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Three-dimensional analysis of the anatomical growth response of European conifers to mechanical disturbance

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Summary Studies on tree reaction after wounding were so far based on artificial wounding or chemical treatment. For the first time, type, spread and intensity of anatomical responses were analyzed and quantified in naturally disturbed *Larix decidua* Mill., *Picea abies* (L.) Karst. and *Abies alba* Mill. trees. The consequences of rockfall impacts on increment growth were assessed at the height of the wounds, as well as above and below the injuries. A total of 16 trees were selected on rockfall slopes, and growth responses following 54 wounding events were analyzed on 820 cross-sections. Anatomical analysis focused on the occurrence of tangential rows of traumatic resin ducts (TRD) and on the formation of reaction wood. Following mechanical disturbance, TRD production was observed in 100% of *L. decidua* and *P. abies* wounds. The radial extension of TRD was largest at wound height, and they occurred more commonly above, rather than below, the wounds. For all species, an intra-annual radial shift of TRD was observed with increasing axial distance from wounds. Reaction wood was formed in 87.5% of *A. alba* following wounding, but such cases occurred only in 7.7% of *L. decidua*. The results demonstrate that anatomical growth responses following natural mechanical disturbance differ significantly from the reactions induced by artificial stimuli or by decapitation. While the types of reactions remain comparable between the species, their intensity, spread and persistence disagree considerably. We also illustrate that the external appearance of wounds does not reflect an internal response intensity. This study reveals that disturbance induced under natural conditions triggers more intense and more widespread anatomical responses than that induced under artificial stimuli, and that experimental laboratory tests considerably underestimate tree response.

Keywords: Abies alba, Larix decidua, Picea abies, reaction wood rockfall, tangential rows of traumatic resin ducts, wood anatomy.

Introduction

In Alpine forest ecosystems, intrinsic factors, such as climatic conditions, concurrence and age structure, constantly influence tree growth. A large variety of disturbing agents and their effects on tree growth and wood anatomy have been investigated in detail. Viveros-Viverosa et al. (2009) studied the effect of altitude on trees. The influence of soil property on tree growth was studied by Oberhuber et al. (1997), and the influence of temperature and precipitation was studied by Wimmer and Grabner (1997, 2000) and Esper et al. (2008). Rigling et al. (2003) analyzed the benefits of irrigation, whereas the changes in radial growth following water-level fluctuations were investigated by Polacek et al. (2006). Oberhuber et al. (1998), Rigling et al. (2002) and Weber et al. (2007) investigated the impact of drought. Tree disturbance due to pest infestation is yet another field of dendroecology that has received attention over the last few years (Weber 1997, Baier et al. 2002). The effect of soil erosion on tree growth assessed by McAuliffe et al. (2006), Hitz et al. (2008) and Spatz and Bruechert (2000) described the impact of wind factors.

In Alpine environments, another major disturbance influencing tree growth is mechanical stress. Macroscopic tree responses to mechanical impact are wounding, tilting and breaking of the stem (Schweingruber 1996). Macroscopic tree response following mechanical disturbance was analyzed in the past using resistance tests – i.e., artificial stem bending, (Moore 2000, Peltola et al. 2000, Stokes et al. 2005, Lundström et al. 2007*a*, 2008) so as to develop energy dissipation models or to obtain maximum stem breaking values. More recently, mechanical full-scale impact experiments were conducted in the field by Dorren and Berger (2005), Dorren et al. (2006) and Lundström et al. (2009) to determine the maximum energy dissipation values of different trees.

On a microscopic scale, trees respond to mechanical disturbance with the formation of callus tissue (Schweingruber 2001) and eccentric growth or with the formation of reaction wood (Timell 1986, Duncker and Spiecker 2008). In addition, different conifer species react to mechanical stress with the formation of tangential rows of traumatic resin ducts (TRD; Bannan 1936, Stoffel 2008). The TRD formation operates as a defence mechanism and assists compartmentalization of the wood after tree damage (Thomson and Sifton 1925, Shigo 1984, Hudgins et al. 2004). Resin ducts appear in tangential rows close to the wound, where the cambium had been partially destroyed due to mechanical stress. The arrangement of TRD is narrowest close to the wound and becomes more dispersed with increasing distance from it (Bannan 1936, Schneuwly et al. 2008). To date, only a very limited number of quantitative studies exist, which focus on the tangential or axial spread of TRD following mechanical stress or artificial decapitation on secondary xylem formation (e.g., Moore 1978, Nagy et al. 2000, Lev-Yadun 2002, Bollschweiler et al. 2008, Schneuwly et al. 2008, Stoffel and Hitz 2008). Another barely studied characteristic of TRD is the intra-annual shift of the ducts within a growth ring with increasing distance from the wound. Bannan (1936) described this phenomenon of delayed onset of TRD differentiation in an axial direction. Radial migration of TRD with increasing distance from the injury was recently confirmed by Bollschweiler et al. (2008), Schneuwly and Stoffel (2008*a*) and Stoffel and Hitz (2008).

