



Thinning reduces late-spring frost impact on stem radial growth in a beech forest stand

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ABSTRACT

Resistance and resilience to multiple stresses depend on competition among trees, thus they can be improved by means of silvicultural practices reducing stand density. However, we often ignore whether thinning is an appropriate practice to increase the resistance and resilience to late-spring frosts. These climatic events can damage tree species, especially when leaf emergence is advanced by warmer springs. Here, we compared the effect of a late-spring frost on crown damage and stem radial growth in beech trees (*Fagus sylvatica*) from areas thinned and not thinned. The study area is a mixed forest of *F. sylvatica*, *Quercus petraea* and *Q. pyrenaica*, and is located in central Spain, near the southern limit of beech distribution. The proportion of trees damaged by frost was not significantly different in thinned vs non-thinned areas. However, severely damaged trees in non-thinned areas showed higher growth reductions and a longer legacy effect than severely damaged trees in thinned plots. Severely damaged trees were those with earlier leaf and stem growth phenology in the frost year. These trees, compared to slightly damaged trees, delayed growth cessation and had a longer growth period in the frost year, and the year afterwards in non-thinned areas. Growth recovery was size-dependent in non-thinned areas, in which bigger trees recovered growth faster. The positive effect of thinning in attenuating frost impact on growth and accelerating growth recovery adds up to other beneficial effects of thinning for stress tolerance. Similar results could occur in other deciduous species highly sensitive to spring temperatures, which are likely to increase with global warming.

1. Introduction

Stand density plays a central role in forest dynamics. Closed, dense stands hinder regeneration of many species and trigger episodes of decline and mortality among adult trees (Bauhus et al., 2017; Linares et al., 2010; Rodríguez-Calcerrada et al., 2017; Rubio-Cuadrado et al., 2021c, 2020). Thus, reducing stand density is a common practice to manage forest dynamics and increase forest resilience to ongoing climate threats. Timely applied thinning can favor regeneration, biodiversity and productivity (Bauhus et al., 2017; del Río et al., 2017; Lust et al., 1998) in addition to alleviating stress intensity (del Río et al., 2017; Moreau et al., 2022). The positive effects of thinning are obviously variable among forests depending on stand age, stand density, dominant species, climate or thinning intensity (del Río et al., 2017; Moreau et al., 2022; Picchio et al., 2020). For example, in dense Mediterranean forests, thinning alleviates competition, drought stress, heat stress and wildfire

risk (Moreau et al., 2022; Moreno and Cubera, 2008; Rodríguez-Calcerrada et al., 2011). Thinning increases the availability of resources to residual trees. On one hand, removed trees no longer consume water, light and nutrients; on the other hand, these resources increase because of higher throughfall, warmer soil temperature and faster organic matter mineralization. This explains the increases in primary and secondary growth (Deng et al., 2019), viable fruit production (Wu et al., 2019; but see Smith et al., 2022) and pest resistance (Moreau et al., 2022) commonly observed in residual trees after thinning. Nevertheless, undesirable effects after thinning at the stand level have also been reported, particularly after heavy thinning, such as tree windthrow (Picchio et al., 2020) and understory colonization by dense thickets that limit regeneration of target species. Other studies did not find any effect of thinning on tree stress resistance and resilience (Bosela et al., 2021), or even negative ones (López et al., 2009). In this sense, our knowledge about the influence of thinning on late-spring frost stress is

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very limited.

The frequency of late-spring frost damage in temperate species at their southern distribution limit has increased in the last decades due to winter and spring warming and associated advance of phenology (Sanguesa-Barreda et al., 2021). The sensitivity of leaf phenology to winter temperature is a strong determinant of probability to suffer late frost damages. Newly emerged leaves are particularly sensitive to frost, much more than leaf primordia within buds and moderately more than older leaves with thicker cell walls and higher amounts of osmoprotectants (Taschler et al., 2004). Thus, a late frost can damage newly flushed leaves, but not leaves that have flushed earlier or buds that remain dormant (Augsburger, 2011). Damaged trees produce a new cohort of leaves from stored nutrient reserves. Although trees have enough carbon reserves to resprout several times after repeated defoliation events (Hoch et al., 2003), this usually comes with the cost of a decrease in diameter growth (Rubio-Cuadrado et al., 2021a). Subfreezing temperatures occurring during late frosts are usually higher (milder) and extend over shorter periods than those that occur during winter frosts. However, damages in the cambium or the new xylem, besides damages in the foliage, can also occur and severely affect tree growth, even beyond the frost year. Both the use of reserves to repair tissues and resprout, and the alteration of xylem anatomy after late frosts (Bräuning et al., 2016), could have long-lasting effects on growth. In fact, the succession of late frosts can have legacy effects that make trees more susceptible to subsequent frosts or other stresses (Rubio-Cuadrado et al., 2021a). In this framework, an evaluation of forestry practices that reduce late-frost damage and/or increase late-frost resilience are needed.

The extent of frost stress depends on the severity of the frost, the vulnerability of the plant, and the recovery rate of the plant. We can expect that more trees will suffer widespread crown damages when experiencing lower freezing temperatures and higher irradiance in an open canopy than in a closed canopy (Aussenac, 2000; Sonoike, 1998). Indeed, tree canopy cover reduces frost damage in understory seedlings (Langvall and Örlander, 2001). In this sense, a trade-off after thinning between increasing individual tree vigor but higher open canopy susceptibility can be assumed. In addition, the interaction between microclimate and leaf phenology complicates any prediction of canopy opening on frost damage. Trees in the understory and the midstory can leaf out earlier than those in the overstory due to lower irradiance and higher winter temperatures, or later if they require higher chilling accumulation for bud break (Augsburger, 2011; Vitasse et al., 2014a). Thus, microclimatic effects of thinning on irradiance, air relative humidity and air temperatures will be determinant of the probability of frost damage. Moreover, leaf spring phenology (and the risk of frost damage) depends on the duration of the previous growing season. Longer growth periods in thinned areas (Capon et al., 2018) can delay leaf senescence, bud set time, winter hardening, and next-spring leaf flush time due to later exposure to chilling required for bud break (Fu et al., 2014). Similarly, predictions of tree recovery from frost impacts are not straightforward. If growth stimulation by thinning is at the cost of accumulated carbon and nutrient reserves (López et al., 2009), the recovery from frost can be slower in thinned areas. But if higher tree growth is accompanied by higher carbon and nutrient reserves too (i.e. higher vigor), the recovery can be faster in thinned areas (Bauhus et al., 2017). The inability to fully recover from repeated and/or intense stress events is at the origin of silent mortality events years or decades later (Rubio-Cuadrado et al., 2021c, 2018).

The objective of our study was to compare the effects of a late frost on beech (*Fagus sylvatica* L.) trees in thinned and non-thinned plots of a natural forests in Spain, where this species is close to its southernmost distribution limit. Thinning was carried out in 2015 and, in April 2017, a late-frost event occurred. We evaluated the impact of this frost event during the following four years. We compared 1) the proportion of trees damaged by the frost; 2) the magnitude and duration of the reduction in stem radial growth; 3) the alteration of stem radial growth phenology (i.

e. growth start and end dates, duration of the growth period and maximum growth rate); and 4) the relation of tree growth phenology and tree diameter with recovery time from frost. We hypothesized that the timing of budbreak and cambium reactivation drives the exposure of vulnerable tissues and explains differences in frost damage.

