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ORIGINAL ARTICLE

Low resistance but high resilience in growth of a major deciduous forest tree (*Fagus sylvatica* L.) in response to late spring frost in southern Germany

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Abstract

Key message **European beech showed low resistance but high resilience in radial growth after an extreme late frost event. Site-specific growth reductions correlated with absolute minimum temperature in May.**

Abstract Late spring frost events occurring after the early leaf unfolding ("false spring") can result in severe leaf damages in deciduous trees. With climate warming, such damages may occur more frequently due to an earlier start of the growing season. While affected, mature trees usually survive, but radial and height growth after the late frost has rarely been quantified in relation to the magnitude of the frost events. The effects of a severe late frost event in the early May 2011, following a warm spring and early bud break, was quantified for European beech (*Fagus sylvatica* L.) at 7 forest stands in Bavaria, Germany. Resistance and resilience of tree growth were quantified based on tree-ring widths of 135 trees. Resistance to the late frost event (comparing tree-ring width in the frost year with the previous 5 years) was on average reduced by 46%. Resistance was positively correlated with May minimum temperature at the study sites, indicating a relationship between growth reduction and frost severity. Partial least-square linear models based on monthly climate data (precipitation, temperature, potential evapotranspiration, and the Standardized Precipitation Evapotranspiration Index) could not explain the growth reduction in 2011, thereby providing evidence for the importance of frost damages on annual growth. *F. sylvatica* showed high resilience after the frost year, with tree-ring widths in the subsequent years being comparable to the previous years. This study suggests that frost events may strongly reduce growth of *F. sylvatica* in the event year, but that carry-over effects on the radial growth of subsequent years are not likely.

Keywords Dendroecology · Tree rings · False spring · European beech · Frost damage

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Introduction

Late spring frost events occurring after the early leaf unfolding, sometimes referred to as "false springs", can result in severe leaf damages in deciduous trees (e.g., Day and Peace 1946; Stahle 1990; Augspurger 2009; Hufkens et al. 2012; Kreyling et al. 2012a; Menzel et al. 2015) and serious economic losses in forestry and agriculture (Gu et al. 2008). Climate models suggest that such conditions can occur more frequently with climate change (Rigby and Porporato 2008), theoretically resulting in more frequent late frost damage (Kramer 1994). Accordingly, increased frequency of late frost damage in deciduous forest trees over recent decades has been observed in long-term monitoring data (Augspurger 2013). Larger-scale analyses of climate records suggest that the risk for late spring frost damage increases with climate change in some regions (e.g., eastern North America), while it may also decrease in other regions (e.g., western North America) (Marino et al. 2011; Allstadt et al. 2015). For Central Europe, earlier occurrence of spring frost events by 2.1 days per decade is reported (Potop et al. 2014), while leaf unfolding of the target species of our study, *Fagus sylvatica* L., advances by 3.6 days per decade across Germany (DWD 2016). These numbers imply that leaf unfolding advances quicker than frost occurrence, resulting in more frequent “false spring” situations and increasing risk of late frost damage.

European beech (*Fagus sylvatica* L.) is the dominant natural tree species of Central Europe across many soil types and along broad gradients of water availability (Leuschner et al. 2006). Beech forests, mainly the old stands, play an important role in the maintenance of biodiversity and are economically important (Gessler et al. 2007; Moning and Müller 2009). Growth of *F. sylvatica* is commonly reported to be limited by summer droughts in Southern (Jump et al. 2006) and in Central Europe (Lebourgeois et al. 2005; Scharnweber et al. 2011; van der Maaten 2012). Compared to other tree species, *F. sylvatica* is considered to be more sensitive to the late spring frost events (Day and Peace 1946), but circumvents this sensitivity by late bud burst dates (Dittmar et al. 2006; Kreyling et al. 2012a). Late frosts affect beech mainly via destruction of the foliage, which—in turn—require assimilates to be used for the formation of new leaves. As these assimilates cannot be used for growth, late frost years generally result in reduced growth, i.e., in narrow tree rings (Dittmar et al. 2006; Dittmar and Elling 2007). Late frost damage is considered one of the main drivers of the northern and upward range limit of *F. sylvatica* and other broad-leaved deciduous tree species in Europe (Kollas et al. 2014a).

