Delay of growth release after a windthrow event and climate response in a light-demanding species (European larch *Larix decidua* Mill.)

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Received: 15 February 2021 / Accepted: 15 September 2021 / Published online: 1 October 2021
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Abstract

Key message Larch trees respond to stand opening with an approximately 4-year delay of growth, and low precipitation in July limits radial growth after a windthrow event.

Abstract Precise cross-dating of disturbance events is crucial to understanding the functioning of forest stands, and may help explain ongoing ecological processes in a forest. Tree rings are very often used to reconstruct the history of disturbances and to study the response of trees to climatic factors. This study analyzed how quickly European larch can benefit from an abrupt change after catastrophic windthrow events and the extent of trees' sensitivity to climate. The study is based on cores from 83 larch trees collected in a post-disturbance 100 ha plot established after a catastrophic windstorm in 2004 in the Slovakian High Tatras. Growth release was calculated from the percentage of growth change (PGC) measured in tree rings. The time lag between the disturbance event and release was related to tree diameter at breast height, tree age, and tree's previous growth. The time lag between the year of the event and the year of growth reaction was 4.6 years on average (median 4 years) in a multi-aged group of trees. The climate analyses employed residual chronology. The new environmental conditions in the post-disturbance area have altered the trees' growth reaction to climate; in particular, they show sensitivity to water deficit in July.

Keywords Climate · Dendroecology · Disturbances · Growth release · *Larix decidua* · Tree rings

Introduction

An increase of annual temperature and changes in the distribution of precipitation due to climate change have recently been recorded across the world (Carrer and Urbinati 2006; Esper et al. 2020; IPCC 2021). In addition, noted is a rise in the number of extreme events such as windthrows, persistent drought, or spring frosts. A better understanding of those changes is needed for assessment of forest diversity, vegetation dynamics, and future forest productivity (Büntgen et al. 2007; Mihai et al. 2021; Larysch et al. 2021).

Natural disturbances are an important element of forest ecosystems. They significantly influence the dynamics of forest stands. Depending on the type, severity, spatial scale, and interval of disturbance events, they shape the structure of a forest stand. A knowledge of precisely cross-dated disturbance events is crucial to understating the functioning of a forest stands, and may help explain ongoing ecological processes in forests (Altman et al. 2013; Svoboda et al. 2011; Vaganov et al. 2006). Tree rings are very often used to reconstruct the history of disturbance events. An ever-increasing number of research papers use various dendrochronological

Communicated by DeMicco.

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techniques to determine the moment of a past disturbance (Svoboda et al. 2011; Trotsiuk et al. 2018; Zielonka et al. 2010; Zielonka and Malcher 2009).

One type of reconstructions is based on cross-dating direct injuries left by the disturbance factor. Dating of scars allows researchers to determine the exact year of a disturbance, because scars form as a result of direct damage to the cambium (Chen et al. 2020; Niklasson et al. 2002; Stambaugh et al. 2011). Another kind of study examines abrupt increases in radial growth following a disturbance. This method is based on the assumption that trees surviving a disturbance respond with the formation of wider rings. Such a reaction is a result of increased resource availability due to decrease competition. The year of the disturbance can be detected in a tree-ring series when an increase of growth due to a disturbance exceeds a given threshold (Fraver and White 2005; Lorimer and Frelich 1989; Nowacki and Abrams 1997; Payette et al. 1990; Stambaugh et al. 2011). Many techniques are used to identify and describe a growth release (Altman et al. 2016; Rubino and McCarthy 2004; Trotsiuk et al. 2018). The following methods are used most often: the radial growth averaging criteria developed by Nowacki and Abrams (1997), the boundary-line method (Black and Abrams, 2003), the absolute-increase method (Fraver and White, 2005), and a combination of radial growth averaging and boundary-line techniques (Splechna et al., 2005). Most methodological papers focus on setting radial growth thresholds to ascertain whether we are really dealing with a release caused by a disturbance (Altman et al. 2016; Rubino and McCarthy 2004; Trotsiuk et al. 2018). The year of occurrence of a disturbance is determined as the first year before the transition from narrow rings in an undisturbed stand and the first wide ring in the stand after a disturbance. However, it may be wrong to assume that a disturbance occurred 1 year before the formation of the first of a series of wide rings within a release. Growth release may be shifted some years after the year of the event. This shift does not depend on the method of calculating a release, but rather seems to be an effect of a tree's lagged physiological reaction and recovery after a disturbance (Chalupová et al. 2020).