2. Material and methods

2.1. Study area and experimental design

The study was conducted in a mixed beech-oak deciduous forest in Spain (3°30'W, 41°07'N). The altitude ranges between 1240 to 1575 m and dominant orientation is east. The soils range from luvisols to humic cambisols, derived from granitic micaceous gneiss (Gil et al., 2009). The climate is sub-Mediterranean, with recurrent summer droughts, coinciding with highest annual temperatures, wet autumns and springs, and cold and dry winters. According to a 27-year series of data recorded with a meteorological station in the forest since 1994, mean annual precipitation is 863 mm and mean annual temperature is 9.7 °C, with a period from November to February in which temperatures usually fall below 0 °C. Late-spring frosts are probable from March to May. In the last decades, late frosts have scorched beech leaves in 23–26 April 1995, 3–6 May 2010, 27–28 April 2013, and in 27–28 April 2017, which is the frost event addressed in this study. Site quality for beech is low, with the study site being included in the group with the worst site index at national level (Moreno Fernández et al., 2018). Despite this and the location of the site near the southern limit of beech distribution (Fig. S1), no resilience risks associated with drought or high temperatures have been detected (Rubio-Cuadrado et al., 2021a, 2020).

Numerous temperate woody and herbaceous species thrive in this forest close to or at their southernmost distribution limit together with Mediterranean taxa (Gil et al., 2009). Banning of livestock grazing in 1961 put an end to a long history of exploitation and boosted regeneration and filling of the open woodland over subsequent decades. Today, stand density and basal area reach values as high as 3947 stems ha⁻¹ and 50.7 m² ha⁻¹ in some areas of the forest. With the aim of increasing fruit production, seedling regeneration, and vigor of remaining trees, including centennial beech trees, 12 plots of 15 m radius were established and thinned in February 2015 using the thinning from below method. By centennial trees we mean those with a diameter at breast height (DBH) of at least 40 cm, with an estimated age of more than 100 years, and therefore present in the forest since before the grazing ban. The plots were selected around centennial beech trees and old clearings densely colonized by beech and oak (*Quercus petraea* [Matt.] Liebl and *Quercus pyrenaica* Willd.) after banning livestock grazing. The plots were randomly distributed over the forest area in which beech was the dominant species. Basal area removed in the 12 plots averaged 41.0 ± 5.6% of total basal area and 61.5 ± 4.4% of basal area of recruits (i.e. all trees except the centennial beech tree). Mean reduction in density was 91.1 ± 1.5% (Table S1 of the Supplementary Material). We retained trees of beech and holly (*Ilex aquifolium* L.) larger than 16 cm of DBH, and trees of *Quercus petraea* of all sizes given its low regeneration and high conservation value in the region. For comparison, we subsequently established 12 control plots of the same size and characteristics that were not thinned, searching for sites with altitudes, slopes and orientations similar to those of the thinned plots (Table 1). The location of all the 24 study plots in the forest can be seen in Fig. S1 of the Supplementary Material.

2.2. Measurements

Secondary growth was measured at breast height using dendrometer bands (DB 20, EMS Brno). The bands were placed on 72 beech trees of similar DBH (20.9 ± 0.5 cm in thinned plots vs 19.4 ± 0.6 in control plots); three trees per plot. However, repeated data loss for one tree left in 71 the number of monitored trees (36 in thinned plots and 35 in

Table 1

Average physiographic, edaphic and tree and stand characteristics of thinned and non-thinned (control) plots. Data are means $\pm$ standard error of 12 replicate plots of 15 m radius per treatment. Four hemispherical photographs were taken per plot to calculate the leaf area index (LAI). All variables were measured in spring 2015, two months after the thinning, except edaphic variables and LAI, measured on early summer 2017. DBH: Diameter at breast height. Dominant tree height is the average height of the 100 highest trees per hectare.

Variable	Thinned plots	Control plots
Altitude (m)	1413 $\pm$ 9	1416 $\pm$ 7
Slope (%)	20.4 $\pm$ 1.2	19.5 $\pm$ 1.0
Orientation (°)	48.8 $\pm$ 10.3	60 $\pm$ 10.1
Organic matter (%)	6.94 $\pm$ 0.41	8.51 $\pm$ 0.57
Carbon to nitrogen ratio	17.0 $\pm$ 0.4	15.5 $\pm$ 0.6
Density (stems ha ⁻¹)	300 $\pm$ 43	2082 $\pm$ 277
Total basal area (m ² ha ⁻¹)	19.5 $\pm$ 1.9	34.4 $\pm$ 2.1
DBH (cm)	18.9 $\pm$ 0.9	11.3 $\pm$ 0.9
Dominant tree height (m)	13.6 $\pm$ 0.6	15.2 $\pm$ 0.7
LAI (m ² m ⁻²)	3.72 $\pm$ 0.15	4.30 $\pm$ 0.18

control plots). The dendrometer bands were installed in March 2015 over the smooth bark of beech, without the need of debarking, and thus avoiding cambium damage. Since May 2015 until October 2021 a total of 61 readings were made, every 2–3 weeks during the growing season, and every 2–3 months during the dormant season.

In the nights of 27 and 28 April 2017 there was an abrupt fall of temperatures below 0 °C for 6 and 8.5 h, respectively. The minimum temperature reached was -4.6 °C in the dawn of 28 April. The frost affected the leaves of the monitored trees, which had already flushed at this time. The evaluation of the damage was made by one observer on April 29, establishing three categories of damage: less than 25% of the crown damaged, 25 to 50% of the crown damaged and more than 50% of the crown damaged.

2.3. Analyses

Girth increment data were transformed to radial increments assuming a cylindrical tree shape. The basal area increments (BAI) were calculated for each tree as:

$$BAI_t = \pi(r_t^2 - r_{t-1}^2) \quad (1)$$

where BAI_t is the basal area increment at time t and r_t and r_{t-1} are the stem radius at times t and $t-1$, respectively.

To compare the intensity of damage caused by the late frost (<25%, 25–50% and >50% of the sprouted leaves scorched) between treatments (thinned and non-thinned plots), we built a table of frequencies in which the number of trees included in each category resulting from crossing these two categorical variables was counted. Subsequently, a chi-square test (contingency table) was performed.

We modeled the growth of each tree every year for the period 2015–2021 to estimate the Julian day of year (DOY) when radial growth starts and ends (DOY_{beginning} and DOY_{end}, respectively), the length of the active growth period (DOY_{end} – DOY_{beginning}), and the time at which the maximum growth rate occurs. A sigmoid function was fitted to growth of each tree by nonlinear least squares using the *nls* function in R statistical software (R Development Core Team, 2022):

$$BAS = a / (1 + e^{(-b * (DOY - c))}) \quad (2)$$

where BAS is the standardized basal area, taking values from 0 to 1 (see Eq. 3), and a , b , c are the model parameters, being c the DOY with maximum growth rate.

$$BAS_{it} = (BA_{it} - \min(BA_i)) / \max(BA_{it} - \min(BA_i)) \quad (3)$$

where BAS_{it} and BA_{it} are the standardized basal area and the basal area, respectively, for tree i at time t . Because the model estimated the start and end of growth asymptotically, we defined the start and the end

of the active growth period as the day when BAS was 10% and 90% of the annual maximum (Moore et al., 2006).