Research has so far focused on the assessment of physical parameters in real-size experiments or on the anatomical growth features following artificial wounding of juvenile plants. In contrast, knowledge of the anatomical response following mechanical disturbance in adult trees is still largely needed, and the type, temporal appearance and spatial extent of tree response in the secondary xylem after natural wounding have not yet been addressed in detail.

This study, therefore, focuses on the types and the intensities of anatomical growth responses of European larch (*Larix decidua* Mill.), Norway spruce [*Picea abies* (L.) Karst.] and Silver fir (*Abies alba* Mill.) following mechanical disturbance induced by the impact of blocks falling from rock faces. The specific aims of this study were to (1) quantify the mean radial and axial extent of rows of tangential resin ducts; (2) investigate the spatial probabilities of the occurrence of TRD; (3) quantify the intra-annual shift of TRD in the axial direction; and (4) analyze the spatial distribution and the intensity of reaction wood.

Materials and methods

Study sites

The response of conifers to mechanical disturbance was analyzed in trees affected by natural rockfall activity. While each of the species was sampled on a different rockfall slope in the Swiss and French Alps, the determining conditions, such as slope angle and boulder size, did not differ considerably between the sites (Table 1). The altitude difference between the three study sites was a given precondition for this study.

Fieldwork and sample preparation

In total, 16 trees with multiple rockfall injuries were selected for the analysis: six *L. decidua*, six *P. abies* and four *A. alba*. For the sampled trees, we recorded tree species, tree height and tree diameter at breast height. We noted the maximum extension, width, height and orientation of each injury before it was photographed. The selected trees were then felled and cut into 820 stem sections of 0.1-m length in the laboratory; they were then air dried and sanded up to grit 400. While the mean tree diameters of *L. decidua* and *P. abies* were similar in size (18.7 and 23.7 cm, respectively), those of *A. alba* trees were much larger (mean diameter 43.1 cm). The average tree ages were 30.4 (*L. decidua*), 20.0 (*P. abies*) and 43.0 (*A. alba*) years (Table 2).

Laboratory analysis

In the laboratory, wood-anatomical features relating to mechanical disturbance were identified using dendrogeomorphic methods described by Stoffel and Bollschweiler (2008) and Stoffel (2008). As a first step, the section with

Table 1. Characteristics of the three different study areas of this study.

Species	*L. decidua*	*P. abies*	*A. alba*
Location	Täsch	Saas Balen	Vaujany
Coordinates	46°04′ N and 7°47′ E	46°09′ N and 7°55′ E	45°12′ N and 6°03′ E
Slope angle	35°	36°	38°
Altitude	1800–1850 m	1550–1650 m	1250–1350 m
Boulder size	About 1 m^3	Maximum 1 m^3	About 1 m^3
Reference	Stoffel et al. (2005*a*)	Schneuwly and Stoffel (2008*b*)	Dorren et al. 2006

Table 2. Number of sampled trees, tree diameters and tree age at the time of wounding.

	Number of trees	Diameter (cm)		Age (years)	
		Mean	SD	Mean	SD
Total	16	24.2	39.3	28.4	15.8
L. decidua	6	18.7	24.9	30.4	17.1
P. abies	6	23.7	23	20	9.1
A. alba	4	43.1	53.5	43	12.9

the maximum lateral extent of the injury was analyzed, followed by the sections above and below the exposed part of the wound insofar as any anatomical growth response could be detected. The width (in degrees) and the intra-annual position of the injury were assessed by noting the earliest evidence of the growth response, such as any change in the structure of tracheids (Stoffel and Hitz 2008), the formation of callus tissue or the appearance of TRD. The TRD were taken into account if they were present (i) in an extremely compact arrangement and (ii) forming continuous rows (Stoffel et al. 2005*a*). For the purpose of assessment of the intra-annual timing of wounding, responses in growth were classified following Stoffel et al. (2005*b*, Figure 1A) into: the first-formed cell layer (resulting from an injury during the dormant season, D), early, middle and late earlywood (EE, ME and LE, respectively, three equal-width sub-units) and early and late latewood (EL and LL, respectively, two equal-width sub-units).

