Climate data were not manipulated to 164 preserve the original interannual pattern of mean daily temperature, maximum, and minimum daily 165 temperature and daily precipitation which were used in this study. We standardised all tree-ring 166 series to remove site effects while preserving interannual patterns within each dataset, allowing us 167 to use original E-OBS data even if these were not possible biases in climate data due to the shift in 168 coordinates between the site and E-OBS grid point did not affect our results. Daily observation data 169 were available only for Kalsa (1960-2009), we compared daily temperature and precipitation 170 between E-OBS and observation data using Pearson's correlation and linear regression (Fig. S2). We 171 found a very good fit between E-OBS and observed temperature, but higher intensity precipitation 172 events are underestimated in E-OBS.

#### 173 2.4 Finding best climate variables to explain tree growth

174 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 175 176 window (time period of the year) that best explained high-frequency variation of tree ring width. All 177 possible windows from the beginning of July of the preceding year to the end of December of the 178 current year were tested. Time windows were 1 to 549 days long and were constructed at a daily 179 resolution to avoid the arbitrary nature of monthly climate data. Linear and quadratic relationships 180 between the climate in the constructed time windows and radial growth were tested. Aggregate 181 statistics describing a climate variable in its optimum time window were tested, the mean was found 182 to be the best predictor and was thus used in further analyses. Best models were selected on the 183 basis of  $\Delta AICc$  (Akaike Information Criterion with a correction for small sample sizes) and the

184 randomisation 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  $P_{\Delta A I C C}$  (the

186 likelihood that a climatic signal is real) was calculated (van de Pol et al., 2016).

#### 187 2.6 Statistical analyses

188 Quadratic regression was used to test the relationships between the climate and RWI, followed by an 189 application of Generalized Additive Models (GAM) to investigate the interactive effects of climate 190 and thinning regimes on the formation of radial growth (RWI) as a linear combination. The sensitivity 191 of radial growth to climate variation was expressed as a long-term correlation between the two. A 192 commonly used resilience index is calculated as the ratio between the ring width in the year of 193 extreme weather and the mean of three preceding years (Lloret et al., 2011). However, this index is 194 strongly affected by the detrending methodology applied to the TRW series, and the arbitrary choice 195 of the period length used to calculate the mean growth during pre-stress years - and thus the 196 potential occurrence of climate extremes during the three years preceding the target year (Schwarz 197 et al., 2020). In this study, the resistance index was therefore defined as the ratio between the ring 198 width in the year of an extreme weather event to the normal growth defined by the spline fit 199 (Section 2.3) and was calculated for the two years with the greatest growth decline (2000 and 2003). 200 At each site, linear mixed models were used to test the interactive effects of site and thinning 201 regimes (fixed effects) on tree resistance. In this analysis, year was used as a random component to 202 remove the effect of temporal autocorrelation.

203





Figure 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).

#### 212 3 Results

### 213 **3.1 Biomass growth and carbon storage of beech forests**

- 214 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
- 218 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
- 220 sites explored in this study, beech is the most productive at the warmest low-elevation site (Kal -
- 221 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 and represent carbon loss (thinning from above).

230



Figure 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.

236

#### 237 3.2 Long-term climate sensitivity of beech forests

- 238 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
- 240 2). Beech trees at two sites were found to be strongly climate-sensitive (Kalsa and Stare Hory), while

241 the randomisation exercise indicates that the climate signal is statistically significant only at the

242 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

245 presence of radial growth climate sensitivity at this site.

246 **Table 2** Identification of optimum time windows predicting beech tree radial growth based on precipitation

247 (Prec), diurnal temperature amplitude (T ampl), mean daily (T day), and maximum daily temperature (T max).

248 ΔAICc is defined as AICc of a full model minus AICc of a baseline model with no climate data (van de Pol et al.,

249 2016). Start and End indicate the beginning and end of the optimum period in each plot (Julian days).

	Prec				T am	pl			T day	/			T ma	x		
Plot	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

250

#### 251 **3.3 Effect of thinning and productivity on the growth-climate sensitivity**

252	The analysis presented in this study does not support H1, suggesting that the reduction of stand
253	density as a result of planned thinning does not impact long-term climate sensitivity in beech (Fig. 4).
254	RWIs, as driven by temperature and precipitation variation, were not significantly different between
255	the two management alternatives (p>0.05, Table S1). Daily temperature amplitude and average daily
256	precipitation were found to be the best predictors of RWI within a given year. Figure 4 shows the
257	relationships between these variables, focusing on time windows identified as the most important by
258	the model comparisons (Table 2). The Kalsa site is interesting as it is sensitive to climate variation,
259	possibly due to being at the trailing edge of beech distribution (the warmest and the driest site, Fig.
260	1c). At this site, increasing daily amplitude causes a continuous decline of RWI (Fig. 4a), confirming
261	hypothesis H2.