On the other hand, case studies describing stand histories concentrate mostly on shade-tolerant species in a situation in which sub-canopy trees are released from suppression by former canopy trees, because light-demanding species would not endure the period of suppression before the disturbance (Fraver and White 2005; Pyttel et al. 2019). In the case of shade-tolerant species, boundary-line release criteria allow us to identify the growth reactions based on the previous growth (PG) dynamic (Black and Abrams 2003, 2004). This method is based on the fact that suppressed, slow-growing trees can react more intensely to an abrupt improvement of habitat conditions (Lorimer and Frelich 1989). Thus, the method can detect whether a tree is strongly suppressed

or not. Still, this procedure does not account for a possible physiological time lag in the trees' growth reaction. In this paper, we analyze growth releases after windthrows in the European temperate montane zone.

The study was conducted in the Slovakian High Tatras. On 19 November 2004, a swathe of forest was flattened by a catastrophic windstorm, which destroyed over 12,000 ha of the stand. As much as 2,500,000 m³ of timber was uprooted or broken. Prior to the windstorm, the stand composed of spruce (ca. 80%), larch (ca. 20%), and single pines. Mortality was highest among the spruces. Most of the larches survived due to having small leafless crowns and a stronger root system (Holeksa et al. 2016; Zielonka and Malcher 2009; Zielonka et al. 2010). Currently, larch is the dominant tree species in the sparse-canopy stand. Local people believe that the 2004 event was unprecedented, but similar events from the past have been documented. The following "catastrophic windstorms" are mentioned in historical sources: 18 November 1915, 287,000 m³ timber volume (Koreň 1994; Vadas 1916); 1 May 1919, 52,000 m³; 1–3 September 1941, ca. 60% (420,000 m³); 23 October 1971, 94,000 m³; and 1981, 295,000 m³ (Vadas 1916). These dates were partly confirmed by dendroecological reconstructions. Tree rings analyses allowed us to detect strong and synchronized growth releases after 1941, in 1915–1919 and at the end of the 1860s (Zielonka and Malcher 2009; Zielonka et al. 2010). A disturbance regime based on the repeated occurrence of windthrows seems to be responsible for the coexistence of spruce and larch within the stand.

In this paper, we ask how light-demanding European larch responds to a very severe disturbance event. The aim of this study was to analyze growth reactions in larch trees 15 years after a severe windthrow in a mixed spruce–larch stand. How quickly can larch benefit from the abrupt change of environment from a closed-canopy forest to an open stand in a post-disturbance plot? How do the biometric characteristics of a tree influence the potential time lag between a disturbance event and growth release? Our study was designed to pinpoint the potential bias inherent in detection of disturbance events based on releases found in tree-ring series.

In analyzing the changes in ring width caused by a disturbance, we cannot neglect the influence of climatic factors, because the formation of tree rings also strongly depends on climate (Fritts 1976; Schweingruber 1996). Trees may respond differently to seasonally distributed temperatures and precipitation in different geographical areas. A substantial number of papers deal with the growth–climate relationship in European larch (Carrer and Urbinati 2006; Büntgen et al. 2007; Koprowski 2012; Oberhuber et al. 2020; Oleksyn and Fritts 1991; Saulnier et al. 2019), but such studies rarely relate the tree response to both climate and disturbances. Widening the focus might prove especially important in large post-disturbance areas, where elimination

of the canopy may lead to substantial changes in insolation, temperature amplitude, water accessibility, anemometric factors, humidity, etc.; it is highly probable that the response of trees to climatic elements will be altered. We might also expect such changes to overlap with the biosocial interactions of survival trees (decrease of competition). Hence, other questions should be addressed. Does the occurrence of a disturbance change the growth response to climatic factors? Does the sensitivity of larch to climatic factors change over time—before and after the occurrence of a disturbance?