Until now, the quantification of late spring frost influence has rarely been considered when studying growth of *F. sylvatica*. Kreyling et al. (2012b) reported a 7% reduction in height growth in 2-year-old saplings when exposed to late frost (−5 °C after leaf unfolding). For mature trees, Dittmar et al. (2006) observed a late frost-induced (temperature under −3 °C) ring-width reduction of up to 90% for trees in the Alps. After complete defoliation due to late frost (minimum temperature −5 °C), recovery of foliage within 3 months is reported for *F. sylvatica* (Menzel et al. 2015). Similarly, high frost sensitivity is reported for the closely related Siebold’s beech (*Fagus crenata* Blume) in Japan, where a late spring frost event in April 2011 killed 80% of fresh leaves in a 40-year-old stand (Awaya et al. 2009). Although new leaves emerged from latent buds after only 36 days, the impact of the late frost was clearly visible in the diameter growth, as some trees grew only 20% compared to the previous years (Awaya et al. 2009).

Dittmar et al. (2006) showed that even after the strongest late frost event with the highest damage potential in the last century, a complete recovery of radial increment in most of the *F. sylvatica* trees was noted in subsequent years. In addition, Awaya et al. (2009) observed a recovery in diameter growth and net primary production of *F. crenata* in the year following late frost. Possibly, beech ensures next year’s growth potential by storing photosynthetic products in the later part of the growing season, rather than using the assimilates during the current year’s growth (Larcher 2003).

In the early May 2011 (May 3rd, 4th, and 5th), unusually low early morning temperature extremes were observed in Germany, reaching −11 °C in some regions of Bavaria (Kreyling et al. 2012a) and affecting plant growth and vitality. The event caused strong leaf damage and reset the spring development of forest greening by 7–9 weeks (Kreyling et al. 2012a). Similarly, Menzel et al. (2015) noticed complete defoliation without visible recovery for an average of 3 weeks (18–34 days) in *F. sylvatica*. In this study, we have focused on the late spring frost event of the early May 2011, which has been the most recent severe and large-scale late frost event in Germany. The impact of the late frost event on tree growth was determined by quantifying tree-ring widths. Tree growth as well as climatic and phenological conditions were studied at seven sites across Bavaria, southern Germany, before, during, and after the 2011 late frost event. We hypothesized decreased growth after the late frost event, i.e., low resistance, with effect sizes increasing with decreasing minimum temperature at the site level. We furthermore expected high resilience in radial growth with no signs of negative carry-over effects of the frost event into the growth of the following year(s).

Materials and methods

Study area

The study area is located in Bavaria, southeastern Germany (Fig. 1a). The sampling was done on mature stands, which were dominated by the target species *F. sylvatica* and were all located within Natural Forest Reserves (NFR; “Naturwaldreservate” see: www.naturwaelder.de) to minimize human disturbance. Overall, seven sites were selected (Fig. 1b) along a gradient of May minimum temperature in 2011 (Table 1). The sites were characterized by an average annual temperature of 7.2–8.1 °C, precipitation sums of 767–851 mm, and elevation between 310 and 653 m a.s.l. (Table 1), representing typical climatic conditions for *F. sylvatica* within the core of its natural distribution range.

