Formation and spread of callus tissue and tangential rows of resin ducts in *Larix decidua* and *Picea abies* following rockfall impacts

DOMINIQUE M. SCHNEUWLY,[1,2] MARKUS STOFFEL[1,3,4] and MICHELLE BOLLSCHWEILER[1,3,4]

[1] *Department of Geosciences, Geography, University of Fribourg, Chemin du Musée 4, CH-1700 Fribourg, Switzerland*

[2] *Corresponding author (dominique.schneuwly@unifr.ch)*

[3] *Department of Environmental Sciences, University of Geneva, Chemin de Drize 7, CH-1227 Carouge-Geneva, Switzerland*

[4] *Laboratory of Dendrogeomorphology, Institute of Geological Sciences, University of Berne, Baltzerstrasse 1-3, CH-3012 Berne, Switzerland*

Summary After mechanical wounding, callus tissue and tangential rows of traumatic resin ducts (TRDs) are formed in many conifer species. This reaction can be used to date past events of geomorphic processes such as rockfall, debris flow and snow avalanches. However, only few points are known about the tangential spread or the timing of callus tissue and TRD formation after wounding. We analyzed 19 *Larix decidua* Mill. (European larch) and eight *Picea abies* (L.) Karst. (Norway spruce) trees that were severely damaged by rockfall activity, resulting in a total of 111 injuries. Callus tissue appeared sparsely on the cross sections and was detected on only 4.2% of the *L. decidua* samples and 3.6% of the *P. abies* samples. In contrast, TRDs were present on all cross sections following wounding and were visible on more than one-third (34% in *L. decidua* and 36.4% in *P. abies*) of the circumference where the cambium was not destroyed by the rockfall impact. We observe different reactions in the trees depending on the seasonal timing of wounding. The tangential spread of callus tissue and TRDs was more important if the injury occurred during the growth period than during the dormant season, with the difference between seasons being more pronounced for callus tissue formation than for TRD formation. We observed an intra-annual radial migration of TRDs with increasing tangential distance from the wound in 73.2% of the *L. decidua* samples and 96.6% of the *P. abies* samples. The persistence of TRD formation in the years following wounding showed that only *L. decidua* trees produced TRDs 2 years after wounding (10.5%), whereas *P. abies* trees produced TRDs 5 years after wounding (> 50%).

Keywords: dendrogeomorphology, European larch, injury, Norway spruce, tangential extension, traumatic resin ducts.

Introduction

Rockfall is a common mass movement process in alpine environments. After Berger et al. (2002), it is defined as the free falling, bouncing or rolling of individual or a few rocks and boulders, with volumes involved generally being $< 5\ m^3$. The collision of a boulder with a tree can cause various damages, such as wounding, tilting and breaking of the stem. Tree responses to collisions include formation of callus tissue (Schweingruber 2001), eccentric growth or the formation of reaction wood (Timell 1986, Braam et al. 1987), abrupt changes in growth (Strunk 1997, Friedman et al. 2005), and multiple leader formation (Mattheck 1996, Schweingruber 1996). In addition, various conifer species react to mechanical damage with the formation of tangential rows of traumatic resin ducts (TRDs, LePage and Bégin 1996, Stoffel and Perret 2006, Bollschweiler et al. 2008). The presence and distribution of TRDs have been used to date past geomorphic events (Bollschweiler 2007, Schneuwly and Stoffel 2008*a*, 2008*b*, Stoffel 2008). Nevertheless, there is still uncertainty about the exact timing and distribution of TRD formation after mechanical impact on the stem. In contrast to widely scattered resin ducts that appear as a common feature in stems of the genus *Larix* (Bannan 1936), TRD formation operates as a defense mechanism that compartmentalizes the wood after tree damage (Thomson and Sifton 1925, Shigo 1984, Hudgins et al. 2004). If the injury occurs during a period of cambial activity, the TRDs differentiate from the cambium with a delay of 4–28 days (Nagy et al. 2000, Franceschi et al. 2002, Luchi et al. 2005). Damage occurring outside the growth period causes formation of TRDs during the following growing season (Fahn et al. 1979). The TRDs normally appear in tangential rows close to the wound where the cambium has been partially destroyed, and their arrangement becomes more dispersed away from the wound (Bannan