Materials and methods

Study area and climate

The study area is in the Slovakian Tatra (the Western Carpathians). Cores were collected in a 100 ha plot established after the windstorm for multidisciplinary studies, the so-called EX-SITE (Fleischer 2008). The soils consist of rocky podzolic cambisols. The plot is on a gentle (15% grade) south-facing slope. Plot elevation ranges from 1000 to 1300 m a.s.l. The ground vegetation composed mostly of *Vaccinium myrtillus*, *V. vitis-idaea*, *Calamagrostis villosa*, and *Homogyne alpina*.

Climatic data were collected in the meteorological station in Tatranská Lomnica (49°9′ N; 20°17′ E, 827 m a.s.l.) located ca. 10 km from the study site. For the period 1926–2019, mean annual precipitation was 805 mm and mean annual temperature was 5.57 °C (January minimum – 4.8 °C, July maximum 15.4 °C). Figure 1 presents climate diagrams of the 15-year periods before the event (1990–2004) and after it (2005–2019). For all months except January and February, mean annual temperature in the second period was 1.0 °C higher than in the first one. Data from the meteorological station in Zakopane also shows an increase of mean annual temperature in respective periods, though a weaker one (0.68 °C). Total annual precipitation after 2004 was only slightly higher than before 2004 (by 18.8 mm/year), but the seasonal distribution changed more markedly (Fig. 1).

Tree-ring data

The locations of the larch trees selected for study were spaced evenly over the whole plot. They were observed to be healthy, without visible stem injury or branch loss. Tree sampling followed the standard dendrochronological protocol (Schweingruber 1996). Two cores were extracted from each tree perpendicularly at ca. 1.3 m height above the ground. The cores were dried, sanded and scanned (2400 DPI resolution). Ring width was measured with WinDendro software (<https://www.regentstruments.com/assets/>

Tatranská Lomnica 827 m a.s.l.
MAT=5.6 °C 1990–2004 MAP=802.0 mm
MAT=6.6 °C 2005–2019 MAP=820.8 mm

Fig. 1 Climate diagrams for the meteorological station in Tatranská Lomnica for 1990–2004 (before the windthrow) and 2005–2019 (after the windthrow); monthly mean temperatures (lines) and total monthly precipitation (bars); MAT mean annual temperatures [°C], MAP mean annual precipitation [mm]

windendro_about.html). During these measurements, we verified the sequences of pointer years (Schweingruber et al. 1990; Yamaguchi 1991). The validity of cross-dating was checked with COFECHA (Grissino-Mayer 2001; Holmes 1983). Time series that did not correlate with others were excluded due to possible errors in cross-dating. The tree-ring width series were averaged between the two cores of each tree. In total, we used 83 cross-dated ring width series for further analyses. In 2019, 15 years after the disturbance, 41 trees were cored. To increase the number of samples, we used 42 cores extracted just after the disturbance in 2005. All series were also used to study the growth response to earlier events in the nineteenth and twentieth centuries.

Growth release

We analyzed the growth response after the disturbance in 2004, as the exact date of stand opening was known, and in 10 years, after the most probable disturbance episodes in 1941, 1915, and 1869, known from historical data and dendroecological reconstructions (Koreň 1994; Zielonka and Malcher 2009; Vadas 1916). For detection of release, we

applied the most commonly used method, based on calculation of percent growth change (PGC) (Nowacki and Abrams 1997). For our purposes, PGC was calculated for each ring according to the formula:

$$\text{PGC} = (M_2 - M_1) / M_1 \times 100, \quad (1)$$

where PGC is the percent growth change for a single year, M_1 is the preceding 10-year mean growth, and M_2 the subsequent 10-year mean growth. Since in this procedure, the last 10 years from the time series must be excluded, for the 2004 event, we additionally used shorter (5-year) windows for M_1 and M_2 (Nowacki and Abrams 1997; Black and Abrams 2003). This allowed us to extend our calculations of releases to 2014.