Climate variables

Daily air temperature series, based on 10-min measurement intervals, were obtained from the weather station network

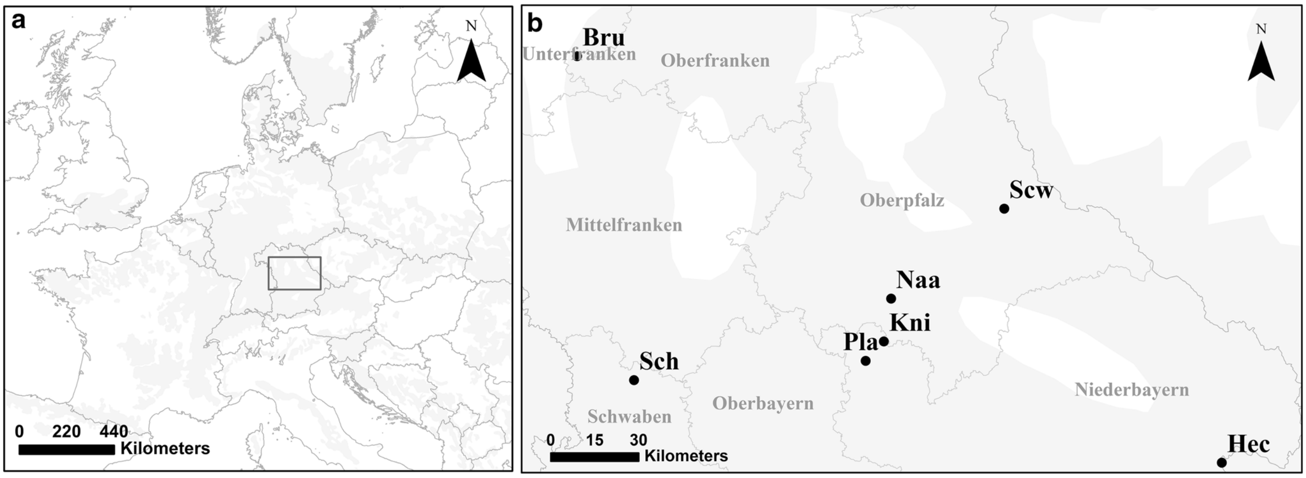

Fig. 1 **a** General location of the study area in Europe within the distribution range of *Fagus sylvatica* (*grey area*; from EUFORGEN (2009)), and **b** location of the seven study sites. More detailed information on the seven sites including the abbreviations and full names is provided in Table 1

Table 1 Characterization of the seven study sites/Natural Forest Reserves (NFR)

Site code	NFR name	Latitude	Longitude	Altitude (m a.s.l.)	May min. temp. 2011 (°C)	Mean temp. (°C)	Precip. (mm)	Mean series length (a)	*H* (m)	DBH (cm)
Hec	Hecke	48.54	13.44	358	−1.2	8	851	151	33.1 (3.4)	57 (7.5)
Kni	Knittelschlag	48.96	11.90	461	−1.3	7.6	767	95	34.5 (1.2)	48 (7.4)
Naa	Naabrangen	49.09	11.94	450	−1.5	7.6	767	124	28.4 (2.2)	42 (9.4)
Pla	Platte	48.90	11.82	450	−1.7	7.6	767	124	28.7 (3.4)	41 (5.8)
Bru	Brunnstube	49.87	10.50	400	−2.3	8.1	716	97	33.1 (1.4)	43 (6.3)
Sch	Schneetal	48.87	10.74	533	−3.1	7.6	767	129	28.8 (2)	44 (5.4)
Scw	Schwarzwihrberg	49.35	12.49	653	−3.2	7.2	800	155	34.1 (3.6)	58 (11.8)

Climate data are shown for the climate normal period 1961–1990 as provided on the NFR Website (www.naturwaelder.de). Sites ordered by decreasing May minimum temperature in the year of the late frost event (2011), which is the mean of the absolute minimum temperature of the nearest three climate stations of the LfL-network

Mean Temp mean annual air temperature, *Precip* annual precipitation sum, *H* tree height, *DBH* diameter at breast height of the sampled trees, [mean values (SD)]

of the Bayerische Landesanstalt für Landwirtschaft (LFL; URL: www.wetter-by.de). For each of the seven sampling sites, the three closest weather stations within a maximum distance of 25 km were selected. Therefore, climate data (daily minimum, mean and maximum air temperature, and precipitation sum) from 20 climate stations were obtained. In our analyses, we used averages calculated from the three closest weather stations as a conservative estimate for each climatic parameter and study site. The climate variables were studied for 2011 and compared with the 10 years before (2001–2010). As tree growth is normally restricted to the period April–September in this region (van der Maaten 2012), the focus was on these months. Confidence intervals at 95% were calculated for the 10-year period preceding the frost event to assess the extremeness of climatic conditions in 2011.