1936). Fahn et al. (1979) had concluded that the number and size of ducts decreases with distance from the injury. There are few published quantitative data on the tangential extent of TRDs (Moore 1978, Bollschweiler et al. 2008, Stoffel and Hitz 2008). The lateral and axial spread of TRDs seems to depend not only on the distance to the injury, but also on the season when wounding occurred. The most pronounced appearance of TRDs after tree damage is observed when the injury occurs during the growing season, whereas wounding during the dormant period results in a weaker spread of TRD in the next growing season (Bannan 1936). Another unknown factor is the intra-annual shift of TRDs within a growth ring with increasing distance from the wound. Bannan (1936) had described the phenomenon of a delayed onset of TRD formation, but had only mentioned an axial shift of ducts. Bollschweiler et al. (2008) and Stoffel and Hitz (2008) had observed, in addition to the axial shift, a radial migration of TRD with increasing distance from the injury. The same authors had also investigated the persistence of TRD formation, but these studies were on juvenile plants or trees that had been disturbed by debris-flow activity.

As a result, there is only limited knowledge on the tangential and intra-annual occurrence and the persistence of TRD formation in trees wounded by falling rocks and boulders. Similarly, there have been no studies on the anatomic responses to natural wounding in *Picea abies* (L.) Karst. (Norway spruce). To improve both the nondestructive investigation of naturally injured trees with increment cores and the accurate dendrogeomorphologic dating of past rockfall activity, it is crucial to improve our understanding of the axial and intra-annual behavior of TRD formation.

The aims of this study were to: (1) investigate and quantify the formation and radial extension of callus tissue and TRDs; (2) determine the influence of seasonality on the formation of callus tissue and TRDs; (3) analyze the intra-annual shift of TRDs with increasing tangential distance from the wound; and (4) assess the persistence of TRD formation in the years following wounding.

Materials and methods

Study site

The study site is situated 5 km north of Saas Fee close to the village of Saas Balen (46°09′06″ N and 7°55′27″ E), Valais, Switzerland. The forest stand is located between 1390 and 1610 m a.s.l. with a mean slope of 36°. Within the forest stand, a thin layer of quaternary talus and morainic deposits covers the bedrock that comprises micaceous schists belonging to the Penninic crystalline layers. The forest consists mainly of *Larix decidua* Mill. (European larch, 90%), some *P. abies* (10%), and a few *Pinus cembra* L. (< 1%) trees. Phenological data from a nearby site (10 km to the east; Müller 1980) indicate that the growth period is initiated around mid-May, latewood formation starts in mid-July and tree-ring growth ceases in mid-October. Mean annual temperature (1987–2007) at the study site is 4.5 °C with a mean annual rainfall of 620 mm (SMI (Swiss Meteorological Institute) 2008).

Vegetation on the study site is strongly influenced by rockfall activity that regularly occurs on the slope (Schneuwly and Stoffel 2008*a*, 2008*b*), mainly outside the growing season. The volume of the falling boulders does not normally exceed 1 m^3, and the anthropogenic influence is negligible in the forest stand.

Field work and sample preparation

At the study site, no geomorphic processes other than rockfall could be identified, and there were no signs of avalanche paths or debris-flow channels on the study slope (Figure 1A). Based on the analysis of processes present on the site, severely injured trees with multiple rockfall injuries were selected for this study. For the study trees, we recorded tree species, tree height and tree diameter at breast height (DBH). All visible defects in each tree's morphology were recorded and pictures of each individual were taken. The maximum extension, width, height and orientation of each injury were noted before a picture was taken of every wound (Figure 1B). Finally, one cross section was sawn from each wound at its maximum lateral extension, resulting in a dataset of 111 injuries (82 for *L. decidua*, 29 for *P. abies*).

Laboratory analysis

In the laboratory, tree reaction after wounding was analyzed. Samples were first air-dried and polished with sandpaper up to 400 grit. In addition, a selected number of samples were used for detailed microscopic examination, and micro-cuts were prepared from the wounded area and the adjacent tissue, as described by Schweingruber (1978) and Clark (1981). The width (in degrees), the year and the intra-annual position of the injury were assessed. We noted the earliest evidence of a reaction, such as changes in cell structure (Stoffel and Hitz 2008), formation of callus tissue and appearance of TRDs. To determine the intra-annual timing of wounding, reactions in the growth ring were subdivided as described by Stoffel et al. (2005) in Figure 2B into: the first-formed cell layer (in which TRD formation usually occurs as the result of an injury during the dormant season, D), early, middle and late earlywood (EE, ME and LE, respectively), and early and late latewood (EL and LL, respectively).