In most cases, a PGC threshold of 25% is regarded as a disturbance (Lorimer and Frelich 1989; Nowacki and Abrams 1997, but we decided to set a PGC threshold of 50% to avoid “false releases”. Values exceeding 100% were treated as strong releases. If a local maximum of PGC exceeded 50% during the 10-year period after the disturbance event, we treated such a signal as a response to a previous event and then calculated the delay of the response. We used regression to relate the time lag to tree diameter, tree age, and previous growth (mean of the 10 ring widths preceding the year of the disturbance event). Tree age and diameter at the moment of disturbance was calculated from the ring width series. The intensity of the release (value of PGC peak) was calculated in the same way.

Climate analysis

As releases were calculated from raw tree-ring series, for the climate study, we used ARSTAN software for standardization. A negative exponential curve or a linear regression line or a horizontal line through the mean ring widths was fitted to all tree-ring series and then the measurement values were divided by the values of the fitted lines (Holmes 1994). Autoregressive modeling was performed for the indexed series to remove autocorrelation and to enhance the common signal. The residual chronology was used for calculating the growth response to climatic conditions in Tatranská Lomnica (mean monthly air temperature and monthly sums of precipitation). Analyses of the correlation and response function between tree growth and climate values employed DendroClim2002 (Biondi and Waikul 2004). Bootstrapping process was applied to assess the statistical significance of the correlations. In the program, we analyzed changes in the relationship between tree growth and the same climatic factors in period 1926–2019 over 30-year intervals. The correlations were calculated for moving intervals shifted progressively by 1 year in the analyzed period. The climate data covered periods from October of the previous year to

September of the current year. This procedure aimed to find all changes in growth response of trees to climate in the whole analyzed period (1926–2019). Mean monthly temperature and sums of monthly precipitation were calculated for periods 1990–2004 (before the windthrow) and 2005–2019 (after the windthrow). Pearson’s correlations were used to determine the climate–growth relationships in these two periods. In addition, the climate data from the meteorological station in Zakopane (49°17′ N; 19°57′ E, 846 m a.s.l.) were compared with data from Tatranská Lomnica, an undisturbed site located in the same mountain range. Zakopane is located on the other side of the Tatra range at approximately the same elevation.

Results

Chronology characteristics

The chronology contained 239 years in the period of 1781–2019 (Fig. 2). From 1815, the chronology was based on at least 11 trees. Mean tree-ring width was 1.34 mm (± 0.85 SD) and the mean index value was 1.0 (± 0.3 SD). Mean sensitivity to tree-ring widths was 0.287, and for the index value it was 0.4, values suitable for dendroclimatic research. The mean value of the first-order autocorrelation was 0.77 computed for tree-ring widths and 0.0 for index value. The expressed population signal (EPS) for 1926–2019 was 0.96, and the mean inter-series correlation value (Rbar) was 0.412.

Releases

Over the 2004–2009 period, 18% of trees responded with growth release; most of the trees showed a reaction in 2007 (PGC calculated using 10-year windows). Using shorter (5-year) intervals for PGC calculation made it possible to extend the period of observation to 2014. During this time (2004–2014), 78% of trees responded with growth release of over 50% of PGC, and 34% with reactions over 100% PGC. There was no immediate growth reaction. No release indicated the correct year of disturbance in 2004. The highest number of trees (29%) showed peak PGC in 2007, 3 years

Fig. 2 Chronologies based on raw measurements and indexed series

Fig. 3 Percentage of trees showing growth reaction after the 2004 windthrow. PGC values over 50% and 100% indicated. Calculation of PGC based on 5-year intervals of preceding and subsequent mean growth

after the event. Single trees continued the response to the following years until 2014 (Fig. 3).

The time lag between the year of event (2004) and the year of growth reaction was 4.9 years on average (median 3.5 years). This lag for individual trees extended to even 10 years (Table 1).

In linear regression the time lag between 2004 and the growth reaction (as the dependent variable) was not significantly related to diameter ($R^2=0.0442$) or tree age ($R^2=0.0159$) (Fig. 1a, b in Supplementary Material). The time lag significantly depended on previous growth (PG) [Fig. 1c (Supplementary Material) and Table 2]. Trees having smaller average previous ring width responded later than those with larger average width of previous rings [Fig. 1c (Supplementary Material)].