The starting day of leaf unfolding was estimated for each study site to confirm the early leaf unfolding of *F. sylvatica* in 2011. Therefore, we overlapped the study site locations with phenological maps of beech provided by the German Weather Service (DWD; http://www.dwd.de/DE/fachnutzer/freizeitgaertner/2_pflanzenentwicklung/_node.html). The same procedure was followed to obtain estimates of leaf unfolding for the years 2006–2010.

Tree growth

In late March 2014, 15–20 mature and dominant trees were selected in each of the seven sites. From each tree, two 5.15 mm-thick cores were extracted at breast height, in two opposite and slope-parallel directions, using an increment borer. Overall, we collected 270 cores from 135 trees. The wood samples were air-dried, sanded, scanned using a high-resolution scanner (Epson Perfection V700 Photo scanner at 2000 dpi), measured, and cross-dated (visually and statistically) using CDendro/CooRecorder v.7.7 (Cybis Elektronik & Data AB, Sweden). No missing rings were detected.

To analyze tree-growth responses during and after the extreme late frost event of 2011, resistance and resilience were calculated (Lloret et al. 2011). Resistance, which measures the degree of radial growth loss following a disturbance, was estimated by taking the ratio between the growth during and before an extreme event (i.e., 2011). Resilience, which measures the recovery in radial growth following a disturbance, was calculated using the ratio between the growth after and before an extreme event. For resistance, we related the growth of individual trees during the frost year to their average growth in the five preceding years (2006–2010), whereas for resilience, we related the average growth in 2012–2013 to the average growth in 2006–2010. We used raw tree-ring widths for these analyses, because no general trend which could hint at any ageing effect was evident for the studied period (Fig. S1). To calculate resistance and resilience indices, we used an adapted version of the "res.comp" function of the R package "pointRes" (van der Maaten-Theunissen et al. 2015).

A linear least-squares regression was performed correlating the resistance index of the seven study sites with four climatic variables (mean, minimum and maximum air temperature, and precipitation sum) that were measured at daily resolution during the growing season. Confidence intervals at 95% and linear regressions were calculated with the software R version 3.2.3 (R Core Team 2016) and the packages "plyr" (Wickham 2011) and "Rmisc" (Hope 2013).

To test whether the growth depression observed in 2011 was mainly caused by the late frost and could not be explained by other climatic conditions in that year, we built partial least-squares (PLS) regression models with monthly climate parameters over the period 1950–2010. We compared model predictions for 2011 with observed growth, assuming that actual growth levels are lower than model predictions, because the PLS models may not capture short-term extreme events (like late spring frost). In the models, site chronologies were used as dependent and climate parameters as independent variables. In building site chronologies, ring-width series of individual trees were detrended by fitting a cubic smoothing spline with 50% frequency cutoff at 30 years. This detrending highlights climate-induced growth fluctuations in tree growth while removing longer term trends that might, for example, relate to forest management activities or tree ageing. Indices were then calculated by dividing the observed by the predicted values.

Climate predictors considered as independent variables in the models included, amongst others, monthly temperature (mean monthly minimum, mean, and mean monthly maximum) and precipitation variables for April of the previous to September of the current year. As the aforementioned daily temperature and precipitation series (cf. Section 'Climate data') were too short to build reliable models, we extracted monthly temperature and precipitation data for each site from a gridded climate surface (1 km × 1 km) of the German Weather Service (DWD). From these primary climate data, Potential Evapotranspiration (PET) and a Standardized Precipitation Evapotranspiration Index (SPEI) integrated over 6 months, representing shorter-term fluctuations of soil water content, were computed as additional parameters. For PET, we excluded the variables for December, January, and February, since PET often showed small or zero values in these months with low inter-annual variations. In total, 105 monthly climate parameters were used in our modeling exercise.