263

Figure 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

267 period of 1950-2017 was used to calculate the relationships.

268

#### 269 **3.4 Growth trends and responses to climate extremes**

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

272 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			
R <sup>2</sup> marginal	0.11				
R <sup>2</sup> conditional	0.13				

273

274 High temporal synchrony of radial growth reductions across the sites clearly shows that the identified

275 trends are driven by large-scale weather patterns (Fig. S3). However, Ciganka - the oldest stand

276 typical for its lowest radial increment in this experiment - did not share this pattern. Probably, factors 277 other than the annual variation of weather may be affecting climate sensitivity of radial growth. 278 Compared to the long-term average, TRW of beech stands across all sites have decreased in the 279 2000s and 2010s. Radial growth rate of trees in the youngest stand located at high elevation (Stare 280 Hory, 670 m a.s.l.) significantly decreased between 2000 and 2019 (Mann-Kendal trend test p-value = 281 0.039 (thinned) and 0.003 (control)). Similarly, radial expansion of beech trees at the most productive 282 site (Kalsa) decreased during the drought years 2000 and 2003 by about 40%, compared to previous 283 years, and did not recover since (Fig. S3). In general, the extreme 2000 and 2003 summer droughts 284 reduced radial growth by 15–43% (or by 28% and 32% for control and thinned variants, respectively). 285 These finding support acceptance of hypothesis H3. Comparison between marginal and conditional r-286 squared values shows that growth responses to extreme weather events differ between 2000 and 287 2003 and that the resistance to extreme heat and drought events strongly depends on tree size and 288 is site-specific (Table 3; Fig. 5b). Interestingly, the larger a tree is (compared to the mean of its 289 cohort), the smaller its resistance to drought. Again, the Ciganka site stands out in comparison to the 290 others, the resistance index is strongly influenced by stand management at this site only (Fig. 5a), 291 partially supporting hypothesis H1. However, thinning did not lead to changes in resistance at the 292 other sites, a fact which diminished our ability to draw general conclusions. Moreover, beech trees 293 found at the Ciganka site were taller on the thinned plot than on the control, despite being the same 294 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).



303 Figure 5 (A) Effects of European beech stand management in thinned (T) and control (C) plots on radial growth 304 resistance to the 2000 and 2003 extreme droughts on individual sites (Ciganka (Cig), Kalsa (Kal), Motycky (Mot) 305 and Stare Hory (StH)). Values represent mean for each site ± 95% confidence interval, p-values were estimated 306 by post-hoc pairwise comparisons. (B) Relationship between tree productivity (average radial growth in three 307 years preceding the most severe drought of 2000) and the resistance index (calculated as the ratio between the 308 ring width in the year of extreme weather event to the normal growth defined by spline fit set with time period 309 = 30 years and smoothing parameter = 0.5).

310

#### 311 Discussion

- 312 An analysis of data from a long-term thinning experiment, in combination with advanced
- 313 dendrochronological coring, shows that the effect of thinning on climate sensitivity of beech trees is
- 314 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).

317

#### 318 Long-term trends of growth-climate sensitivity

319 In Slovakia, there is evidence of beech radial growth already being affected by drought defined as a 320 combination of higher temperature and less precipitation. This effect is prominent at warmer sites, 321 but not as pronounced at upper-elevation sites with colder mountain conditions (600 – 800 m a.s.l.). 322 At Kalsa, the warmest and the driest site observed here, the strongest driver of annual growth 323 variation was the amount of precipitation in the period from the beginning of May until half July, 324 squarely in line with a recent finding from Central Europe (Kolář et al., 2017). Here, beech bud burst 325 usually starts during the second half of April (Vitasse and Basler, 2013), while radial growth peaks in 326 the second half of June and terminates around mid-August (Bošel'a et al., 2013). The sensitivity of 327 radial growth to summer precipitation ties in with the period of maximum growth and has recently 328 been shown to increase at a multi-decadal scale (Kolář et al., 2017). In this study, an expected 329 positive response of growth to annual temperature variation at the higher-elevation sites was 330 however not seen. Only a weak negative effect of daily temperature amplitude on beech growth was 331 detected in forests growing at upper elevations in a colder environment, suggesting that today they 332 are less climate-sensitive than those growing in warmer locations. Moreover, the growth-climate 333 relationship at the most climate sensitive and the most productive site did not change between the 334 two analysed periods (1951-1983 and 1984-2017; Fig. S5), corresponding with the principles of James 335 Hutton's theory of uniformitarianism as applied to dendroclimatology (Fritts, 1976). The 336 uniformitarianism theory posits that the growth-climate sensitivity does not change over time and 337 forms a crucial condition for tree-ring-based reconstructions of climate variation to the past. 338 However, evidence of the variation in growth-climate relationships is widespread in tree-ring studies 339 (Wilmking et al., 2020).