Although we initially established three categories of crown damage, we tested differences in growth and growth-related phenological variables between trees with more and less than 50% of leaves scorched (hereafter severely damaged and slightly damaged trees). We made this reduction in the number of groups due to the small number of trees in some of the original groups. Mann-Whitney U tests were used after determining that the data did not meet the assumption of normality. Relationships between tree stem growth-related phenological variables, diameter and growth were tested using Pearson or Spearman correlations depending on whether the basic assumptions of parametric analysis were met. In the multi-year analyses, i.e. those in which all years were included in the same group, the values for each year were standardized prior to the analyses as follows:

$$V_{iy}' = (V_{iy} - \bar{V}_y) / s_y \quad (4)$$

where V_{iy} is the i value of growth or a growth-related phenological variable for year y , $\bar{V}_y$ is the mean of the variable for the year y , and s_y is the standard deviation of the variable for the year y . Likewise, in those analyses in which variables were analyzed jointly without differentiating between treatments, the values for each year and treatment were standardized prior to the analyses as follows:

$$V_{iyt}' = (V_{iyt} - \bar{V}_{yt}) / s_{yt} \quad (5)$$

where V_{iyt} is the i value of growth or a growth-related phenological variable for year y and treatment t , $\bar{V}_{yt}$ is the mean of the variable for the year y and treatment t , and s_{yt} is the standard deviation of the variable for the year y and treatment t .

3. Results

3.1. Proportion of trees damaged by the frost

Only 12 out of 71 beech trees with dendrometers experienced damage to less than 25% of the crown during the late frost of 2017 (9 and 3 in thinned and non-thinned plots, respectively), 8 showed damage to 25–50% of the crown (4 in thinned and 4 in non-thinned plots) and 51 trees to more than 50% of the crown (23 and 28 in thinned and non-thinned plots, respectively) (Fig. 1). The results of the contingency table showed that there was no significant relationship between the treatment (thinned vs non-thinned plots) and the distribution of trees in the different damage categories (Pearson's chi-square = 1.806; p -value = 0.179).

Due to the small number of trees in some of these groups, only two levels of damage were considered for the subsequent analyses: < 50% of the leaves scorched by the late frost (slightly damaged trees) and > 50%

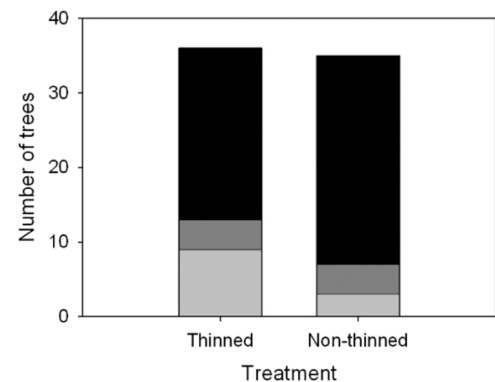


Fig. 1. Percentage crown damage (<25%, light gray, 25–50%, medium intensity gray, and >50%, dark gray) caused by a late frost in 71 beech trees in 2017. Results are shown for thinned and non-thinned plots.

of the leaves scorched (severely damaged trees). The diameter at breast height of the selected trees was similar in the four resulting groups: 20.52 cm (standard deviation 2.42) for slightly damaged trees from thinned plots, 21.15 cm (3.25) for severely damaged trees from thinned plots, 20.24 cm (2.72) for slightly damaged trees from non-thinned plots and 19.40 cm (3.40) for severely damaged trees from non-thinned plots.

3.2. Magnitude and duration of the reduction in stem radial growth

The late frost affected the 2017 growth of severely damaged trees compared to slightly damaged trees in both thinned and non-thinned plots (Table 2). However, the following year (2018), only trees growing in non-thinned plots still showed lower growth. These growth reductions occurred especially during the months of maximum growth (late June and early July) and were less important (non-significant differences) during the rest of the growing season (Fig. 2). In 2017 the growth reduction in severely damaged trees was 47% and 61% (both significant) in the thinned and non-thinned plots, respectively, while in 2018 it was 8% (not significant) and 42% (significant), respectively. Considering growth in 2017 and 2018 together, severely damaged trees grew 21% less than slightly damaged trees in the thinned plots, while in the non-thinned plots growth was 45% lower in severely damaged compared to slightly damaged trees. In the non-thinned plots, during 2019 the severely damaged trees still had a 10% lower growth than the slightly damaged ones, although the difference was not statistically significant (Fig. 3 and Table 2). In contrast, during 2015, 2016, 2021 and, especially, 2020, growth was generally higher in those trees that were severely damaged during the 2017 late frost (Table 2), with significant differences in 2020 in thinned plots (Table 2; Fig. 2). Considering these four years together, and without differentiating between treatments, severely damaged trees grew significantly more than slightly damaged trees ($p = 0.024$). This allowed severely damaged trees to recover part of the growth lost due to the effect of the late frost in the non-thinned plots and especially in the thinned plots, where growth surpassed the accumulated growth of the slightly damaged trees from 2020 onwards (Fig. 4).

3.3. Alteration of stem radial growth phenology

Growth-related phenological variables showed higher variability in 2017 and 2018 in severely damaged trees than in slightly damaged trees,

Table 2

Average basal area increment (BAI, in cm^2 , with standard error in parentheses) of beech trees in thinned and non-thinned plots of a forest stand during seven years, two before the 2017 frost and five afterwards. Results are shown for severely damaged (>50% crown damaged) and slightly damaged (<50% crown damaged) trees. The p -value is the result of the Mann-Whitney U tests performed to analyze the differences between groups (severely damaged vs. slightly damaged). Values with significant differences (p -value < 0.05) are in bold.

Year	Thinned plots			Non-thinned plots		
	Slightly damaged	Severely damaged	p -value	Slightly damaged	Severely damaged	p -value
2015	14.57 (1.78)	16.13 (1.46)	0.537	9.72 (1.66)	10.41 (0.67)	0.672
2016	10.26 (2.34)	11.45 (1.35)	0.415	5.46 (1.11)	6.65 (0.85)	0.643
2017	6.32 (1.33)	3.37 (0.65)	0.037	2.57 (0.58)	0.99 (0.2)	0.015
2018	13.18 (1.33)	12.07 (1.24)	0.344	10.99 (1.68)	6.42 (0.58)	0.017
2019	14.02 (0.92)	14.64 (1.5)	0.415	8.46 (1.64)	7.62 (0.71)	0.558
2020	8.58 (2.42)	12.85 (1.82)	0.093	4.91 (1.31)	6.18 (0.73)	0.505
2021	13.05 (1.45)	17.06 (2.23)	0.344	8.85 (2.14)	8.95 (0.9)	0.856

which prevented finding significant differences between groups (Fig. 5). In 2017, the growth period started earlier ($p < 0.05$ in both thinned and non-thinned plots) and ended later in severely damaged trees than in slightly damaged trees ($p < 0.10$ and $p > 0.10$ in thinned and non-thinned plots, respectively), implying longer growth periods ($p < 0.05$ and $p < 0.10$ in thinned and non-thinned plots, respectively). In 2018, trees in non-thinned plots severely damaged in the 2017 late frost showed longer growth periods ($p < 0.10$) due to later growth cessation ($p < 0.05$) compared to slightly damaged trees. The delay in growth cessation caused severely damaged trees to have higher relative growth in autumn than slightly damaged trees (Fig. 6a). However, due to large variability in growth phenology among severely damaged trees, this difference was not significant. While some trees reacted to frost damage by lengthening the growth period, others had very small growth periods or even did not grow at all during the whole year (Fig. 6b). These differences were partially explained by the treatment, with thinned plots having a lower percentage of non-growing trees.