Thereafter, the nature of the TRDs was determined and subdivided into three classes: in Class 1, TRDs were formed as extremely compact and continuous rows; in Class 2, TRDs were very compact but not formed in completely continuous rows; in Class 3, TRDs were tangentially aligned but with clearly observable gaps between single ducts.

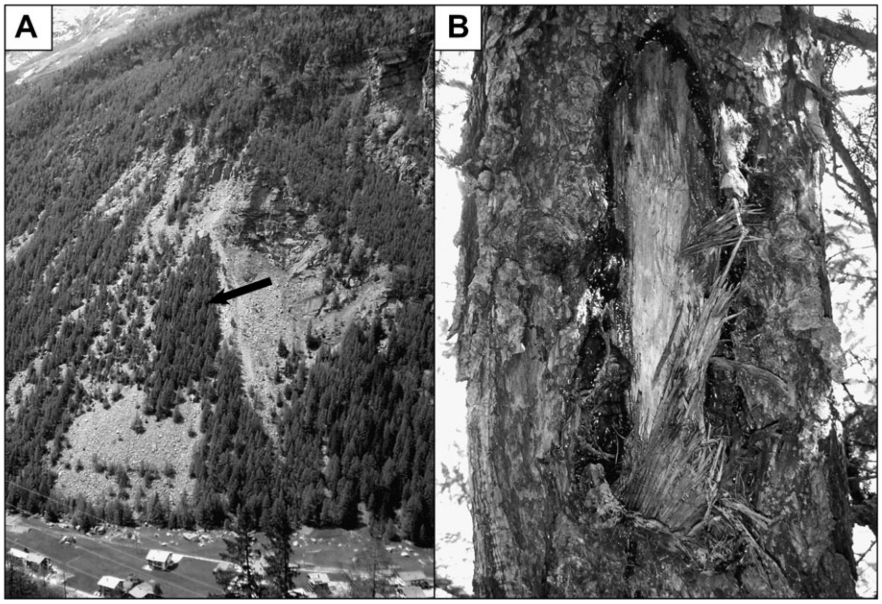

Figure 1. (A) General view of the rockfall slope, with the investigated forest stand indicated by an arrow. (B) Typical rockfall injury, notice the wood chipped off by the impact.

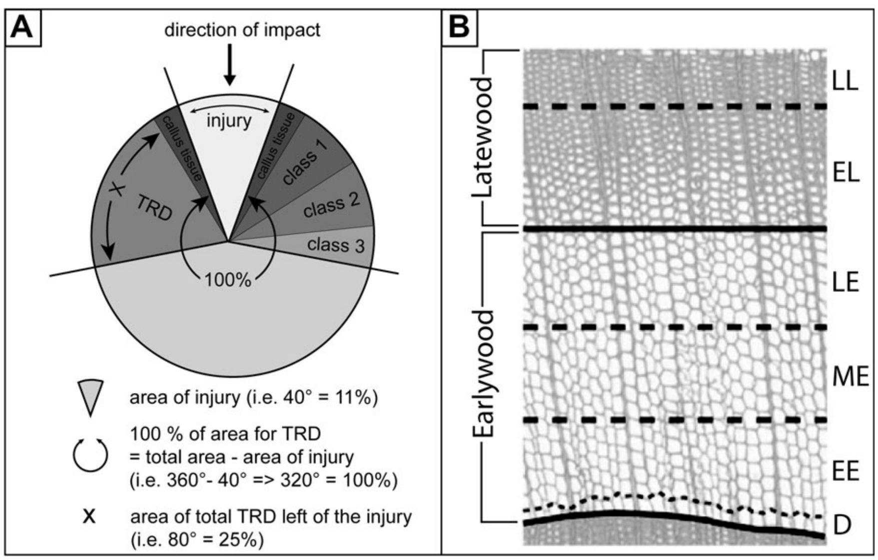

Figure 2. (A) Schematic illustration of the tangential TRD analysis. (B) Intra-annual subdivisions of a growth ring into: dormancy (D), early earlywood (EE), middle earlywood (ME), late earlywood (LE), early latewood (EL) and late latewood (LL).