The PLS regression method effectively handles co-linearity problems in such a large climate data set by decomposing the matrix of independent variables into scores and loadings to construct principal components (PCs), which are then used in a regression in such a way that the predicted variation in the dependent variable (i.e., tree growth) is maximized with a minimum number of PCs (Garthwaite 1994). We built PLS regressions for individual sites using standardized variables and leave-one-out cross-validation, and selected those PCs that explained at least 5% in the tree-growth variation. For processing the tree-ring data, calculating PET and SPEI, and performing the PLS regressions, we used the R packages "dplR" (Bunn 2008), "SPEI" (Vicente-Serrano et al. 2010), and "pls" (Mevik and Wehrens 2007).

Results

Climate conditions

The climatic conditions during the growing season of 2011 differed from the previous years. While the mean temperature in 2011 was generally similar to the 10 previous years, July temperature was lower, and April temperature was higher (Fig. 2a). However, the absolute minimum temperature of May 2011 had a strong deviation from the 95% confidence interval of the 10 previous years. The May minimum temperature (−2.2 °C, minimum temperature registered at the day with the lowest temperature averaged across all climate stations) corresponded to the late spring frost event of May 2011 (Fig. 2c). Compared with the last ten years, it was 2.7 °C colder than the 5th percentile for

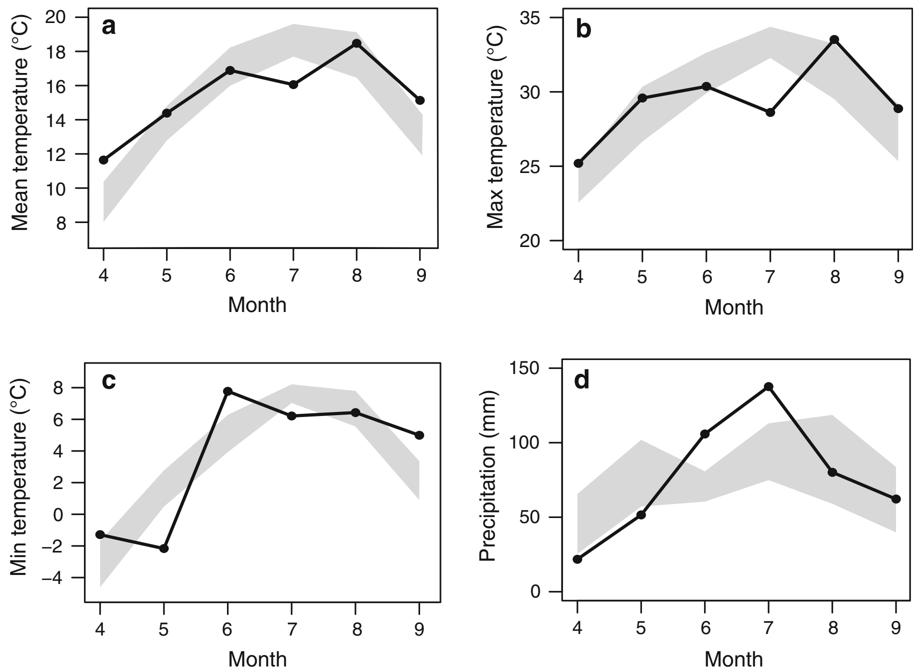

Fig. 2 Monthly climate data for 2011 compared to the period 2001–2010 (growing season: April to September). *Black lines* represent the year 2011 and the *shaded polygon* the 95% confidence intervals of the climate variable for the period 2001–2010 for **a** mean temperature, **b** absolute minimum temperature, **c** absolute maximum temperature, and **d** precipitation sum. All figures are based on averages of 20 weather stations in close vicinity to the study sites

that time of the season. Furthermore, maximum temperature in mid-summer in 2011 was relatively low (Fig. 2b) and the summer rather wet (Fig. 2d).