The tangential extension of TRD at the maximum extent of wounds was calculated by measuring the distance between the wound's boundary and the farthest point where the TRD still occurred. Following Bollschweiler et al. (2008), the radial distance of TRD formation was given as a percentage of the ring's total circumference, excluding that portion where the cambium had been destroyed (Figure 1B). Above and below the injury, the radial spread of TRD was analyzed as well, but the values were divided by 2 to obtain data for both sides of the wound. In the next analytical step, the intra-annual season of the earliest tree response was noted, and the axial shift of TRD with increasing vertical distance from the wound was

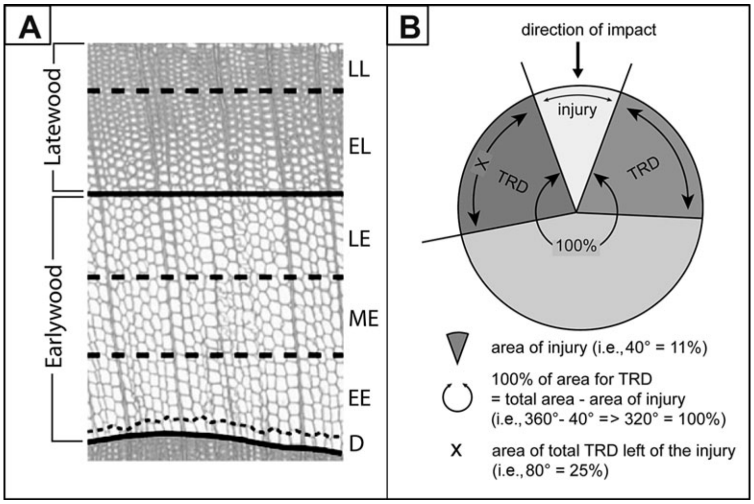

Figure 1. (A) Intra-annual subdivisions of a growth ring into dormancy (D), early earlywood (EE), middle earlywood (ME), late earlywood (LE), early latewood (EL) and late latewood (LL). (B) Schematic illustration of the tangential TRD analysis at the height of injury.

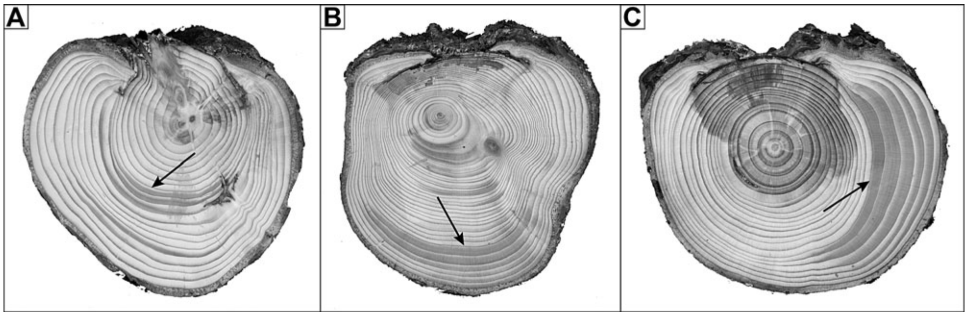

Figure 2. Illustration of the reaction wood intensity classes represents: (A) class 1 (weak), (B) class 2 (medium) and (C) class 3 (intense). The black arrows point at the first year of reaction wood formation. As can be seen in (C), the reaction wood does not necessarily appear opposite the direction of the injury.

assessed. For this analysis, we only considered injuries showing first growth responses in the dormant season (D) and tracked the earliest appearance of growth responses in all sections above and below the wound. So as to provide representative results, at least 10 responses had to be present at each vertical distance from the wound to be considered.

The analysis of TRD formation concentrated particularly on the first year of appearance, but its presence in subsequent years was also noted. In the last analytical step, the occurrence of reaction wood was investigated, and its intensity was divided into three classes, with class 1 representing weak (weak appearance, little spread and few years), class 2 medium and class 3 intense (strong appearance, wide spread and several years) formation of reaction wood (Figure 2).

As some of the rockfall impacts were located close to ground level, it was not always possible to track growth responses to the level where they would have disappeared if they had occurred at a higher point on the stem. Similarly, anatomical growth responses were recorded only if they could be clearly attributed to a specific wound; in the case of proximity to another wound, ambiguous tree sections were not analyzed, and 'absent' sections were systematically removed from our calculations.

Results

Characteristics of rockfall wounds

The impacts of rockfall resulted in 54 wounds on the investigated trees, meaning that most of the trees showed multiple wounds. Most of them were identified in *L. decidua* with 26, followed by *P. abies* with 20 and *A. alba* with 8 wounds. The mean wound height was 86.5 cm and the standard deviation (SD) was 88.3 cm (Table 3). The seasonality of wounding reveals a strong peak in D (79.6%), implying that the highest rockfall activity does not occur during the vegetation period. In *L. decidua*, 88.5% of all injuries occurred outside the vegetation period, whereas scarring in dormancy was found to be 60% in *P. abies* and 100% in *A. alba*.