The intensity of the growth reaction, measured as the PGC peaks value (dependent variable), depended significantly on tree diameter ($R^2=0.2328$) (Table 2). Higher diameter trees responded with lower PGC, while thinner ones reacted with higher PGC [Fig. 2a (Supplementary

Material)]. A similar inverse relationship was found for, age and previous growth, but these relationships were not significant for the 2004 event [Fig. 2b, c (Supplementary Material) and Table 2].

In the period prior to 2004, episodes of synchronized releases overlap with historically known windthrows (Fig. 4). The oldest one, reflected in a higher percentages of trees showing release, began in 1869. The next two release episodes began after 1915 and 1941. Low-intensity releases were observed in the 1990s, but as we had no information about intensive wind damage in the area, we excluded them from further analyses. In the 10-year period after 1869, 67% of the trees responded with growth reactions and a third of the trees exhibited a reaction over 100% PGC. After the windthrow in 1915, 43% of the trees responded with growth reactions and 29% had reactions higher than 100% PGC. After 1941, 38% of the trees reacted with growth release and 14% had PGC greater than 100%.

The time lag between year of event and year of growth reaction calculated for events in 1869, 1915, and 1941 (taken together) shows a slightly negative, but significant relation to tree diameter ($R^2=0.072$) [Fig. 3a (Supplementary Material)] and tree age ($R^2=0.0717$) [Fig. 3b (Supplementary Material) and Table 2]. Older and thicker trees seem to have reacted faster than younger and thinner ones. The time lag was not related to previous growth ($R^2=0.0046$) (Table 2). For those dates, the time lag between a disturbance year and release varied from 3.4 to 5.5 years on average (median 2–5.5) (Table 1).

The intensity of release (PGC of local maximum) was negatively correlated with tree diameter ($R^2=0.1423$) [Fig. 4a (Supplementary Material)] and previous growth ($R^2=0.1485$) [Fig. 4b (Supplementary Material) and Table 2]. The reactions of larger trees and those with greater previous growth were smaller than those of young and suppressed trees.

Climate

Over the whole analyzed period (1926–2019), the trees responded positively to high February, March, May and June temperature, but the correlations were significant only

Table 1 Time lag between the calendar year of disturbance event and occurrence of release, calculated for the 2004 windthrow event and for probable events in 1941, 1915 and 1869

Year	Mean $\pm$ SD	Median
2004	49. $\pm$ 2.8	3.5
1941	3.4 $\pm$ 2.6	2
1915	4.7 $\pm$ 1.5	4
1869	5.5 $\pm$ 2.7	5.5
All	4.6 $\pm$ 2.5	4

Table 2 Correlation coefficients for the relationship between time lag of growth release and tree DBH, tree age, and previous growth (PG) for the windthrow in 2004, and for the disturbance events of 1941, 1915, and 1869 taken together

Year		DBH	AGE	PG
2004	Time lag	0.21	0.13	−0.47
	Max PGC	−0.48	−0.17	−0.21
1941	Time lag	−0.27	−0.27	−0.07
	Max PGC	−0.38	−0.18	−0.39

Significant values with $p < 0.01$ are in bold

Bold values are significant

Fig. 4 Distribution of release signals in trees. PGC calculations employed 10-year intervals for preceding and subsequent mean growth. These PGC values were used to determine the disturbance pattern after the events in 1869, 1915, and 1941

Fig. 5 Bootstrapped correlation coefficients (bars) and response function coefficients (lines) between residual chronology and mean monthly air temperature and total monthly precipitation for 1926–2019 period. Grey bars and markers denote significance $p \leq 0.05$

for March and June. Temperature of the previous autumn as well as the second half of the current vegetation season (July, August, and September) seems to have had a negative influence on growth, but none of those correlations was significant (Fig. 5).

Larch responded positively to precipitation in the November of the previous year and negatively to the current

September, both of those correlations being significant. The growth response to precipitation in the other months was highly variable and not significant: slightly negative in January, March, and May, and weakly positive in July (Fig. 5).