#### 340 Thinning and growth sensitivity to climate

No evidence confirming the hypothesis that thinning from above makes the remaining canopy trees 341 342 more or less vulnerable to climate variation was found in this study. The hypothesis tests the 343 assumption that by removing direct competition for light, water and nutrients, the target trees that 344 remain in the stand will enhance their fitness and thus reduce vulnerability to adverse climate 345 conditions (Andrews et al., 2020; Bottero et al., 2017). Similarly, and in contrast to a recent finding 346 from beech ecosystems elsewhere (Mausolf et al., 2018), this research shows that leaving the stand 347 to natural development and self-thinning increases climate resilience in beech. Clearly, forest stand 348 dynamics have a role in attenuating climate sensitivity of closed-canopy beech forests typical for 349 intense competition. The suppressed trees that are usually harvested during thinning from below 350 interventions are considered to be less climate-sensitive (Bosela et al., 2016). Removing these trees 351 thus may increase the mean climate variation sensitivity of the remaining beech stand. Thinning from 352 above, as applied in this study, leaves the supressed trees in situ and subjects them to natural 353 mortality very much akin to the self-thinning of unmanaged forests. The type of thinning applied to 354 the plots used in this study may thus partly explain the finding that the climate sensitivity of canopy 355 trees was not significantly affected by the thinning regime. Indeed, the effects of silviculture (density 356 regulation) depend on multiple factors and are known to range from negative (Mausolf et al., 2018), 357 through no effect (this study), to positive (Bottero et al., 2017; Manrique-Alba et al., 2020). Species 358 mixture can also reduce vulnerability of beech to drought compared to monospecific stands (Mölder 359 and Leuschner, 2014). Beech trees growing in a mixture often have larger crowns and higher crown 360 plasticity compared to trees in pure stands (Pretzsch et al., 2016). However, the effect of species 361 mixture depends on various factors including, for example, soil type and quality (Mölder and 362 Leuschner, 2014). In our study, a combined effect of site and species mixture is likely but their 363 individual contribution to explaining climate sensitivity and responses to extreme weather events 364 cannot be unequivocally quantified. Nevertheless, growing species in a mixture can significantly 365 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.

#### 370 Growth reactions to extreme weather events

371 This study shows that the resistance of beech trees to extreme weather events is strongly negatively 372 affected by tree size and site quality. Fast-growing, taller, and larger trees typically have greater 373 xylem vessel diameter, leading to a higher probability of embolism under extreme conditions (Micco 374 et al., 2019; Olson and Rosell, 2013; Rosell et al., 2017). Faster-growing trees rely on higher hydraulic 375 conductivity to support growth, which trades-off as a higher risk of cavitation and vulnerability to 376 drought (Rosell et al., 2017). The faster growth rate of the youngest forest stands in this study (StH) 377 may therefore explain their lower resistance, compared to the nearby older forest stand (Mot). 378 Documented age-related changes in tree sensitivity to climate variation do not paint a consistent 379 picture (Esper et al., 2008a; Zang et al., 2014), suggesting the possibility of different extreme weather 380 coping strategies evolved by different species (Micco et al., 2019; Rennenberg et al., 2006). 381 The tenet underlying forest thinning dictates that removal of canopy trees improves resource 382 availability for the remaining stand and stimulates its growth rate. This study shows that in some 383 conditions, faster growth comes at the expense of higher vulnerability to extreme weather events 384 (the Ciganka site, Fig. 5). This effect was not observed at the other three sites, alluding to an 385 interaction between stand management and site conditions, as suggested by Lévesque et al. (2015). 386 However, contrasting results and interpretations limit the understanding of the general mechanism 387 (D'Amato et al., 2013; Esper et al., 2008b; Martínez-Vilalta et al., 2012a; Metz et al., 2016; Pretzsch et 388 al., 2013; Thurm et al., 2016), the type of tree species mixture has also been indicated to affect 389 drought response (Martínez-Vilalta et al., 2012b). Beech trees have been shown to produce more 390 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.

#### 394 Effect of thinning on carbon uptake in beech forests

395 Van Deusen (2010) has shown that unmanaged forest stands store more carbon in living trees than 396 their managed counterparts and this study confirms that finding. Here, thinning has resulted in a 397 slower accumulation of carbon in living biomass (Fig. 2e), but the total timber production over the 398 rotation period does not differ significantly between the thinning regimes, as recently indicated by 399 Bosela et al. (2016). The discrepancy can be explained by the off-take of tree stems during regular 400 thinning interventions. If added to the carbon stored in the remaining forest, the total usually 401 exceeds carbon storage of unmanaged forests (Van Deusen, 2010), but its climate mitigation impact 402 is driven by the half-life of resulting wood products (Profft et al., 2009).