Radial and axial arrangements of TRD in the year of injury

In the uninjured tissues adjacent to the wounds, the radial extent of TRD strongly depends on the species (Table 4). At the height of the wound, TRD were observed in all *L. decidua* and *P. abies* trees. In the case of *A. alba*, however, TRD were not present in two of eight injuries. The spread of the mean TRD proportion of the tree

Table 3. Number of wounds, wound heights and intra-seasonal distribution of wounding.

	Number of wounds	Wound height (cm)		Intra-annual season of wounding					
		Mean	SD	D	EE	ME	LE	El	LL
Total (%)	54	86.5	88.3	79.6	14.8	1.9	1.9	1.9	1.9
L. decidua (n)	26	91.2	92.8	23	1	1	0	1	0
P. abies (n)	20	93	91.6	12	7	0	1	0	0
A. alba (n)	8	55	64.6	8	0	0	0	0	0

Table 4. Radial (%) and axial (cm) arrangements of TRD in *L. decidua*, *P. abies* and *A. alba* trees in the tree ring following mechanical disturbance.

	Samples	Minimum	Maximum	Mean	SD
Radial arrangement (%)					
L. decidua	26	3.8	59	20.5	18.2
P. abies	20	4.5	100	27	22.8
A. alba	8	0	4.2	3.7	3.3
Axial arrangement (cm)					
L. decidua					
Above	25	0	60	22	13.5
Below	22	0	−50	−12.3	11.1
P. abies					
Above	20	10	130	38	31.2
Below	11	10	−60	−35.5	15.7
A. alba					
Above	8	0	20	10	9.3
Below	4	0	−10	−2.5	5

circumference where the cambium has not been destroyed again varied among the species. While TRD in *L. decidua* and *P. abies* can be found on 20.5% and on 27%, respectively, its occurrence was only very localized in *A. alba* with 3.7% of the circumference. The analysis of the axial extension reveals tendencies similar to those observed for the radial arrangement, with TRD extensions above and below, respectively, the injury of +22 and −12.3 cm for *L. decidua*, +38 and −35.5 cm for *P. abies* and +10 and −2.5 cm for *A. alba*. The maximum axial extension for *L decidua* accounts for +60 and −50 cm. The TRD in *P. abies* was identified to be maximal up to +130 cm/−60 cm away from the wound. The smallest values are again noted for *A. alba*, with maximum vertical distances at +20 cm/−10 cm.

The arrangement of TRD in the radial direction is illustrated in Figure 3 and is given as the mean radial proportion affected at each 10-cm interval from the central height of the injury. The lateral and axial spread of TRD is largest in *P. abies*, followed by *L. decidua* and *A. alba*, and the highest values are observed just above the injury. The results also indicate that more TRD are normally formed above, rather than below, the injury after mechanical disturbance.

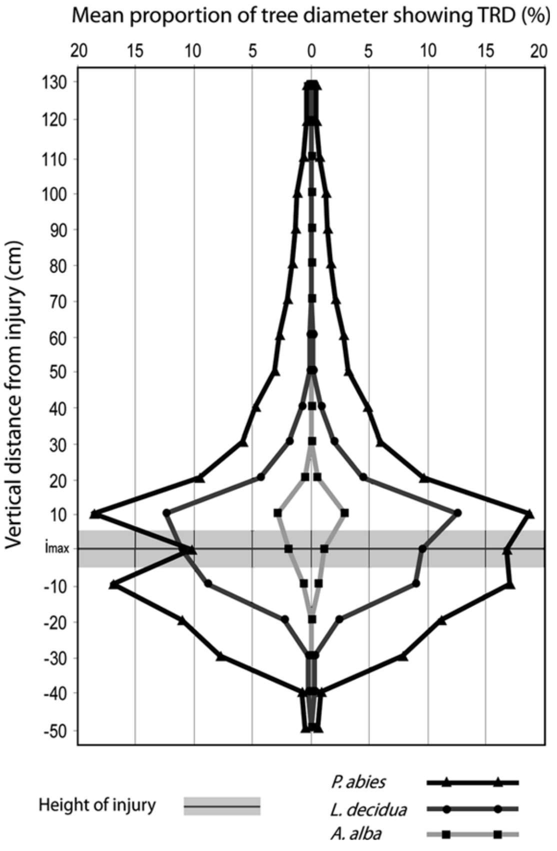

Figure 3. Mean spatial arrangement of TRD in the radial and axial directions for *L. decidua*, *P. abies* and *A. alba* following mechanical disturbance.