Pooling all years, we found that growth phenology was weakly related to frost damage and strongly related to thinning. The median start-of-growth day occurred earlier in severely damaged than in slightly damaged trees (143 vs 145; $p = 0.067$), the median end-of-growth day occurred later in thinned plots than in the non-thinned plots (216 vs 210; $p < 0.001$), and the growth period was longer in the thinned plots (71 vs 65 days; $p < 0.001$).

3.4. Importance of growth phenology for annual growth

The higher growth showed by severely damaged trees in 2020 (33% and 22% higher than in slightly damaged trees in thinned and non-thinned plots, respectively; Fig. 3) was related to their longer growth period during this year (Fig. 5). In this sense, a significant relationship was found between the length of the growing period and the BAI in 2020 for trees in the thinned plots (Pearson correlation = 0.431, $p = 0.011$; data not shown). This result was not maintained in other years, though.

Pooling all years, an early onset of growth was related to increased annual growth (Table 3). However, no relationship of growth with time at growth cessation or length of the growth period was found. As expected, the DOY at the beginning and end of the growth period were strongly related to the growth length. A weak inverse relationship (p -value = 0.069) was found between the DOY of growth beginning and DOY of growth end, and, therefore, an early onset of growth did not imply an early growth termination. Tree stem diameter was related to the length of the growing period, so that the larger the diameter, the earlier the growth started and the later the growth ended.

3.5. Relation of tree growth phenology and tree diameter with the recovery from frost

Diameter was an important trait explaining growth recovery after late frost in non-thinned plots. For severely damaged trees, considering the 2017–2021 period, growth relative to the two years prior to the late frost (2015–2016) was directly related to diameter in non-thinned plots (Spearman correlation = 0.194, p -value = 0.021), but not in thinned plots (Spearman correlation = 0.002, p -value = 0.986). Considering all trees (both from thinned and non-thinned plots), diameter was also directly related to growth (Table 3). Considering the years separately, no significant relationships was found between diameter and relative stem growth, due to the high variability in growth across trees (Fig. 7).

4. Discussion

A late-spring frost reduced stem radial growth in adult beech trees. The impact of the frost on growth was higher in those trees whose crown was severely scorched (i.e. > 50% crown damaged), as compared to trees with < 50% of the crown damaged. In addition, growth reduction was greater and lasted longer in trees growing in non-thinned, dense

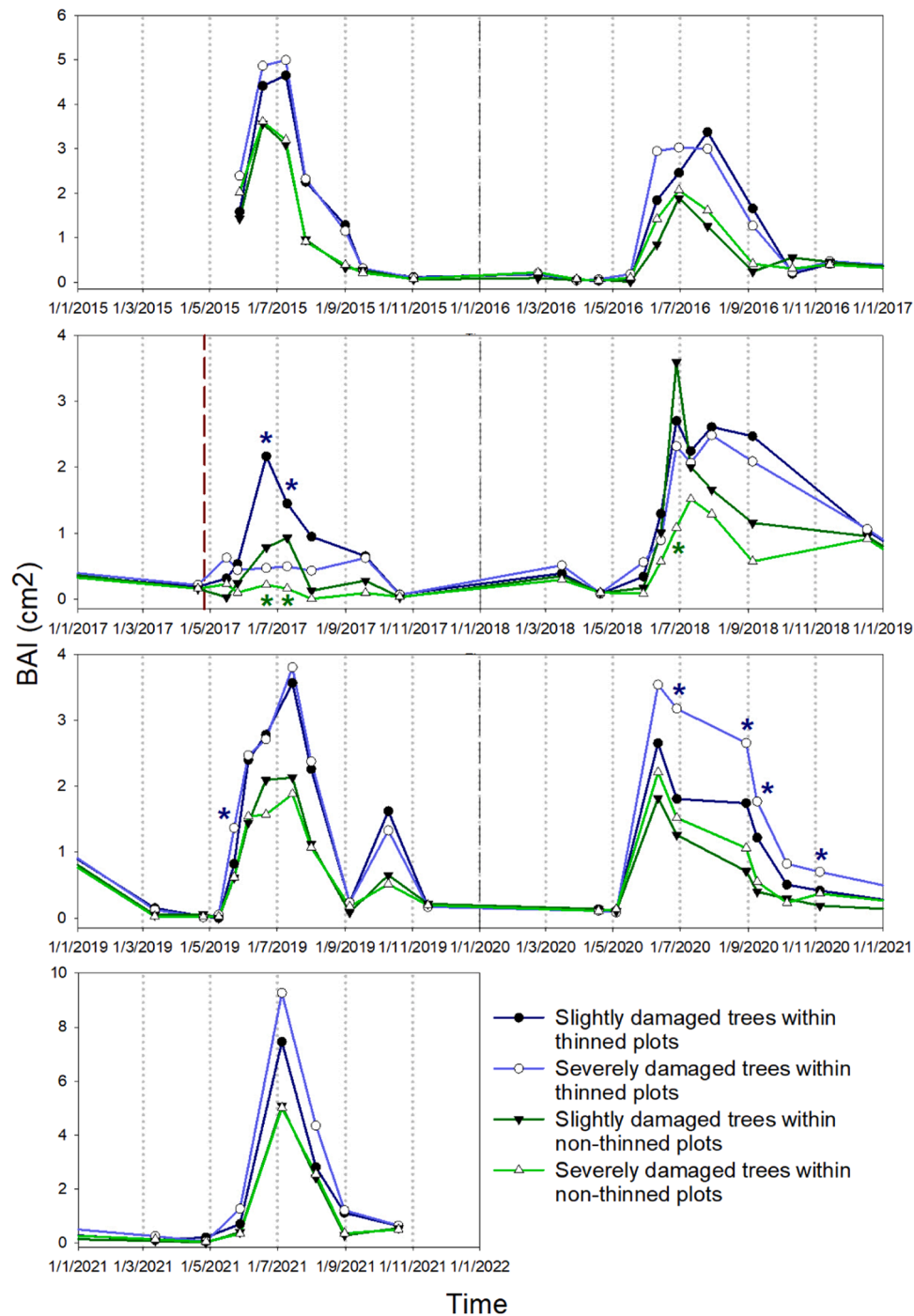


Fig. 2. Annual basal area increment (BAI) of beech trees in thinned and non-thinned plots of a forest stand over seven years, two before the 2017 frost and five afterwards. Results are shown for severely damaged (>50% crown damaged) and slightly damaged (<50% crown damaged) trees. The late frost is highlighted with a dark red dashed vertical line. Asterisks indicate significant differences ($p < 0.05$ with Mann-Whitney U test) between severely and slightly damaged trees within thinned (blue asterisks) and non-thinned (green) areas. Error bars are not displayed for clarity.

areas, as compared to trees growing in thinned areas. Severely damaged trees showed earlier phenology and higher growth during the years not affected by the frost, especially in thinned plots, which made these trees recovered the growth lost due to frost in a few years. To our knowledge, this is the first work showing that thinning alleviates the impact of frost on growth. Two methodological aspects may limit the generalization of our results, with possibly opposing influences. On the one hand, the study has been carried out in a single forest where it has already been shown in previous studies that late frosts have a great effect on beech growth (Rubio-Cuadrado et al., 2021a). It is possible that in other

forests, under other environmental and site quality conditions, the effect of frost, and therefore the differences between treatments, would be smaller. On the other hand, the relatively small size of the plots may mean that, due to the edge effect, the differences between treatments are smaller than would be found if thinning had been carried out over a larger area.