The tangential extension of each TRD class was assessed on both sides of the injury by measuring the distance between the wound's boundary and the farthest point at which TRDs of the different classes occurred. Following Bollschweiler et al. (2008), these distances are given as a percentage of the ring's total circumference, excluding that portion where the cambium had been destroyed (Figure 2A). In addition, the seasonality of TRD occurrence was noted for each class. During the analysis of TRD formation, we focused on the first year of appearance but also noted the presence of TRDs in subsequent years and for how many years they were present. In a last analytic step, the radial shift in TRDs with increasing distance from the wound was assessed. We noted the maximum extent (in mm) of TRDs on both sides of the wound and noted the intra-annual position (Figure 2B) of TRDs next to the injury and at the outermost position. We then counted the number of seasonality classes (D, EE, ME, LE, EL and LL) between the injury and the intra-annual position of the outermost TRDs. These shifting values, summarized in categories, were finally related to the mean distance between the injury and the outermost TRDs measured previously.

Results

General aspects and seasonal distribution

We investigated 27 trees that were severely injured by rockfall (Table 1), comprising a total of 111 injuries. The distribution of tree ages and DBH of the individuals at the time of wounding as well as an overview on injury widths is

Table 1. Number of *L. decidua* and *P. abies* trees and injuries sampled.

	Total	*L. decidua*	*P. abies*
Number of trees	27	19	8
Number of injuries	111	82	29

provided in Table 2. Tree age at the moment of wounding averaged 11.3 years for the *L. decidua* trees and 15.2 years for the *P. abies* trees. The age distribution showed a maximum number of injuries when the trees were 6–8 (*Larix*) and 12–14 (*Picea*) years old. The mean DBH at the time of injury averaged 45 mm for *L. decidua* (peak at 21–30 mm) and 47.2 mm for *P. abies* (peak at 41–50 mm). Mean injury widths were similar between species, with 85.7° for *L. decidua* and 92.7° for *P. abies*. The distribution of injury widths reached a maximum at 41–60% (*L. decidua*) and 61–80% (*P. abies*). Thus, tree age and DBH at the time of injury as well as injury widths were comparable between the study species.

The distribution of the intra-annual position of the earliest response after wounding revealed that most reactions started at the very beginning of the growth ring. In 76.6% of all injuries, no cell rows were formed before the formation of callus tissue or TRDs, implying that most of the impacts were induced outside the growth period between mid-October and mid-May. Although 19.8% of tree reactions were observed during the earlywood period (mid-May to mid-July), only 3.6% were initiated during the formation of latewood cell layers (mid-July to mid-October) (Table 3).

Arrangement of callus tissue and TRD in the year of injury

In general, TRD formation represented the most common growth feature following wounding. Following an injuring event, TRDs appeared on all samples without exception. In contrast, callus tissue was present on only 45.1% of *L. decidua* samples and 41.4% of *P. abies* samples.

Table 3. Season of wounding. Intra-annual position of the earliest response after wounding (dormant season (D), early (EE), middle (ME) and late earlywood (LE), early (EL) and late (LL) latewood). The distribution reveals a strong peak in rockfall activity in the dormant season which lasts from mid-October to mid-May.

Season	D	EE	ME	LE	EL	LL	Total
Proportion (%)	76.6	9	9	1.8	1.8	1.8	100

Table 4 shows that the radial spread of TRDs was identified on 34% (*L. decidua*) and 36.4% (*P. abies*) of the ring's circumference that was remaining vital after impact. Callus tissue was, in contrast, detected only on 4.2% (*L. decidua*) and 3.6% (*P. abies*) of the circumference where the cambium was not destroyed. There was less difference between species in either feature (Figures 3 and 4).

Influence of the seasonal timing of wounding on callus tissue and TRD formation

Eighty-five injuries were inflicted during the dormant season and only 26 injuries occurred during the growth period. The formation of callus tissue and TRDs differed between trees injured during the dormant season and those damaged during the growing season. As illustrated in Table 5, the formation of callus tissue was much more pronounced, by a factor of 2.25, in the samples that were injured during the growth period. Similarly, the tangential extension of TRDs was more pronounced, by a factor of 1.25, if the impact occurred during the growing season. Thus, callus tissue formation depended much more on the seasonality of the event than TRD formation.

Table 2. Distribution of age (years) and DBH (mm) at time of wounding and distribution of injury widths (°) in the *L. decidua* and *P. abies* trees (%) studied. Minimum values are given in italics, maximum values are highlighted in bold.