The comparatively low values for the radial extent of TRD at the height of the injury are given because the proportion of the circumference occupied by the wound itself cannot produce TRD, and therefore does not appear in Figure 3.

Probability for TRD being formed in the year of injury

Figure 4 illustrates the probability of TRD being formed in the stem following mechanical disturbance. The highest probability for the occurrence of widespread TRD formation is observed in *P. abies* (Figure 4A). In the immediate lateral and upper neighborhood of the injury, the probability of TRD being formed exceeds 90% in *P. abies*. It also appears that the probability of TRD formation is generally higher above rather than below the injury in *P. abies*, but the differences in occurrence probabilities become much more comparable with increasing distance from the wound. Similar probability patterns can be observed for *L. decidua*, where the chances of TRD formation are again > 90% in the lateral and axial proximity of the wound (Figure 4B). When compared to the TRD pattern of *P. abies*, *L. decidua* shows more rapid decreasing rates with increasing distance from the wound in both the radial and axial directions. Based on our data, it also appears that TRD in *L. decidua* is, in general, more commonly formed above, rather than below, the wound.

The probability of TRD being formed following mechanical disturbance is considerably smaller in *A. alba* than in the other two species (Figure 4C). The probability of finding TRD is again highest in the tissues adjacent to the wound at around 60–75%. At the height where the wounds exhibit their maximum radial extension, the probability of identifying TRD in 5% of the circumference remaining vital after disturbance already falls below 30%. Again, the probability of TRD formation is higher above rather than below the injury, and the slight radial decrease at the height of the injury is because the injury itself does not appear in the illustration.

Long-term production of TRD

Data on the long-term production of TRD are illustrated in Table 5 for the height of the injury as well as for the cross-sections just above and below the wound. At the height of the injury, 69% of the natural disturbance events induced in *L. decidua* resulted in TRD formation for more than one growth period. In *P. abies*, 95% of the samples showed TRD for over > 1 year, whereas in *A. alba* 75% of the tissues adjacent to the wounds revealed TRD in the increment rings that were formed in the years after mechanical disturbance. The proportion of trees forming TRD above and below the wound for more than one season was, in contrast, considerably smaller for all species. Continuous TRD formation is most important for *P. abies*, where TRD is being produced for over 3.5 years

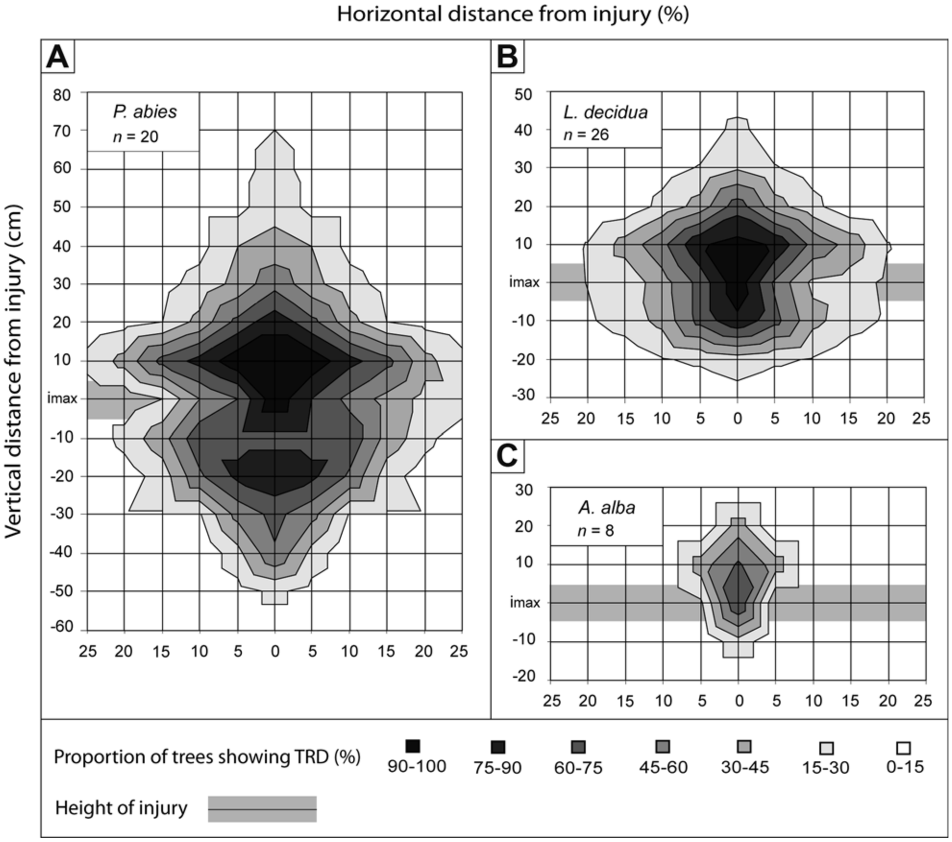

Figure 4. Probability of TRD being formed following mechanical disturbance in *L. decidua*, *P. abies* and *A. alba*. Values are given for the tree ring formed after mechanical disturbance.