4.1. Frost damage influences radial growth

Late frosts cause a generalized reduction in stem radial growth

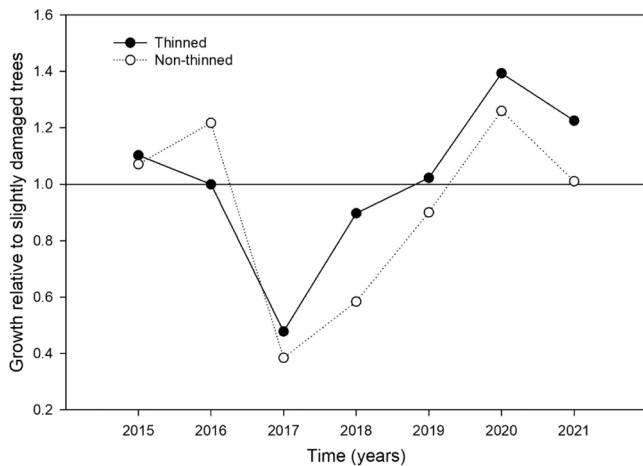


Fig. 3. Relative change of annual stem radial growth caused by frost, calculated as the average stem radial growth exhibited by severely damaged (>50% crown damaged) beech trees relative to that of slightly damaged (<50% crown damaged) beech trees, in thinned and non-thinned plots of a forest stand.

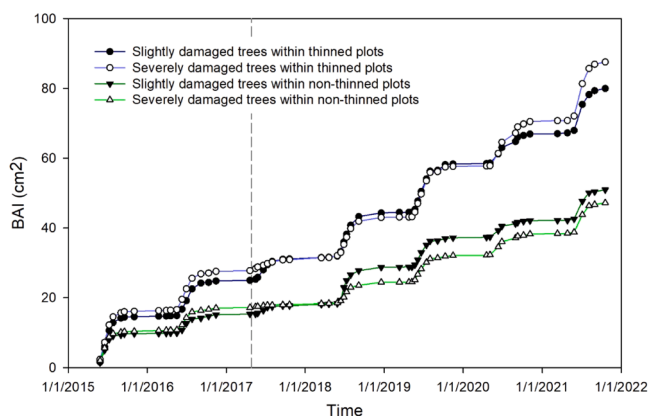


Fig. 4. Annual cumulative basal area increment (BAI) of beech trees in thinned and non-thinned plots of a forest stand over seven years, two before the 2017 frost and five afterwards. Results are shown for severely damaged (>50% crown damaged) and slightly damaged (<50% crown damaged) trees. The late frost is highlighted with a dark grey dashed vertical line. Error bars are not displayed for clarity.

(Dittmar et al., 2006), even in little- or non-frost-damaged trees (Rubio-Cuadrado et al., 2021b), although this reduction increases with increasing frost damage (Table 2). This loss of growth is due not only to the damage itself but also to the decrease in photosynthetic activity. After the frost, trees compensate partial or total defoliation by producing a second leaf cohort, but this second leaf flushing can take longer than a month, with the corresponding loss of C gain (D'Andrea et al., 2019; Nolè et al., 2018). In addition, new leaves produced after the scorch of the first leaf cohort can be thinner and assimilate less C per unit leaf area than those of non-damaged trees (Rubio-Cuadrado et al., 2021b). Likewise, in non-damaged trees, temperature drop delayed leaf flushing, reducing the vegetative period in a similar way as in damaged trees (Rubio-Cuadrado et al., 2021b). Despite the loss of foliage in severely damaged trees, the cambium remained active after the frost (Fig. 2). Although frost defoliation was not complete in the monitored trees, previous studies showed that growth after frost occurs (at low level) even during a period of complete defoliation (D'Andrea et al., 2020), probably due to old C reserves (D'Andrea et al., 2019).

4.2. Tree competition determines the effect of frost on growth

Management and silviculture, through modification of competition, have a major influence on the effect of climate on tree growth. Our results show that the growth reduction of frost-damaged trees was considerably lower in thinned plots. However, thinning did not influence the percentage of damaged leaves (Fig. 1). Although stand density have a major effect on the microclimate created in the canopy (Ausse-nac, 2000), during the dormancy or during early phenological stages of leaf development, the influence of the microclimate is limited both because of the lower coverage provided and the lower transpiration rates.

The response of severely damaged trees to the 2017 frost was divergent according to tree characteristics. While in some trees the growth period was lengthened, in others the growth period was reduced and, according to our results, this variability would be determined by competition and tree size. In this sense, thinned plots and trees with higher DBH had longer growth duration and higher growth. Both factors, stem diameter and tree-tree competition, are related. Since the sampled trees are even-aged, the differences in diameter are mainly determined by competition and sociological position (Maleki et al., 2015; Perot et al., 2010).

4.3. The relationship between foliar phenology and growth phenology

Leaf phenology is related to secondary growth phenology (Kraus et al., 2016). Beech is a diffuse-porous tree and stem water transport occurs in several outermost growth rings, unlike ring-porous species where stem water transport is limited to the youngest rings (Schume et al., 2004). Thus, in diffuse-porous species, carbon allocation to current year wood may not be as decisive as in ring-porous species for water transport for bud break and leaf flushing. Consequently in beech, new photosynthates at the beginning of the growing season are preferentially used for fine root production and foliage growth (Campioli et al., 2013; Merganičová et al., 2019) while radial growth starts within days to weeks after leaf flushing (Cufar et al., 2008; D'Andrea et al., 2020; Michelot et al., 2012).

In the studied area, most trees severely damaged by the 2017 frost sprouted earlier, and showed an advanced stem growth phenology. Moreover, these trees showed a delayed growth cessation compared to slightly damaged trees (although differences were only significant in the thinned area); thus, they had a significant longer growth period, which agrees with frost damage delaying leaf senescence (Rubio-Cuadrado et al., 2021a, 2021b). However, this frost-induced delay in leaf senescence and stem growth cessation has not been found in other works (D'Andrea et al., 2021, 2020), possibly due to the influence of climate. In other temperate, mixed beech-oak forests, a positive relationship between leaf sprouting and senescence has been found (Fu et al., 2014; Liu et al., 2016). Because of the relationship between leaf and growth phenology, it would be expected to find a positive correlation between the onset and end of growth, but we did not find this relationship.