#### 403 Limitations and future work

404 The balance of carbon that ends up in long-lasting wood products against that which joins stable soil 405 organic matter pools is currently unknown. Thus, the overall impact of thinning on carbon storage 406 and its contribution to climate change cannot be easily estimated. Further, the issue of the broad 407 distribution of European beech must be considered when selecting sample sites. We were not able to 408 take this into account, covering only a limited range of climatic conditions affecting beech across 409 Europe. As a result, we can draw conclusions specific to these conditions only. Future research 410 should include various species mixture types, a range of soil conditions, latitude, longitude and 411 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.

420 A widely used resistance index calculation approach defines the index as the ratio between the ring 421 width in the year of extreme climate event to the average of TRW in three years preceding the target 422 year (Bose et al., 2020; Gazol et al., 2016; Lloret et al., 2011). Using this approach, however, some 423 issues arise (Schwarz et al., 2020). First, the question of the definition of an extreme climate event 424 (Zang et al., 2020): here we used a combination of climate data (summer temperature and 425 precipitation, de Martone aridity index), tree-ring data itself and a literature search to identify years 426 with high climatic stress. An important additional point is that there is no standard definition of 427 drought in ecological studies (Slette et al., 2019). Second, the standard index may be as much 428 influenced by the stress experienced in the year of stress as by the vagaries of the growing conditions 429 in the preceding years. To reduce this shortcoming, we first used the spline fit to define a "normal" 430 growth and then calculated the resistance index as the ratio between the annual ring width and the 431 spline fit. Even this approach is not fully free from potential misinterpretation, the signal of the spline 432 fit is driven by the selection of the reference period and the smoothing parameters to set up the 433 function. The trade-off between filtering out inter-annual fluctuations to derive the spline trend 434 while preserving the long-term environmental change signal remains unresolved and may form a 435 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

441	form the nearest E-OBS grid point. The inability of describing the weather for the exact location of
442	each site was balanced by the fact that the interpolation did not remove interannual variation from

the weather record.

#### 444 Conclusions

- 445 This study shows that more carbon is stored *in-situ* in tree biomass of unmanaged beech stands
- 446 when compared to those under a thinning regime. Dominant and co-dominant trees in the canopy
- 447 layer supported by thinning are the most productive, but also the most climate-sensitive and the
- 448 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
- 450 conclusion, light thinning regimes might be preferable to more intensive interventions at sites with a
- 451 higher incidence of heat and drought events, highlighting the attractiveness of close-to-nature
- 452 forestry practice.
- 453

#### 454 Acknowledgement

- 455 We acknowledge the E-OBS dataset from the EU-FP6 project UERRA (https://www.uerra.eu) and the
- 456 Copernicus Climate Change Service, and the data providers in the ECA&D project
- 457 (https://eca.knmi.nl). The work was supported by the Slovak Agency for Research and Development
- via the projects no. APVV-15-0032, APVV-15-0265, APVV-18-0195 and APVV-19-0183. We further
- 459 acknowledge networking support by the COST (European Cooperation in Science and Technology)
- 460 Action CLIMO Forestry (Climate-Smart Forestry in Mountain Regions— CA15226) financially
- supported by the EU Framework Programme for Research and Innovation HORIZON 2020. Martin
- 462 Lukac received support from the European Social Fund EVA 4.0 (OP RDE,
- 463 CZ.02.1.01/0.0/0.0/16\_019/0000803). Last but not least we would like to thank four reviewers for
- their relevant criticism.
- 465
- 466 References
- Andrews, C.M., D'Amato, A.W., Fraver, S., Palik, B., Battaglia, M.A., Bradford, J.B., 2020. Low stand
  density moderates growth declines during hot droughts in semi-arid forests. J. Appl. Ecol. n/a.
  doi:10.1111/1365-2664.13615
- 470 Babst, F., Bouriaud, O., Papale, D., Gielen, B., Janssens, I.A., Nikinmaa, E., Ibrom, A., Wu, J.,
- 471 Bernhofer, C., Köstner, B., Grünwald, T., Seufert, G., Ciais, P., Frank, D., 2014. Above-ground
- 472 woody carbon sequestration measured from tree rings is coherent with net ecosystem
- 473 productivity at five eddy-covariance sites. New Phytol. 201, 1289–1303. doi:10.1111/nph.12589