Table 5. Long-term persistence of TRD in *L. decidua*, *P. abies* and *A. alba* following mechanical disturbance.

	Samples	TRD + y (N)	TRD + y (%)	Minimum (y)	Maximum (y)	Mean (y)	SD
L. decidua							
Above	25	12	48	0	11	1.1	2.3
Height injury	26	18	69.3	0	5	1.5	1.4
Below	23	9	39.1	0	2	0.6	0.8
*P. abies**							
Above	20	16	80	0	9	2.3	2.2
Height injury	20	19	95	0	11	3.5	2.3
Below	14	9	64.3	0	11	2.9	3.1
*A. alba**							
Above	8	2	25	0	1	0.3	0.5
Height injury	8	6	75	0	4	1.5	1.3
Below	4	1	25	0	1	0.3	0.5

y = Additional years of TRD formation, absolute (N) and proportion values (%) are given.
*Minimum values as some of the trees were observed before TRD formation ceased.

after the year of impact at the height of the injury. In *L. decidua* and *A. alba*, continuous TRD formation persists over 1.5 growth rings that are formed after the year of injury.

Intra-annual radial shift of TRD in axial direction

The intra-annual radial shift of TRD with increasing axial distance from the wound was investigated for all injuries induced before the onset of the local growing period in dormancy (D). As can be seen from Figure 5, an axial shift of TRD proves to be common for all species.

Although wounding occurred outside the vegetation period, and the earliest growth response was identified in the first tracheid cell layer of the new increment ring, we observed a systematic intra-annual radial shift to EE cell layers at only 10 cm above the injury for *L. decidua* and *A. alba*. In contrast, TRD formation in *P. abies* differs from

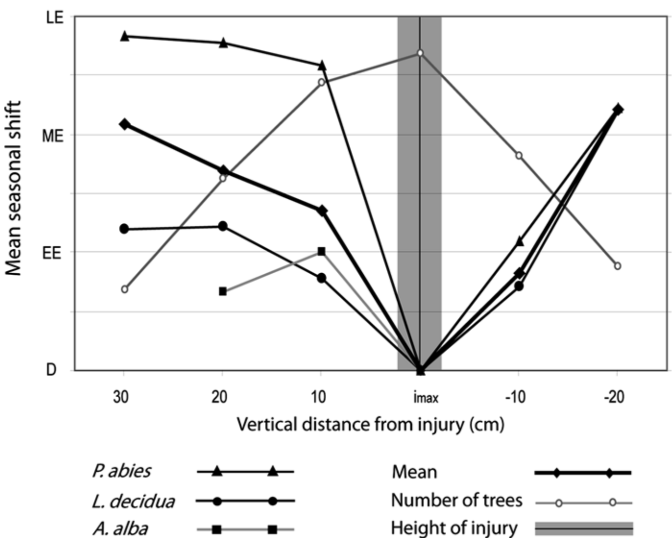

Figure 5. Axial intra-annual shift of TRD in *L. decidua*, *P. abies* and *A. alba* following mechanical disturbance.

those in *L. decidua* and *A. alba* for the cross-sections above the injury, where radial shifting is much more pronounced. At an axial distance of 10 cm above the wound, TRD are formed slightly in ME and approach LE cell layers at 30 cm.

Below the wound, the magnitude of intra-annual radial shifting is larger than that of above the injury, and similar values are observed between the species. In an axial distance of −10 cm below the wound, TRD appear in EE, whereas they are formed in ME and LE cell layers in an axial distance of −20 cm.

Arrangement and intensity of reaction wood following wounding

The axial position and the intensity of reaction wood were investigated, and the results are illustrated in Table 6. Interestingly, major differences exist between the species in appearance frequency and intensity. Simultaneously, reaction wood in all species can be found most commonly at the height of the injury. Reaction wood is also being formed in some of the segments above, but much less frequently below, the injuries. In *L. decidua*, reaction wood was present in only 7.7% of the samples at the height of the injuries, and the intensities were always small (class 1). In *P. abies*, in contrast, reaction wood seems to be more common and was observed in 50% of the samples at injury height. Reaction wood also exhibits a much more pronounced axial spread, with 50% of the samples above and with 42.9% of the samples below the wounds showing it. Moreover, the intensity in *P. abies* was more important than that in *L. decidua*, and regularly reached class 3.