Coupling between leaf phenology and growth phenology depends on the relationship between carbon sources and sinks. After the interruption of the carbon source, trees can limit the loss of stored carbohydrates by down-regulating the C sink strength, including growth rates. In this way, carbohydrates would be redirected from radial growth to the buds to form the second cohort of leaves and, once this cohort is photosynthesizing, trees would prioritize carbohydrate storage over growth (Dietze et al., 2014; Miranda et al., 2020; Wiley et al., 2017). However, the regulation of carbon source/sink relationships under stress or after perturbations is still unclear, and there is no consensus on whether tree growth is limited by carbon assimilation (i.e. source limitation) or cambial activity (i.e. sink limitation) (Guillemot et al., 2015; Lempereur et al., 2015). Körner (2015) points out that, in general, photosynthetic rates are controlled by tissue growth and, therefore, growth reduction would be mostly due to a shorter growing season caused by the frost

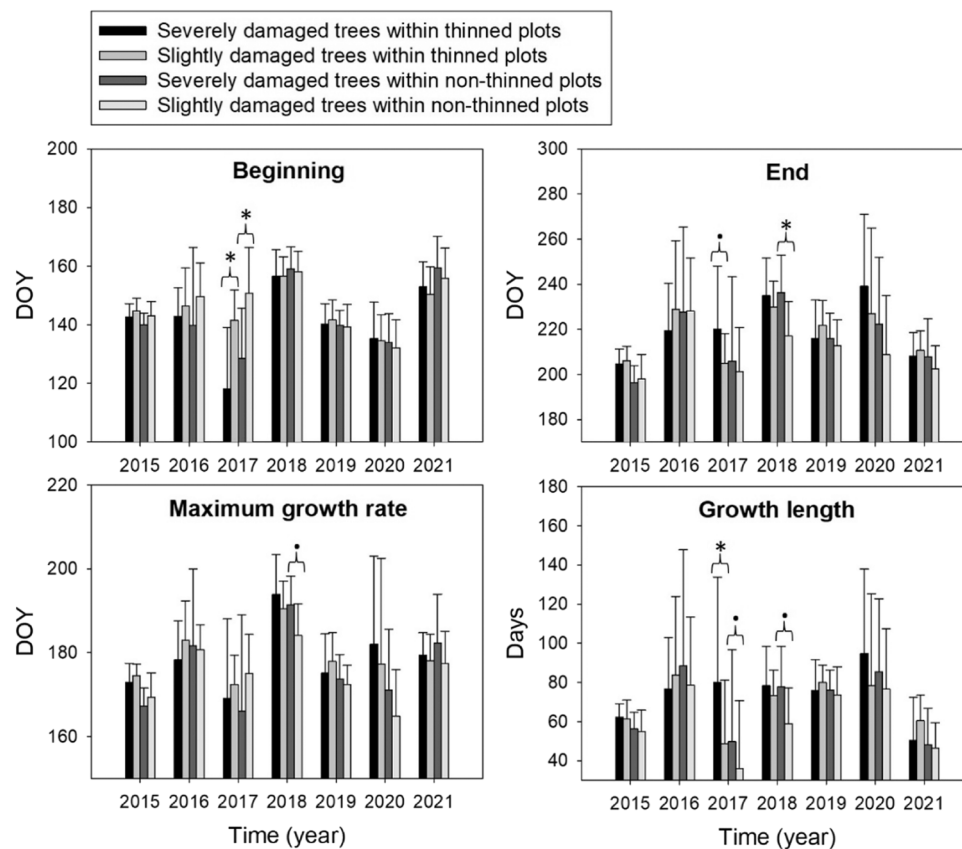


Fig. 5. Start and end of stem radial growth (Day of Year; DOY), day with the maximum growth rate (DOY) and length of the stem growth period (number of days based on start- and end-dates of stem radial growth) in beech trees in thinned and non-thinned plots of a forest stand, modeled from dendrometer data over seven years, two before the 2017 frost and five afterwards. Results are shown for severely damaged (>50% crown damaged) and slightly damaged (<50% crown damaged) trees. Error bars show the standard deviation. Asterisks and points indicate significant differences ($p < 0.05$ and $p < 0.10$, respectively, with Mann-Whitney U test) between severely and slightly damaged trees within thinned and non-thinned plots.

(arrest of cell division by low temperatures and hormonal signals) rather than to a limitation in carbohydrate availability. After the occurrence of a late frost, frost-damaged beech trees would have a shorter vegetative period than non-damaged beech trees (Rubio-Cuadrado et al., 2021b) and this time lag would be the cause of differences in growth between damaged and non-damaged beech trees. Two facts support this hypothesis: 1) the production of the second cohort of leaves can hardly involve any additional carbohydrate cost (Lenz et al., 2014), given the early C-autonomy of opening buds (Keel et al., 2007; but see D'Andrea et al., 2019), and 2) late-summer and autumn growth in the frost year were barely affected (Figs. 2 and 6a).

4.4. Phenology influences growth

Delayed growth cessation did not imply higher annual radial growth (Table 3). Previous studies showed the importance of late growth, produced in summer or autumn, in explaining the variability of annual growth in Mediterranean-influenced climates (Camarero et al., 2021), given that in these environments water stress is the main determinant of radial growth (Cabon et al., 2018). However, in the studied forest, in general, there is no evidence of water stress in beech trees (Cano et al., 2013; Rodríguez-Calcerrada et al., 2019; Rubio-Cuadrado et al., 2021a). In fact, only in 2019 did radial growth exhibit the typical bimodality produced by growth cessation in summer due to water limitation and resuming in autumn after the first rains in this season (Fig. 2). On the contrary, an earlier onset of growth would increase total annual growth (Table 3), confirming the results obtained by Delpierre et al. (2017) for beech, where early phenology was directly related to higher growth, while the timing of the end of the vegetative period (leaf senescence)

was not. In this study Delpierre et al. (2017), showed that tree phenological ranks repeat from year to year due to genetic or epigenetic differences, although small-scale environmental variations, such as differences in soil water content, can also influence phenology. Other studies (Cufar et al., 2015) comparing different populations showed no relationship between growth and leaf phenology, probably because of environmental differences (climate, soil, etc.) among populations may have a greater effect than possible genetic differences. In the absence of late frosts, early phenology provides a competitive advantage in terms of light harvesting (Jolly et al., 2004) and nutrient assimilation (Nord and Lynch, 2009), while this competitive advantage is reversed in years when late frosts occur. Thus, optimal leaf phenology is likely to be shaped by frost risk and competition: late frosts would exert a selective pressure on trees with early budburst (Lenz et al., 2013; Vitasse et al., 2014b), whereas late leaf phenology would reduce C gain and competitive potential. The ongoing increase in temperatures may alter this balance by changing the frequency of occurrence of late frost damage (Ma et al., 2019; Zohner et al., 2020).