Time-dependent analysis showed that the response of trees to climate has varied during the last hundred years. The most striking change in the reaction to temperature is observed during the last ca. 15 years, during which the positive influence of May and June temperature disappears and a significantly negative influence of July temperature becomes evident (Fig. 6). This stands in contrast to 1965–1987, when trees positively responded to July temperature. The 1970s and 1980s show a negative influence of January temperature. During recent years, the trees seemed to have reacted positively to February temperature (Fig. 6). It should be noted that the mentioned decades are considered here as ends of 30-year windows. Precipitation in the previous November had a positive influence on growth for the studied period as a whole (Fig. 5), but this pattern does not hold for the intervals that end before 1987 (Fig. 7). The strongest negative influence of September precipitation ended before 2000. Over the last few years, July rainfall has had a positive influence on growth (Fig. 7).

Due to our use of 30-year windows for the time-dependent series, the correlation coefficients for the years in 1990–2019 do not clearly separate the growth reactions to climate before and after the 2004 windthrow. The differences in growth reactions to climate calculated for 1990–2004 (before the windthrow) and 2005–2019 (after the windthrow) are presented in Fig. 8. Since 15-year period since the windthrow is too short for response function analyses, we used Pearson's correlations. The only significant positive correlation between growth and climate appearing after the windthrow is for July precipitation ($r = 0.52$, $N = 15$, $p = 0.045$). In the period before the windthrow, this correlation was slightly

Fig. 6 Moving-interval correlation computed using DendroClim2002 for residual chronology and mean monthly air temperature. The 30-year window was progressively shifted through the total available years from 1926–1955 to 1990–2019. The window starts with the October of the previous year and ends with the September of the current year

Fig. 7 Moving-interval correlation computed using DendroClim2002 for residual chronology and total monthly precipitation. The 30-year window was progressively shifted through the total available years from 1926–1955 to 1990–2019. The window starts with the October of the previous year and ends with the September of the current year

negative. Changes in the correlation values can be seen in Fig. 8 but none of them is statistically significant.

Discussion

Growth release

Growth releases are commonly used for reconstruction of disturbances event, and very often are the only source of information on the history of forest disturbances. Most of those studies focus on shade-tolerant species, because suppressed trees can react abruptly and immediately to a forest-opening event (Hanson and Lorimer 2007; Kuosmanen et al. 2020). There are far fewer dendroecological reconstructions based on the growth reactions of light-demanding tree species, because such trees are not able to

survive periods of suppression. Moreover, most methodological questions about growth release involve setting the criteria for establishing threshold values of growth increase, aimed at separating real disturbance-induced releases from “false negative” and “false positive” releases (Trotsiuk et al. 2018). Less attention is usually given to the temporal precision of disturbance dating, because such calibration requires long-term experiments. However, it has been observed that a growth response can be shifted away from the actual year of the event (Chalupová et al. 2020). The temporal precision of disturbance dating is critical to the reliability of forest history reconstructions (Altman 2020), but it is rarely addressed.

The windstorm on 19 November 2004 is very well documented. In our sampling plot, the EX-SITE, most of the trees were knocked down, broken and uprooted. The only surviving trees were the larches. After the storm

Fig. 8 Correlation between residual chronology and mean monthly air temperature and total monthly precipitation for 1990–2004 (before the windthrow) and 2005–2019 (after the windthrow). Grey shading denotes significance ($p \leq 0.05$)