- Bose, A.K., Gessler, A., Bolte, A., Bottero, A., Buras, A., Cailleret, M., Camarero, J.J., Haeni, M., Hereş,
  A.-M., Hevia, A., Lévesque, M., Linares, J.C., Martinez-Vilalta, J., Matías, L., Menzel, A., SánchezSalguero, R., Saurer, M., Vennetier, M., Ziche, D., Rigling, A., 2020. Growth and resilience
  responses of Scots pine to extreme droughts across Europe depend on predrought growth
  conditions. Glob. Chang. Biol. 26, 4521–4537. doi:https://doi.org/10.1111/gcb.15153
- Bošel'a, M., Pajtík, J., Konôpka, B., Šebe\vn, V., Vida, T., Bošeľa, M., Pajtík, J., Konopka, B., Šebeň, V.,
  Vida, T., 2013. Modelling effects of weather condition on seasonal dynamics of the stem
  circumference increment in a mixed stand of Norway spruce and European beech. For. J. 59,
  180–188. doi:10.2478/v10114-011-0025-8
- Bosela, M., Sedmak, R., Marusak, R., Sedmakova, D., Petras, R., Barna, M., Bošeľa, M., Sedmák, R.,
  Marušák, R., Sedmáková, D., Petráš, R., Barna, M., Bošeľa, M., Sedmák, R., Marušák, R.,
  Sedmáková, D., Petráš, R., Barna, M., 2014. Evaluating similarity of radial increments around
  tree stem circumference of European beech and Norway spruce from Central Europe.
  Geochronometria 41, 136–146. doi:10.2478/s13386-013-0152-3
- Bosela, M., Štefančík, I., Petráš, R., Vacek, S., 2016. The effects of climate warming on the growth of
  European beech forests depend critically on thinning strategy and site productivity. Agric. For.
  Meteorol. 222, 21–31. doi:10.1016/j.agrformet.2016.03.005
- Bosela, M., Tobin, B., Šebeň, V., Petráš, R., Larocque, G., 2015. Different mixtures of Norway spruce,
  silver fir, and European beech modify competitive interactions in central European mature
  mixed forests. Can. J. For. Res. 45. doi:10.1139/cjfr-2015-0219
- Bottero, A., D'Amato, A.W., Palik, B.J., Bradford, J.B., Fraver, S., Battaglia, M.A., Asherin, L.A., 2017.
  Density-dependent vulnerability of forest ecosystems to drought. J. Appl. Ecol. 54, 1605–1614.
  doi:10.1111/1365-2664.12847
- 497 Candel-Pérez, D., Lo, Y.-H., Blanco, J.A., Chiu, C.-M., Camarero, J.J., González de Andrés, E., Imbert,
  498 J.B., Castillo, F.J., 2018. Drought-Induced Changes in Wood Density Are Not Prevented by
  499 Thinning in Scots Pine Stands. For. . doi:10.3390/f9010004
- Cornes, R., van der Schrier, G., van der Besselaar, E.J.M., Jones, P.D., 2018. An Ensemble Version of
   the E-OBS Temperature and Precipitation Datasets. J. Geophys. Res. Atmos. 123, 9391–9409.
   doi:doi:10.1029/2017JD028200
- D'Amato, A.W., Bradford, J.B., Fraver, S., Palik, B.J., 2013. Effects of thinning on drought vulnerability
   and climate response in north temperate forest ecosystems. Ecol. Appl. 23, 1735–1742.
   doi:10.1890/13-0677.1
- de Rigo, D., Caudullo, G., Houston Durrant, T., San-Miguel-Ayanz, J., 2016. The European Atlas of
  Forest Tree Species: modelling, data and information on forest tree specie, in: San-MiguelAyanz, J., de Rigo, D., Caudullo, G., Houston Durrant, T., Mauri, A. (Eds.), European Atlas of
  Forest Tree Species. Publ. Off. EU, Luxembourg, p. e01aa6.
- Eggleston, H.S., Buendia, L., Miwa, K., Ngara, T., Tanabe, K., 2006. 2006 IPCC Guidelines for National
   Greenhouse Gas Inventories. Japan. doi:4-88788-032-4
- 512 Esper, J., Niederer, R., Bebi, P., Frank, D., 2008a. Climate signal age effects—Evidence from young
  513 and old trees in the Swiss Engadin. For. Ecol. Manage. 255, 3783–3789.
  514 doi:https://doi.org/10.1016/j.foreco.2008.03.015
- 515 Esper, J., Niederer, R., Bebi, P., Frank, D., 2008b. Climate signal age effects—Evidence from young
  516 and old trees in the Swiss Engadin. For. Ecol. Manage. 255, 3783–3789.
  517 doi:https://doi.org/10.1016/j.foreco.2008.03.015