Reaction wood seems to be a more frequent response to mechanical disturbance following rockfall impacts in *A. alba,* and was present in the vast majority (87.5%) of the samples at injury height. Above the wound, half of

Table 6. Axial position and intensity of reaction wood in *L. decidua*, *P. abies* and *A. alba* following mechanical disturbance.

	Samples	Rw (N)	Rw (%)	N 1	N 2	N 3	Mean
L. decidua							
Above	26	1	3.9	1	0	0	0.04
Height injury	26	2	7.7	3	0	0	0.12
Below	23	0	0	0	0	0	0
P. abies							
Above	20	7	50	3	1	3	0.7
Height injury	20	7	50	1	3	3	0.8
Below	14	6	42.9	3	0	3	0.9
A. alba							
Above	8	4	50	3	1	0	0.6
Height injury	8	7	87.5	3	1	3	1.8
Below	4	0	0	0	0	0	0

Rw = Reaction wood, absolute (N) and proportion values (%) are given.
1–3 = Intensity of reaction wood (1 = weakest and 3 = strongest).

the segments still exhibited reaction wood, but none was observed below the injuries. The intensity of reaction wood largely varied in *A. alba,* and all classes were present on the samples.

Discussion

In this study, 54 injuries due to natural rockfall activity were analyzed in six *L. decidua*, eight *P. abies* and four *A. alba* trees to identify and quantify anatomical growth response in the form of tangential rows of TRD and reaction wood following mechanical disturbance.

The results indicate that all *L. decidua* and *P. abies* responded to mechanical disturbance with the formation of TRD at the height of the injury. Similar to the results presented by Schneuwly et al. (2008), we observe TRD on one-fifth and one-fourth, respectively, of the circumference remaining vital after wood-penetrating impacts. In agreement with Schweingruber (2001), we also observe that formation in the radial direction in *A. alba* is much less pronounced (3.7%). The inhibited TRD formation of *A. alba* trees is not the consequence of a different mechanical behavior, but solely of the genetic make-up (Schweingruber 1996); *L. decidua* and *P. abies* also produce much more TRD above and below the wound.

It has also become evident that the mean axial extension of TRD following naturally induced mechanical disturbance (+22 and −12.3 cm for *L. decidua*, +38 and −35.5 cm for *P. abies*, +10 and −2.5 cm for *A. alba*) largely exceeds the values observed after artificial treatments, where the axial extension ranging from 5 cm (Franceschi et al. 2002) to 10 cm (Lev-Yadun 2002) or 12 cm (Luchi et al. 2005) has been reported. The considerably lower values of the studies cited above can be explained by the different nature of disturbance, as trees were artificially treated with hormones or decapitation in these studies and were not subjected to short-lived, but high-intensity, impacts. In contrast, our data seem to be comparable to the results reported by Bollschweiler et al. (2008), who observed TRD at vertical distances of +43 and −14 cm. Although similar to our trees, their samples were wounded by natural mechanical disturbance (debris flows).

The TRD formation in the axial direction was more important above, rather than below, the injury and therefore confirms the findings of Fahn et al. (1979) and Bollschweiler et al. (2008). We believe that the higher frequency of TRD above the wound results from an upward propagation of impact shock waves through the stem (‘hula-hoop effect’; Dorren et al. 2006). Downward from the wound, the effects of shock waves may have been partially extenuated by the root system and the subsurface (Lundström et al. 2007*b*, 2007*c*). While this may explain the uneven axial distribution of TRD following natural mechanical disturbances, it may not elucidate the unequal arrangement of TRD after hormonal treatment, as reported by Fahn et al. (1979). As a result, it is also feasible that the signaling agents leading to TRD formation would more easily propagate in the upward direction.

It has also been demonstrated that TRD formation varies between the species and the nature of disturbance. Previous studies report on correlations between TRD formation and wound size (Fahn et al. 1979), wound size effects (area and length) on axial TRD extension (Bollschweiler et al. 2008) or on the influence of injury width on the radial extension of TRD (Schneuwly et al. 2008). We therefore tested the influence of injury size – categorized into three classes: smallest third, medium third and largest third – on TRD occurrence for *L. decidua* and *P. abies*. As can be seen in Figure 6A, the probability of TRD being formed in *L. decidua* is neither a function of size (Figure 6A) nor a function of maximum wound width (Figure 6B). Figure 6C and D illustrates that the findings for *P. abies* show a very similar response (the sample depth for *A. alba* did not allow for similar investigations).

The TRD in *P. abies* not only appeared more extensively in the radial and axial directions and with higher probabilities, but they also persisted over a larger number of years after wounding. While our findings on *P. abies* and on *L. decidua* agree with the results of Schneuwly et al. (2008), it should also be mentioned that TRD formation was ongoing at the time of sampling in several *P. abies* and *A. alba* trees.