in the winter of 2004/2005, the site was cleared. The logs were cut and salvaged. The heavily damaged trees were removed, including individual spruces because of the threat of a bark beetle (*Ips typographus*) outbreak (Fleischer et al. 2016, 2017). The stand was transformed from closed-canopy forest with dominant spruce to an open stand composed of sparsely distributed single larch trees; whole trees, including crowns and stems, were now newly exposed to sunlight. We expected that this light-demanding species would immediately benefit from such conditions and that this would be reflected in increased radial growth already in 2005. According to Nowacki and Abrams (1997), a local PGC peak indicates a disturbance year, which will be followed by an increase in the width of the next tree ring. None of the trees we studied responded with increase growth in 2005; in the greater number of trees the response came 3 years later, and single trees kept responding over the following 10 years. A similar pattern of delayed response was observed for the events of 1869, 1915, and 1941. Judging from our historical and recent data, on average the release of growth was shifted away from the actual disturbance year by about 4–5 (Table 1). Such time lags have been observed in other species as well (Altman et al. 2013; Pyttel et al. 2019; Rentch et al. 2002; Samonil et al. 2009). Our results generally seem to show that thinner and younger trees need more years to respond with release after a disturbance, up to even 10 years, while larger and older trees may react in 2–3 years, but this trend did not hold 2004 event. The reason may be that tree rings examined to study the 2004 event represented older, thicker classes, unlike the earlier rings of the same trees used to assess the response to previous disturbances. In addition, those relationships were statistically significant but not strongly so, and can be treated only as a general

trend. On the other hand, the time lag in response significantly depended on previous growth: more suppressed trees reacted later than those with wider rings. This correlation was stronger for the 2004 windthrow.

Larches growing in close-canopy forests, especially those mixed with spruce, tend to produce small crowns. The suppression of their previous growth was related to limited access to sunlight. As a consequence, suppressed trees were more likely to have smaller crowns which could not suddenly spread out to take advantage of easy access to light. The first reaction to opening is investment in production of foliage and branches rather than in radial growth of the stem. This period may last 7 years or more before a suppressed tree responds with stem growth release. It is worth noting that the dynamics of previous growth are not necessarily related to tree diameter. A similar mechanism may explain the late response of the oldest generation of trees after 2004. Although they dominated in the stand, their previous growth was limited due to aging.

We observe a stronger reaction to disturbance (higher release) in thinner and suppressed trees, supporting well-known observations (Lorimer and Frelich 1989; Nowacki and Abrams 1997). The percent growth change values strongly depended on previous growth. The highest PGC values are observed only in the most suppressed trees, because PGC expresses the growth increase over previous growth. Trees that have formed wide rings before a disturbance (most likely the dominant trees) cannot increase ring widths very much: they have already occupied a favorable place in the canopy and cannot benefit from canopy opening as much as suppressed ones can (Black and Abrams 2003, 2004; Lorimer and Frelich 1989; Nowacki and Abrams 1997).

The trees we chose for sampling were free of visible damage of the crown and stem, but damage such as windstorm-caused injury of the root system cannot be ruled out. A heavy mechanical impact on the stem may cause unseen damage to the root system, which can be reflected in a decreased radial growth (Gärtner 2007).

Climate

Our dendroclimatic analysis seems to show a change in reaction of larch to climatic factors after the 2004 windthrow. In the period before it, May and June temperature positively influenced radial growth, but this relationship became weaker after the windthrow. In subsequent years, higher February and March temperature seems to have started the vegetation season earlier.

After the windthrow, high April temperature negatively influenced radial growth. Most likely this can be related to the significant decrease of precipitation in 2005–2019 during that month (Fig. 1, Fig. 8), when foliage develops and flowering occurs (Bednářová et al. 2013). Similarly, after the windthrow the positive effect of June temperature on growth decreased, while for July temperature it changed from positive to negative (Fig. 7). More distinct differences in climate–growth relationships are seen between the 15-year periods before and after 2004 (Fig. 6); however, these analyses are based on very short time series and must be considered with caution.

These climate–growth relationships can be interpreted in two ways. First, after the windthrow, the stand became fully open, and surviving scattered trees received direct access to sunlight not only on the crowns but also along stems. This may have decreased their requirement for warmth. On the other hand, the lower sensitivity to summer temperature might be an effect of the previously mentioned putative mechanical damage to surviving, impeding regular growth. The negative reaction to July temperature that began to appear after the windthrow, as well as the positive influence of precipitation observed over the last few years, speak in favor of the first explanation.