Age classes	*L. decidua*	*P. abies*	DBH classes	*L. decidua*	*P. abies*	Injury width classes	*L. decidua*	*P. abies*
3–5	14.6	6.9	≤ 20	15.9	10.3	≤ 20	2.4	*0*
6–8	**30.5**	10.3	21–30	**19.5**	13.8	21–40	9.8	10.3
9–11	20.7	13.8	31–40	13.4	6.9	41–60	**22**	20.7
12–14	7.3	**24.1**	41–50	17.1	**31**	61–80	14.6	**24.1**
15–17	9.8	17.2	51–60	11	13.8	81–100	20.7	10.3
18–20	4.9	6.9	61–70	3.7	13.8	101–120	13.4	10.3
21–23	4.9	10.3	71–80	9.8	*0*	121–140	11	10.3
24–26	*2.4*	*0*	81–90	6.1	10.3	141–160	2.4	3.4
27–30	*2.4*	3.4	91–100	*1.2*	*0*	161–180	*1.2*	3.4
> 30	*2.4*	6.9	> 100	2.4	*0*	> 180	2.4	6.9
Overall statistics (years)			Overall statistics (mm)			Overall statistics (°)		
Mean	11.3	15.2	Mean	45	47.2	Mean	85.7	92.7
Minimum	3	3	Minimum	12	15	Minimum	13	23
Maximum	30	32	Maximum	150	89	Maximum	315	240
SD	6.86	7.33	SD	25.4	20.3	SD	47	53.5

Table 4. Tree reaction to wounding assessed as injury width (°), spread of callus tissue and classes of TRD in the *L. decidua* and *P. abies* samples. Abbreviation: (%*) represents that part of the tree's circumference remaining vital after the impact.

	Injury (°)	Callus tissue (%*)	TRD sum (%*)	TRD I (%*)	TRD II (%*)	TRD III (%*)
L. decidua						
Mean	85.7	4.2	34	22	6.4	5.6
SD	47	7.4	32.4	20	6.8	5.6
P. abies						
Mean	92.7	3.6	36.4	16.2	11.8	8.4
SD	53.5	6.4	44.8	22	14.2	8.6

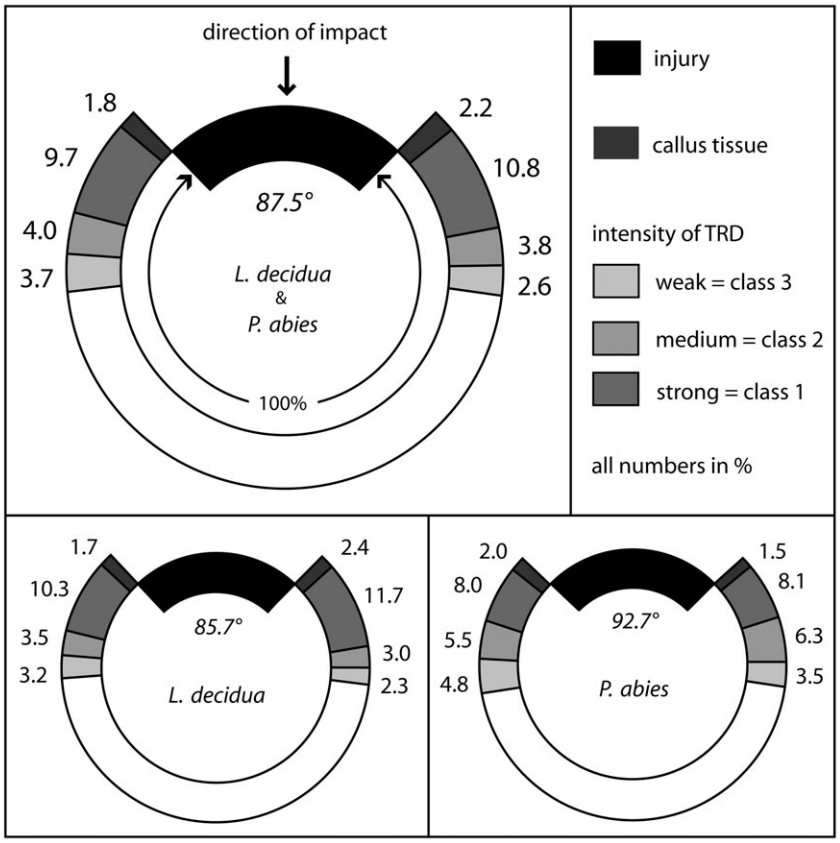

Figure 3. Distribution of callus tissue and intensity of TRD (Classes 1–3) in the year of wounding in *L. decidua* and *P. abies* trees.