The intra-annual radial shift with increasing axial distance from the wound was detected in all species and confirmed the findings by Bannan (1936) and Bollschweiler et al. (2008). This delay in TRD formation might have resulted from the slow propagation of the signaling agent leading to resin production and resin duct formation. Krekling et al. (2004) state that, for *P. abies*, the signal propagates about 2.5 cm day^{-1} in the axial direction. Based on the phenological observations and growth data of *L. decidua* and *P. abies* from the wider study area (Müller 1980), we are led to believe that the formation of EE and ME tracheids lasts for around 30 days. As we had already observed a shift from the growth ring boundary to ME cell layers at 20–30 cm above and below the wound, we are led to assume that the propagation rates obtained after natural mechanical disturbance would be considerably smaller than those of the reactions after artificial treatment.

The formation of reaction wood does not represent a common growth reaction to mechanical disturbance in *L. decidua*, where it was present in only 7.7% of the samples. Our findings agree with those of Stoffel et al. (2005*a*) and Schneuwly and Stoffel (2008*a*), who did not detect large amounts of the reaction either. In *P. abies*, in contrast, 50% of the samples showed reaction wood and at a higher intensity. Reaction wood was most commonly observed in *A. alba*, where it was detected in 87.5% of the samples. While soil characteristics and soil depths are very similar between the sites involved, we consider that the differences in the presence and in the intensity of reaction wood would result from the species-specific

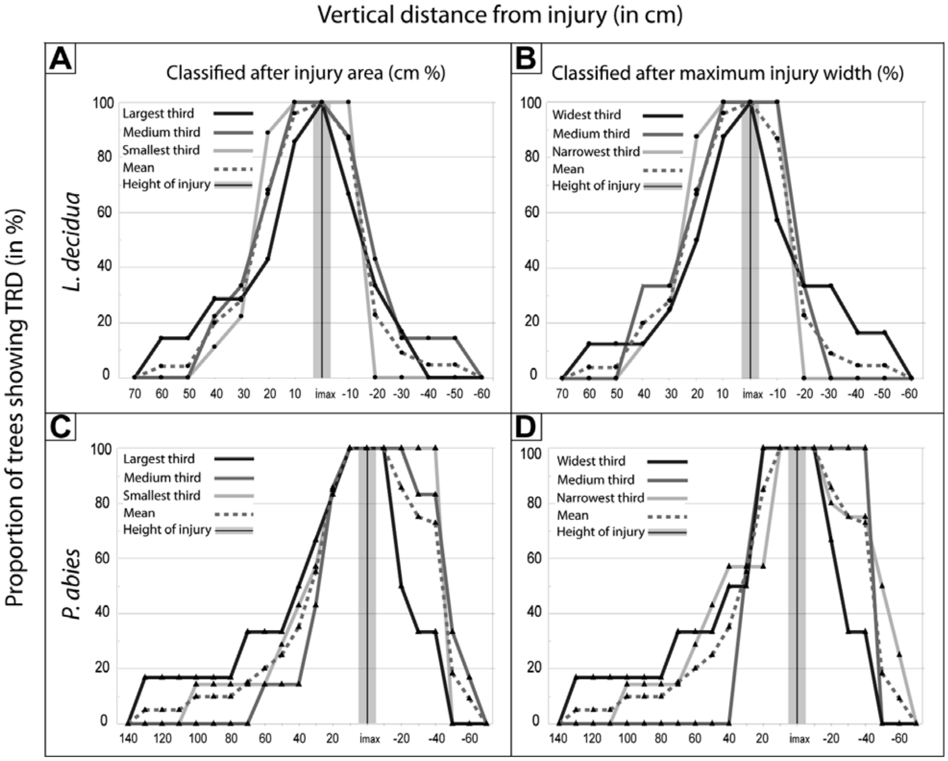

Figure 6. Spatial arrangement of TRD in *L. decidua* and *P. abies* following impact, classified after injury size and injury width.

disparities in root system morphologies and related tree stability.

Conclusion

Growth response to mechanical disturbance resulting from natural rockfall was investigated in *L. decidua*, *P. abies* and *A. alba*. The results provide evidence that natural disturbance induces much stronger and widespread anatomical responses than any wounding produced through artificial stimuli. For the first time, the spatial arrangement, probability of occurrence and intra-annual radial shift of TRD could be quantified, as well as the position and the intensity of reaction wood formation following the impacts assessed. While this study revealed a multitude of new insights into anatomical growth responses of European conifers, it also raises new questions, namely the reasons for the preferential spread of resin ducts above injuries, and concerning the widespread absence of reaction wood in *L. decidua*.

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