The relationship between tree diameter and radial growth phenology, with bigger trees starting to grow earlier and stopping to grow later (Table 3), may in turn be mediated by at least three other relationships: that of size with physiology, that of tree competition with phenology, and that of growth with phenology. Although there are studies that relate tree size to phenology, this relationship seems to be determined more by age than by tree stem diameter per se (Li et al., 2013; Rossi et al., 2008; Zeng et al., 2018). Here, the trees sampled in our study were likely of similar age, having recruited at the same time after the cessation of grazing in 1961, and their differences in diameter were relatively small. In even-aged stands diameter is mainly

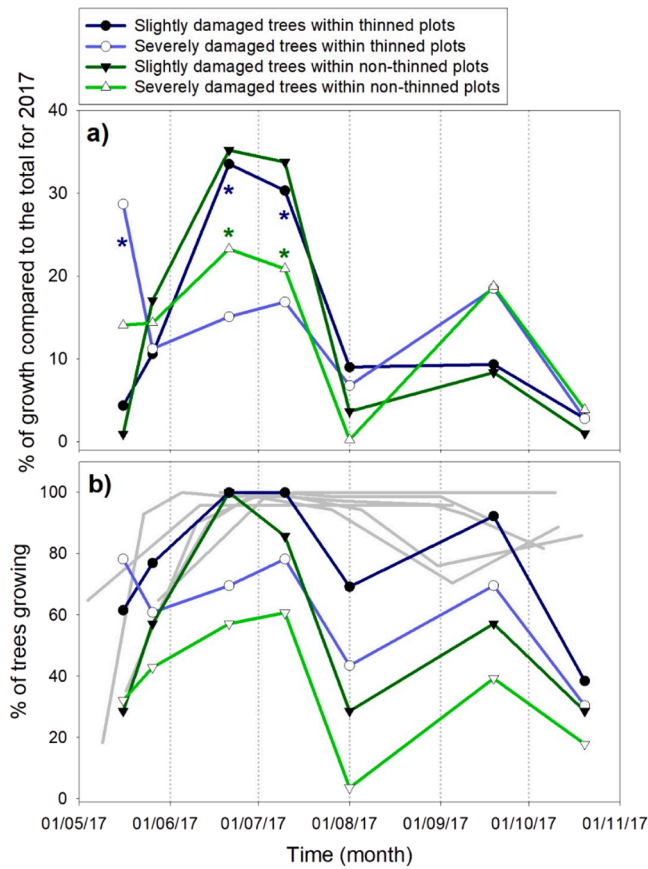


Fig. 6. Distribution of growth in percentage (sum of growth for each series adds up to 100%) since the late frost in April 2017 through November 2017 (a) and percentage of trees with growth (BAI > 0) in each of the measurement dates with respect to the total number of trees in each group for 2017 (b). Significant differences ($p < 0.05$ with Mann-Whitney U test) between severely and slightly damaged trees within thinned (blue asterisks) and non-thinned (green asterisks) plots are shown in a. Error bars are not displayed for clarity. In b, the mean percentage of trees with BAI > 0 for the years 2015, 2016, 2018, 2019, 2020 and 2021 is shown with grey lines.

determined by competition (Maleki et al., 2015; Perot et al., 2010). However, no differences in growth phenology were found between thinned (with less competition) and non-thinned plots (with more competition). Therefore, the relationship between diameter and phenology is related to the fact that trees with early phenology would grow more and, in coetaneous stands, this would produce greater diameters and competitive potential, at least in the absence of late frosts or severe water stress.

Table 3

Spearman correlation coefficients (with p -value in parentheses) relating different growth phenology variables to each other and to diameter, BAI and tree-ring width (TRW). Tree-ring width has been used in addition to BAI because the latter is directly dependent on the diameter. All years have been considered except 2017, to avoid the noise caused by the late frost. Prior to the analyses, all variables (except diameter) were standardized for each year and for each treatment. DOY means the Julian day of year. Values with significant differences (p -value < 0.05) are in bold.

	DOY end	Growth length	BAI	TRW	Diameter
DOY beginning	-0.090 (0.069)	-0.472 (<0.001)	-0.138 (0.005)	-0.128 (0.009)	-0.113 (0.020)
DOY end		0.886 (<0.001)	-0.041 (0.412)	-0.085 (0.084)	0.099 (0.045)
Growth length			-0.005 (0.912)	0.143 (0.004)	0.143 (0.004)
BAI				0.956 (<0.001)	0.414 (<0.001)
TRW					0.179 (<0.001)

4.5. Reduced growth and delayed growth cessation as a legacy of frost on non-thinned areas

Late frosts can have legacy effects, reducing growth beyond the year in which the frost occur (Fig. 2). This is in accordance with a recent study in the same forest (Rubio-Cuadrado et al., 2021a), but is at odds with previous research where late frosts affected growth and growth phenology only in the year of the frost (D'Andrea et al., 2020, 2019; Olano et al., 2021; Sangüesa-Barreda et al., 2021, 2019; Tonelli et al., 2023). There are multiple factors that can influence the impact of a late frost, such as tree vigor status, tree-tree competition, management (Charrier et al., 2015), phenological stage during the frost (Augsburger, 2011), as well as temperatures prior (Sangüesa-Barreda et al., 2021) and during the frost. There may be additional methodological factors influencing the ability to detect frost effects, such as the use of control plots or non-damaged trees for comparison.

The late frost legacy effect found here would influence growth, especially in the trees more damaged by the frost, and the phenology of growth and leaves, with frost delaying leaf senescence (Rubio-Cuadrado et al., 2021a) as well as the end of the radial growth period (Fig. 5). Legacies of extreme climate events on growth have been attributed mainly to damages in the hydraulic system and limitations in the availability of non-structural carbohydrate reserves (Adams et al., 2017; Hacke et al., 2001; Peltier and Ogle, 2019; Schönbeck et al., 2018; Timofeeva et al., 2017). None of these can be excluded when explaining our results. However, the reduction in growth and the delay in growth cessation in the year after the late frost were only significant in the non-thinned plots. Thus, given the importance of competition in limiting the available resources, the hypothesis of growth reduction due to carbon limitation would explain better our results. In a situation of limited resources due to high competition, the reduction in carbohydrate consumption, caused by slower growth, is not enough to maintain stable carbon stocks, resulting in lower carbon reserves at the beginning of the next growing season (D'Andrea et al., 2021), and consequently reducing early growth (Fig. 2). In any case, it is possible that there were other drivers for growth reduction, like water stress, which may result in a situation of sink limitation (insufficient cell turgor to maintain high levels of meristematic and cambial activity) especially in conditions of high competition (Körner, 2015). However, the lack of relationship between the end of the growing season and annual growth (Table 3) suggested that, in the area and the period studied, there was no limitation of growth by water stress [insufficient water resources reduce growth period and total growth (Cabon et al., 2018; Guillemot et al., 2015)].