Growth responses

Overall, the 135 *F. sylvatica* trees sampled in Bavaria showed 46% less growth in 2011 in comparison with the previous 5 years (2006 to 2010) (resistance index = 0.54, SD = 0.23). The resistance indices were positively correlated with minimum temperature at the individual sites ($R^2 = 0.84$, $p = 0.002$; $n = 7$ sites comprising 135 trees; Fig. 3). The other climate variables (mean and maximum temperature, and precipitation) were not significantly correlated with the resistance index.

In May 2011, the lowest minimum temperature within a decade was registered for each site (Fig. 4a). The low temperature combined with an early start of the growing season (Fig. 4b) contributed to the observed late spring frost effect. Leaf onset typically started late April (on average on Julian day 113). In 2011, leaf onset of *F. sylvatica* was at day 106, 5 days earlier than the average of the previous 5 years.

Already 1 year after the late frost event, beech displayed similar growth levels as compared to the 5 years prior to the event (2006–2010), evidenced by an average resilience index of 0.96 (SD = 0.43). An equally high resilience index was found when relating the 2012–2013 to the 2006–2010 growth: 1.02 (SD = 0.40). Interestingly, resilience was highest for those sites strongest affected by the late frost event (Fig. 3). Trees from sites with the highest growth reduction in 2011 even showed higher growth after the frost event than before the frost event.

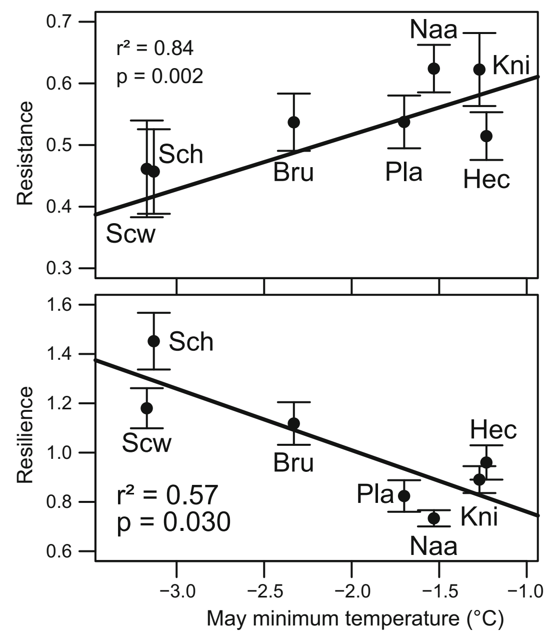

Fig. 3 Resistance (ratio between the growth during 2011 and the growth during the five previous years, from 2006 to 2010) and resilience (ratio between the average growth of the 2 years after and the 5 years before the frost event) of *F. sylvatica* for the seven forest reserves in Bavaria. Average and standard error of resistance index of 2011 plotted against the absolute minimum May temperature averaged across the three closest climate stations for each site, respectively. See Table 1 for site information including the abbreviations