- 518 FAO, 2019. FAO Yearbook of Forest Products 2017. Rome.
- 519 FOREST EUROPE, 2015. State of Europe's Forests 2015.
- 520 Fritts, H.C., 2001. Tree rings and climate. The Blackburn Press, New York and San Francisco.
- 521 Fritts, H.C., 1976. Tree Rings and Climate. Academic Press. doi:10.1016/B978-0-12-268450-0.X5001-0
- Gazol, A., Camarero, J.J., Anderegg, W.R.L., Vicente-Serrano, S.M., 2016. Impacts of droughts on the
   growth resilience of Northern Hemisphere forests. Glob. Ecol. Biogeogr. doi:10.1111/geb.12526
- Gschwantner, T., Alberdi, I., Balázs, A., Bauwens, S., Bender, S., Borota, D., Bosela, M., Bouriaud, O.,
  Cañellas, I., Donis, J., Freudenschuß, A., Hervé, J.-C., Hladnik, D., Jansons, J., Kolozs, L.,
  Korhonen, K.T., Kucera, M., Kulbokas, G., Kuliešis, A., Lanz, A., Lejeune, P., Lind, T., Marin, G.,
  Morneau, F., Nagy, D., Nord-Larsen, T., Nunes, L., Pantić, D., Paulo, J.A., Pikula, T., Redmond, J.,
  Rego, F.C., Riedel, T., Saint-André, L., Šebeň, V., Sims, A., Skudnik, M., Solti, G., Tomter, S.M.,
  Twomey, M., Westerlund, B., Zell, J., 2019. Harmonisation of stem volume estimates in
  European National Forest Inventories. Ann. For. Sci. 76, 24. doi:10.1007/s13595-019-0800-8
- Hlásny, T., Mátyás, C., Seidl, R., Kulla, L., Merganičová, K., Trombik, J., Dobor, L., Barcza, Z., Konôpka,
  B., 2014. Climate change increases the drought risk in Central European forests: What are the
  options for adaptation? Cent. Eur. For. J. 60, 5–18. doi:https://doi.org/10.2478/forj-2014-0001
- IPCC, 2018. Summary for policymakers, in: Masson-Delmotte, V., Zhai, P., Pörtner, H.O., Roberts, D.,
  Skea, J., Shukla, P.R., Pirani, A., Moufouma-Okia, W., Péan, C., Pidcock, R., Connors, S.,
  Matthews, J.B.R., Chen, Y., Zhou, X., Gomis, M.I., Lonnoy, E., Maycock, T., Tignor, M.,
  Waterfield, T. (Eds.), Global Warming of 1.5°C. An IPCC Special Report on the Impacts of Global
  Warming of 1.5°C above Pre-Industrial Levels and Related Global Greenhouse Gas Emission
  Pathways, in the Context of Strengthening the Global Response to the Threat of Climate
  Change,. World Meteorological Organization, Geneva, Switzerland, p. 32.
- Jacoby, G.C., D'Arrigo, R.D., 1997. Tree rings, carbon dioxide, and climatic change. Proc. Natl. Acad.
   Sci. 94, 8350 LP 8353. doi:10.1073/pnas.94.16.8350
- 543 Jevšenak, J., 2019. Daily climate data reveal stronger climate-growth relationships for an extended
  544 European tree-ring network. Quat. Sci. Rev. 221, 105868.
  545 doi:https://doi.org/10.1016/j.quascirev.2019.105868
- Kolář, T., Čermák, P., Trnka, M., Žid, T., Rybníček, M., 2017. Temporal changes in the climate
  sensitivity of Norway spruce and European beech along an elevation gradient in Central Europe.
  Agric. For. Meteorol. 239, 24–33. doi:http://dx.doi.org/10.1016/j.agrformet.2017.02.028
- Lévesque, M., Walthert, L., Weber, P., 2015. Soil nutrients influence growth response of temperate
   tree species to drought. J. Ecol. 1, n/a-n/a. doi:10.1111/1365-2745.12519
- Lloret, F., Keeling, E.G., Sala, A., 2011. Components of tree resilience: Effects of successive low growth episodes in old ponderosa pine forests. Oikos 120, 1909–1920. doi:10.1111/j.1600 0706.2011.19372.x
- Manrique-Alba, À., Beguería, S., Molina, A.J., González-Sanchis, M., Tomàs-Burguera, M., del Campo,
   A.D., Colangelo, M., Camarero, J.J., 2020. Long-term thinning effects on tree growth, drought
   response and water use efficiency at two Aleppo pine plantations in Spain. Sci. Total Environ.
   728, 138536. doi:https://doi.org/10.1016/j.scitotenv.2020.138536
- Martínez-Vilalta, J., López, B.C., Loepfe, L., Lloret, F., 2012a. Stand- and tree-level determinants of the
  drought response of Scots pine radial growth. Oecologia 168, 877–888. doi:10.1007/s00442011-2132-8