4.6. Growth recovery from frost

In our study, trees more damaged by the frost tended to have higher growth than slightly damaged trees in the years before and after (from two years after) the frost, but grew less the frost year and the following year (2017 and 2018). The growth advantage acquired before the frost was lost over the next two years due to the effect of the frost, but two years afterwards, damage was quickly compensated, especially in the thinned plots, where growth recovery was not affected by tree size. Tree

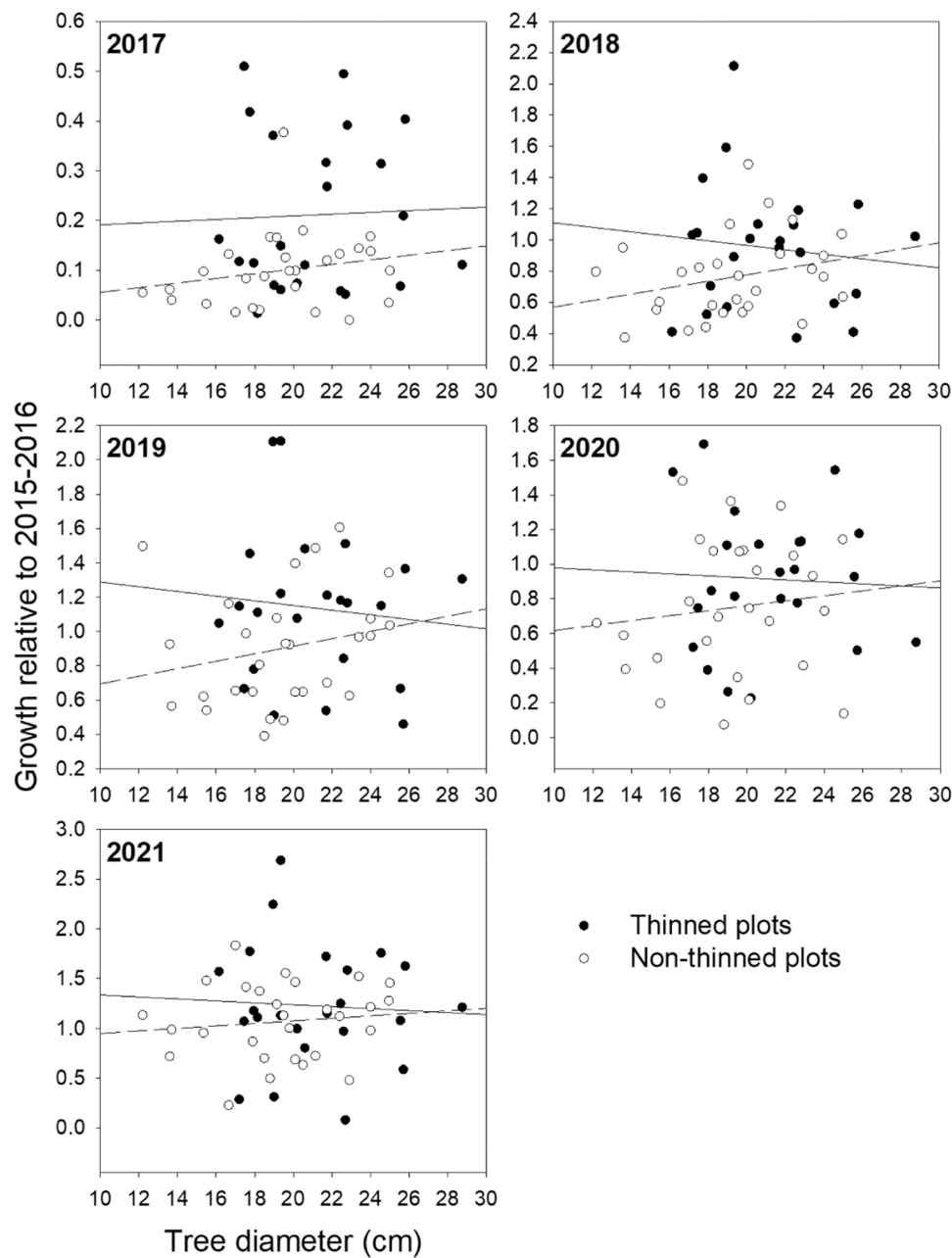


Fig. 7. Scatter plots relating tree stem diameter to relative stem radial growth of each severely damaged beech tree (>50% crown damaged). The relative stem radial growth was calculated as the stem radial growth exhibited by each tree in the 2017–2021 period relative to its average growth in the 2015–2016 period (prior to the occurrence of the late frost). Slightly damaged trees were not considered for this analysis. Solid (thinned plots) and dashed lines (non-thinned plots) show non-significant ($p > 0.1$) trends.

stem diameter, on the contrary, determined the recovery after frost in non-thinned plots (Fig. 7). Since diameter acts as a proxy of growth and competitive ability in this study (see above), its effect will be more important in dense, non-thinned plots where competition is higher.

The higher growth of the most damaged trees was not due to the damage itself, as these trees were already showing higher growth before the frost. One possible explanation for the tendency of severely damaged trees to grow more in 2015–2016 and 2019–2021 is that these trees tend to sprout earlier. This earlier phenology would give the trees some advantage by lengthening the vegetative period and minimizing competition of trees with later phenology, which would result in higher growth rates (Table 3; see also Delpierre et al., 2017). In this sense, previous studies show that differences in phenology between trees of the same species have an important genetic component (Jayawickrama

et al., 1998; Pelgas et al., 2011; Quesada et al., 2017; St Clair et al., 2005); although phenological behavior varies from year to year depending on climatic conditions, a tree will tend to maintain its relative position in the ranking of phenology comprising all trees (Delpierre et al., 2017). In line with this, here, severely damaged trees showed an advanced phenology during the studied period (see section *Alteration of stem radial growth phenology* in Results). Anyway, it should be noted that our phenological measurements are estimates from a model, with the consequent error, and based on stem growth phenology, not leaf phenology.

5. Conclusions

Late frosts are climatic disturbances with a great effect on radial

growth in damaged trees. Given the predictions of an increase in these disturbances in certain areas, it is necessary to find ways to mitigate their damage. Reducing competition by thinning reduced damage during the frost year and especially during the following year. In both years, the reduction in growth suffered by the severely damaged trees occurred mainly during the beginning of the growing season, while late growth was not affected, possibly due to the delay in the end of the growing season. The trees severely damaged by frost were those showing an early phenology. The maintenance of this early phenology from year to year, and the strong inverse relationship between the day of growth start and annual growth, allowed them to maintain higher growth rates during normal years, especially in thinned areas, causing these trees to compensate (or even exceed), at the end of the study period, all the growth lost with respect to the slightly damaged trees. Therefore, thinning is an appropriate tool to reduce the effects of late frosts on sensitive species, especially recommended to improve resilience in those places where an increase in the occurrence of late frosts is expected.

CRediT authorship contribution statement

Rodríguez-Calcerrada Jesús: Conceptualization, Methodology, Writing – original draft, Writing – review & editing. **Rubio-Cuadrado Álvaro:** Conceptualization, Formal analysis, Investigation, Methodology, Software, Writing – original draft, Writing – review & editing. **G. Gordaliza Guillermo:** Data curation, Investigation. **Gil Luis:** Funding acquisition, Writing – review & editing. **López Rosana:** Writing – review & editing.

Declaration of Competing Interest

The authors declare the following financial interests/personal relationships which may be considered as potential competing interests: Alvaro Rubio Cuadrado reports financial support was provided by Polytechnic University of Madrid. Rosana Lopez reports financial support was provided by Spain Ministry of Science and Innovation.

Data Availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.foreco.2023.121675](https://doi.org/10.1016/j.foreco.2023.121675).

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