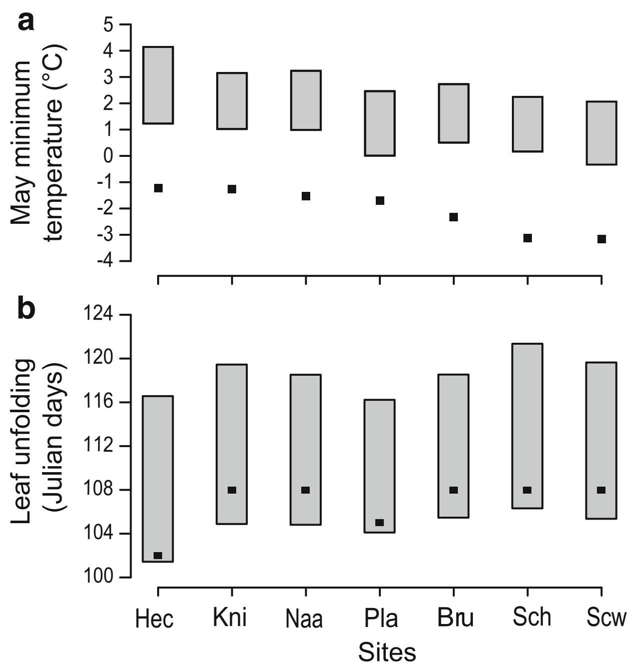

Fig. 4 **a** Absolute May minimum temperature and **b** day of leaf unfolding of *F. sylvatica* at the 7 forest reserves. *Black squares* represent the year 2011 and the *grey bar* the 95% confidence intervals of the climate variable for the period 2001–2010 for the minimum temperature and 2006–2010 for leaf unfolding

Finally, our PLS regression models, which explained between 67 and 75% of the variance in radial growth with only three to four PCs (Table S1), substantiate that late spring frost is the likeliest cause of the observed growth depression in 2011. Namely, model predictions consistently overestimated actual growth in 2011, with an average difference in growth index of 0.52 (SD = 0.19).

Discussion

The dendroecological observations for *F. sylvatica* at seven different sites in Bavaria showed a significant reduction in tree-ring width (46%) in 2011 when compared to the prior 5 years. The minimum temperature registered in May 2011 for the sites was significantly correlated with tree resistance in 2011. Furthermore, our partial least-squares regression (PLS) models based on monthly climate data (precipitation, temperature, potential evapotranspiration, and the Standardized Precipitation Evapotranspiration Index) consistently overestimated the actual growth in 2011 by 100%. We interpret this as evidence for the late frost being responsible for the observed growth reduction. In line with earlier findings (Day and Peace 1946; Stahle 1990; Augspurger 2009; Hufkens et al. 2012; Kreyling et al. 2012a; Menzel et al. 2015), the late frost occurred after an early leaf unfolding due to warm conditions in the early spring followed by an extremely low minimum temperature that damaged the freshly developed leaves. The observed growth reduction can be explained by a reduction of active leaf area, a shortening of the growing season, and requirements of additional resources for reparation of damaged leaves and the development of new leaves (Gu et al. 2008; Augspurger 2009; Kreyling et al. 2012a; Menzel et al. 2015). Moreover, the new-formed leaves after a late frost event can be considerably smaller and less efficient for photosynthesis than 'normal' leaves (Awaya et al. 2009).

Precipitation during the growing season, frequently shown to be a determinant factor for *F. sylvatica* growth (Čufar et al. 2008; Scharnweber et al. 2011; van der Maaten 2012), was not found to have limited growth in 2011 at the studied sites. It should be noted that in June and July 2011, precipitation was even higher than normal and that temperatures during summer were relatively cool, thereby excluding drought stress as a possible cause. Masting, on the other hand, might have aggravated the growth depression of beech in 2011. Namely, a relatively strong fruit production was observed in this late frost year throughout Bavaria (Bayerisches Staatsministerium für Ernährung and Landwirtschaft und Forsten 2011), with possible negative effects on growth (Drobyshev et al. 2010). Although masting is often reported to be triggered by high temperature and (or) drought in the preceding year (Piovesan and Adams 2001; Drobyshev et al. 2010; Mund et al. 2010), this was not the likely cause in 2010, which was a comparably cool and wet year. More recently, it has further been suggested that masting in *F. sylvatica* is triggered by high radiation totals in the previous growing season and the high N status (Müller-Haubold et al. 2015). Despite the co-occurrence of late frost and masting in 2011, we are confident that the observed growth depression can be largely attributed to late frost as growth was significantly lower in 2011 compared to 2006 and 2009, 2 years also known as strong regional masting years (Fig. S1; Bayerisches Staatsministerium für Ernährung and Landwirtschaft und Forsten 2011).