In interpreting time-dependent growth–climate analyses, however, we must bear in mind that we are dealing with 30-year intervals, and briefly, lasting significant correlation might be due to temporary climate variability. In July, the trees apparently suffered from high temperature and water deficit. The observed change in the response to climatic factors might be a result of environmental stress after the windthrow. Increased mean annual temperature was observed at the other meteorological station in the Tatras in Zakopane, used as an example of an undisturbed site, but this rise was not so strong. This may suggest that the post-disturbance opening after 2004 may have additionally boosted the general increase of temperature locally. Indeed,

the 2004 windthrow most likely influenced the meteorological observation in Tatranská Lomnica as the station is located in the vicinity of 12,000 ha destroyed forest. In the Alps at the higher elevations (1600–2200 m a.s.l.), larch growth positively depends on the June and July temperatures (Büntgen et al. 2007; Carrer and Urbinati 2006; Saulnier et al. 2019), perhaps attributable to the cooler climate of that zone. In our study, the positive influence of high July temperature ends in the 1980s. After the 2004 windstorm, the opposite trend appears, whereby a warm July negatively affects the radial growth of larch. This is most likely linked to water deficit, as confirmed by high and significant correlations with July precipitation in the last period. A similar pattern was reported from lower elevations of the Alps (1200–1450 m a.s.l.), where mid-summer drought is a limiting factor for larch growth (Saulnier et al. 2019). In the Alps, high February and March temperatures have been found to influence larch growth negatively (Büntgen et al. 2007; Carrer and Urbinati 2006; Saulnier et al. 2019), contrary to our results. This may be explained by the earlier occurrence of the vegetation season in the Tatras, so that trees benefit from the higher temperatures at winter's end. In our plot, we observed a positive reaction to high precipitation in July only in the last period after 2004. There the tree response to climate after the windthrow shows the same effect as lowering of elevation in the Alps. In lowland Poland, the most important factor limiting larch growth is precipitation in May–July, especially June (Koprowski 2012; Oleksyn and Fritts 1991). In our opinion, the altered growth reaction of trees in the post-disturbance period can be related directly to the windthrow event of 2004, through not only via decrease competition with surviving trees but also via the change in local climate due to post-disturbance opening (IPCC 2014, 2018, 2021). In other regions, increased temperature was not accompanied by increased tree growth (Oberhuber et al. 2020).

Conclusions

The European larch responds to severe windthrows with growth release, but the releases occur several years after the event (ca. 4–5 years). For thinner, younger or suppressed trees up to 10 years. Larger, older trees and those with better average growth before the event may react much faster. This means that in a mixed stand with spruce, larch trees that have access to light in the canopy and relatively good radial growth may still benefit from an abrupt opening and respond with a relatively rapid growth release.

Intense, large-scale disturbances like the 2004 windthrow are responsible for at least strengthening the general trend of climate change, and may influence the trees' sensitivity to climatic factors. The main change after the windthrow can

be related to the water deficit in open canopy stand in the summertime. This is confirmed by significant positive correlations between growth and July precipitation.

The growth reaction of surviving larches after a windthrow can be compared to a similar reaction correlated with a shift towards a lower elevation in the mountains or with a shift toward more continental climate, where mid-summer high temperatures and a water deficit are factors limiting of growth.

Author contribution statement KI, EM, and TZ designed the research and methodology. KI and PF conducted fieldwork. KI was responsible for preparation of samples and for tree-ring measurements. KI and EM conducted data analysis. KI, EM, and TZ led the writing of the manuscript. All the authors gave final approval of the manuscript.

Supplementary Information The online version contains supplementary material available at <https://doi.org/10.1007/s00468-021-02218-4>.

Acknowledgements We are grateful to two anonymous reviewers who suggested many improvements and ideas presented in the final version of this paper. Input from Michael Jacobs who line-edited the final text for submission.

Funding The study was supported by NCN Grant no. N N309 71124 and Ministry of Science and Higher Education of the Republic of Poland statutory project no. BN.610–350/PBU/2020; BSM-204/G/2019 of the Institute of Biology, Pedagogical University in Kraków, and statutory activities SUB/040011-D019/2020 of the Department of Forest Biodiversity, University of Agriculture in Krakow.

Declarations

Conflict of interest The authors declare no conflict of interests.

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