- Martínez-Vilalta, J., López, B.C., Loepfe, L., Lloret, F., 2012b. Stand- and tree-level determinants of
   the drought response of Scots pine radial growth. Oecologia 168, 877–888.
   doi:10.1007/s00442-011-2132-8
- Mausolf, K., Wilm, P., Härdtle, W., Jansen, K., Schuldt, B., Sturm, K., von Oheimb, G., Hertel, D.,
  Leuschner, C., Fichtner, A., 2018. Higher drought sensitivity of radial growth of European beech
  in managed than in unmanaged forests. Sci. Total Environ. 642, 1201–1208.
  doi:10.1016/j.scitotenv.2018.06.065
- McCullough, I.M., Davis, F.W., Williams, A.P., 2017. A range of possibilities: Assessing geographic
   variation in climate sensitivity of ponderosa pine using tree rings. For. Ecol. Manage. 402, 223–
   233. doi:https://doi.org/10.1016/j.foreco.2017.07.025
- McDowell, N.G., Allen, C.D., Anderson-Teixeira, K., Aukema, B.H., Bond-Lamberty, B., Chini, L., Clark,
  J.S., Dietze, M., Grossiord, C., Hanbury-Brown, A., Hurtt, G.C., Jackson, R.B., Johnson, D.J.,
  Kueppers, L., Lichstein, J.W., Ogle, K., Poulter, B., Pugh, T.A.M., Seidl, R., Turner, M.G., Uriarte,
  M., Walker, A.P., Xu, C., 2020. Pervasive shifts in forest dynamics in a changing world. Science
  (80-.). 368, eaaz9463. doi:10.1126/science.aaz9463
- 576 Metz, J., Annighöfer, P., Schall, P., Zimmermann, J., Kahl, T., Schulze, E.D., Ammer, C., 2016. Site577 adapted admixed tree species reduce drought susceptibility of mature European beech. Glob.
  578 Chang. Biol. 22, 903–920. doi:10.1111/gcb.13113
- 579 Micco, V. De, Carrer, M., Rathgeber, C.B.K., Camarero, J.J., Voltas, J., Cherubini, P., Battipaglia, G.,
  580 2019. From xylogenesis to tree rings: wood traits to investigate tree response to environmental
  581 changes. IAWA J. 40, 155–182. doi:https://doi.org/10.1163/22941932-40190246
- 582 Mölder, I., Leuschner, C., 2014. European beech grows better and is less drought sensitive in mixed
  583 than in pure stands: tree neighbourhood effects on radial increment. Trees 28, 777–792.
  584 doi:10.1007/s00468-014-0991-4
- Naudts, K., Chen, Y., McGrath, M.J., Ryder, J., Valade, A., Otto, J., Luyssaert, S., 2016. Europe's forest
  management did not mitigate climate warming. Science (80-.). 351, 597–599.
  doi:10.1126/science.aad7270
- Nechita, C., Čufar, K., Macovei, I., Popa, I., Badea, O.N., 2019. Testing three climate datasets for
  dendroclimatological studies of oaks in the South Carpathians. Sci. Total Environ. 694, 133730.
  doi:https://doi.org/10.1016/j.scitotenv.2019.133730
- Nehrbass-Ahles, C., Babst, F., Klesse, S., Nötzli, M., Bouriaud, O., Neukom, R., Dobbertin, M., Frank,
   D., 2014. The influence of sampling design on tree-ring-based quantification of forest growth.
   Glob. Chang. Biol. 20, 2867–2885. doi:10.1111/gcb.12599
- Noormets, A., Epron, D., Domec, J.C., McNulty, S.G., Fox, T., Sun, G., King, J.S., 2015. Effects of forest
   management on productivity and carbon sequestration: A review and hypothesis. For. Ecol.
   Manage. 355, 124–140. doi:https://doi.org/10.1016/j.foreco.2015.05.019
- 597 Olson, M.E., Rosell, J.A., 2013. Vessel diameter–stem diameter scaling across woody angiosperms
  598 and the ecological causes of xylem vessel diameter variation. New Phytol. 197, 1204–1213.
  599 doi:10.1111/nph.12097
- Pérez-de-Lis, G., García-González, I., Rozas, V., Arévalo, J.R., 2011. Effects of thinning intensity on
   radial growth patterns and temperature sensitivity in Pinus canariensis afforestations on
   Tenerife Island, Spain. Ann. For. Sci. 68, 1093. doi:10.1007/s13595-011-0125-8
- Petráš, R., Pajtík, J., 1991. Sústava česko-slovenských objemových tabuliek drevín [Tree volume
   equations for main tree species in Czechoslovakia]. Lesn. časopis 37, 49–56.