Resilience after the late frost growth depression was generally high with tree-ring width in the 2 years after the late frost event being, on average, as high as in the years before the event. Interestingly, the most affected trees showed the highest resilience with their growth after the frost event even surpassing their mean growth before the frost. Overcompensation after defoliation is a well-known phenomenon (e.g., Jaremo et al. 1996) which might explain this finding. More importantly, this strong recovery even in the most affected trees emphasizes the very high level and speed of resilience to growth reductions induced by late spring frost in *F. sylvatica*. Similarly, high resilience is also reported by other authors (Dittmar et al. 2006; Awaya et al.

2009). The high precipitation and mild temperatures during the end of the 2011 growing season have probably created optimal conditions for production and accumulation of photosynthetic compounds to invest in tree growth of the next season, explaining the high resilience in the year after the late frost. However, if the late frost events become more frequent, their impact on tree-ring width could become economically important. Dittmar et al. (2006) registered an unexpectedly strong decrease in ring growth in the second year of two subsequent years with the late frost events. Moreover, indirect effects could potentially lead to negative long-term responses, such as late spring frost damage, followed by summer drought creating opportunities for pathogen infestations which eventually result in tree mortality (Bendixsen et al. 2015). Finally, the late spring frost events may cause alterations in wood anatomy, such as formation of frost rings, i.e., distorted callous tissue damaged by late frost which might also be found in *F. sylvatica* (Bräuning et al. 2016), or white rings, i.e., pale-colored rings with low wood density following carbon reallocation to foliage production after defoliation (Hogg et al. 2002). As the late spring frost events result in defoliation in *F. sylvatica* (Menzel et al. 2015; Kreyling et al. 2012a), such wood anatomical reactions suggest future investigations in wood anatomical responses to the late spring frost damage in relation to carbon reallocation or potentially decreased structural stability of the wood. In this study, we did not focus on possible late frost-related signatures in the wood anatomy of beech. During the optical measurement of tree-ring width, no obvious peculiarities were observed for the year 2011.

Concerning temperature thresholds for damage of unfolded leaves in forest trees, the 2007 late spring frost across the southeastern United States caused widespread damage at air temperatures of around −7 °C (Gu et al. 2008). A threshold of −3 °C is suggested for damage of *F. sylvatica* leaves (Dittmar et al. 2006). In our study, most of the minimum temperature values registered were higher than −3 °C. However, minimum temperature was not recorded on site and could have been colder at leaf level in the studied forests than the air temperature at the LFL climate stations. The weather stations are usually located at some distance to the forest stands, in flat and open terrain, which creates a deviation between the forest microclimate and the weather station conditions (Kollas et al. 2014b). More importantly, however, we expect that relative differences among the sites are correctly captured. Here, we tested only linear relationships between frost resistance and the absolute minimum temperatures (Fig. 3). The true underlying pattern, however, will not be linear as crossing zero resistance is impossible and also projections beyond one are not meaningful. A more probable sigmoid function has not been tested given the low number of sites. The linear representation, though, should clearly not be extrapolated but might reflect the quasi-linear part of an underlying sigmoid function.

Conclusion

In a changing climate, the late frost damage might occur more frequently due to earlier leaf unfolding. Our data imply strong reductions in tree-ring width following a spring frost event (46% growth reduction across our sites in 2011), i.e., a low resistance of *F. sylvatica* to late frost. The reduction of tree-ring width increased with decreasing minimum temperature during the late frost event. Frost resilience of growth in *F. sylvatica* was very high, as growth one and two years after the spring frost event returned to pre-frost growth rates even in the most severely affected sites. Nonetheless, as increased frequency of the late frost damage with climate change is possible, the question whether resilience remains high after repeated late frost events needs further investigation.

Author contribution statement Writing the paper: AP with all other authors contributing. Field work: AP, JK, TS, and EM. Laboratory work: AP, EM, and MMT. Analyzing the data: AP, EM, and MMT. Coordinating the research project: JK.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

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