- Pretzsch, H., del Río, M., Schütze, G., Ammer, C., Annighöfer, P., Avdagic, A., Barbeito, I., Bielak, K.,
  Brazaitis, G., Coll, L., Drössler, L., Fabrika, M., Forrester, D.I., Kurylyak, V., Löf, M., Lombardi, F.,
  Matović, B., Mohren, F., Motta, R., den Ouden, J., Pach, M., Ponette, Q., Skrzyszewski, J.,
  Sramek, V., Sterba, H., Svoboda, M., Verheyen, K., Zlatanov, T., Bravo-Oviedo, A., 2016. Mixing
  of Scots pine (Pinus sylvestris L.) and European beech (Fagus sylvatica L.) enhances structural
  heterogeneity, and the effect increases with water availability. For. Ecol. Manage. 373, 149–
- 611 166. doi:https://doi.org/10.1016/j.foreco.2016.04.043
- Pretzsch, H., Schütze, G., Uhl, E., 2013. Resistance of European tree species to drought stress in
  mixed versus pure forests: Evidence of stress release by inter-specific facilitation. Plant Biol. 15,
  483–495. doi:10.1111/j.1438-8677.2012.00670.x
- Profft, I., Mund, M., Weber, G.-E., Weller, E., Schulze, E.-D., 2009. Forest management and carbon
  sequestration in wood products. Eur. J. For. Res. 128, 399–413. doi:10.1007/s10342-009-0283-5
- Rennenberg, H., Loreto, F., Polle, A., Brilli, F., Fares, S., Beniwal, R.S., Gessler, A., 2006. Physiological
  responses of forest trees to heat and drought. Plant Biol. 8, 556–571. doi:10.1055/s-2006924084
- Rosell, J.A., Olson, M.E., Anfodillo, T., 2017. Scaling of Xylem Vessel Diameter with Plant Size: Causes,
   Predictions, and Outstanding Questions. Curr. For. Reports 3, 46–59. doi:10.1007/s40725-017 0049-0
- Schwarz, J., Skiadaresis, G., Kohler, M., Kunz, J., Schnabel, F., Vitali, V., Bauhus, J., 2020. Quantifying
  Growth Responses of Trees to Drought—a Critique of Commonly Used Resilience Indices and
  Recommendations for Future Studies. Curr. For. Reports 6, 185–200. doi:10.1007/s40725-02000119-2
- Slette, I.J., Post, A.K., Awad, M., Even, T., Punzalan, A., Williams, S., Smith, M.D., Knapp, A.K., 2019.
  How ecologists define drought, and why we should do better. Glob. Chang. Biol. 25, 3193–3200.
  doi:https://doi.org/10.1111/gcb.14747
- Tei, S., Sugimoto, A., Yonenobu, H., Matsuura, Y., Osawa, A., Sato, H., Fujinuma, J., Maximov, T.,
  2017. Tree-ring analysis and modeling approaches yield contrary response of circumboreal
  forest productivity to climate change. Glob. Chang. Biol. 23, 5179–5188. doi:10.1111/gcb.13780
- Thurm, E.A., Uhl, E., Pretzsch, H., 2016. Mixture reduces climate sensitivity of Douglas-fir stem
  growth. For. Ecol. Manage. 376, 205–220. doi:10.1016/j.foreco.2016.06.020
- van de Pol, M., Bailey, L.D., Mclean, N., Rijsdijk, L., Lawson, C.R., Brouwer, L., 2016. Identifying the
  best climatic predictors in ecology and evolution. Methods Ecol. Evol. 1246–1257.
  doi:10.1111/2041-210X.12590
- Van Deusen, P., 2010. Carbon sequestration potential of forest land: Management for products and
  bioenergy versus preservation. Biomass and Bioenergy 34, 1687–1694.
  doi:https://doi.org/10.1016/j.biombioe.2010.03.007
- 641 Vitasse, Y., Basler, D., 2013. What role for photoperiod in the bud burst phenology of European
  642 beech. Eur. J. For. Res. 132, 1–8. doi:10.1007/s10342-012-0661-2
- Wilmking, M., van der Maaten-Theunissen, M., van der Maaten, E., Scharnweber, T., Buras, A.,
  Biermann, C., Gurskaya, M., Hallinger, M., Lange, J., Shetti, R., Smiljanic, M., Trouillier, M., 2020.
  Global assessment of relationships between climate and tree growth. Glob. Chang. Biol. 26,
  3212–3220. doi:10.1111/gcb.15057
- Zang, C., Hartl-Meier, C., Dittmar, C., Rothe, A., Menzel, A., 2014. Patterns of drought tolerance in
   major European temperate forest trees: Climatic drivers and levels of variability. Glob. Chang.

- 649 Biol. 20, 3767–3779. doi:10.1111/gcb.12637
- Zang, C.S., Buras, A., Esquivel-Muelbert, A., Jump, A.S., Rigling, A., Rammig, A., 2020. Standardized
  drought indices in ecological research: Why one size does not fit all. Glob. Chang. Biol. 26, 322–
  324. doi:https://doi.org/10.1111/gcb.14809
- Zweifel, R., Zimmermann, L., Zeugin, F., Newbery, D.M., 2006. Intra-annual radial growth and water
   relations of trees: implications towards a growth mechanism. J. Exp. Bot. 57, 1445–1459.
- 655 doi:10.1093/jxb/erj125