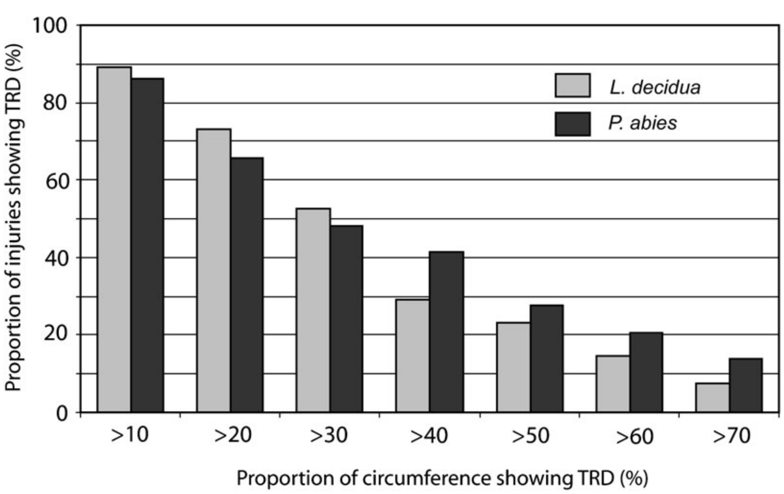

Figure 4. Radial spread of TRDs in that portion of the tree ring remaining vital in the first year following wounding.

Table 5. Reaction to wounding in *L. decidua* and *P. abies* depends on season of wounding.

Injury	No.	TRD (%)	Callus tissue (%)
During dormant season	85	32.7	18.8
During growth period	26	40.7	42.3

Intra-annual shift of TRD

An intra-annual shift of TRDs with increasing tangential distance from the wound was observed in 73.2% of the *L. decidua* samples and 96.6% of the *P. abies* samples. There was a relationship between the tangential distance from the injury and the importance of the intra-annual shift of TRDs in *P. abies* (Figure 5), but no such dependence was observed in the *L. decidua* samples, indicating that distance is not the only factor that induces the intra-annual shift.

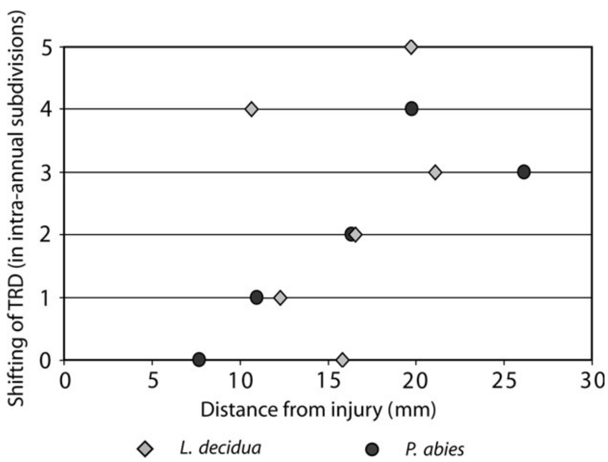

Figure 5. Relation between tangential distance from injury and radial migration of TRDs toward later portions of the tree ring (for the intra-annual subdivision, see Figure 2B).

Persistence of TRD formation

The persistence of TRD formation in the years following the injuring events differed between the species. In the year of the event, both species reacted to the injury with the formation of tangential TRDs (Figure 6). The proportion of *L. decidua* showing TRDs was reduced by about 50% every year after injury. Thus, 1 year after wounding, 56.3% of the samples showed TRDs, 22.1% were showing TRDs 2 years after the impact, and 3 years later, TRDs were present in 10.5% of the samples. In contrast, TRD formation persisted much longer in *P. abies*, with ducts being present in 93.1% of all samples 1 year after the impact. Two years after the injuring event, TRDs were still produced in 69% of the samples and even 5 years after the disturbance, more than half of the *P. abies* (53.6%) samples had TRDs.

Discussion

We analyzed 111 rockfall injuries from 19 *L. decidua* Mill. and eight *P. abies* (L.) Karst. trees and assessed the anatomic changes in tree growth following wounding. The TRDs were always formed after wounding in the investigated samples. Most wounds (76.6%) were inflicted during the dormant season, resulting in TRD formation at the very beginning of the growth ring formed during the following growth period. These findings are in agreement with the studies by Bannan (1936), Fahn et al. (1979) and Bollschweiler et al. (2008).

It also appears from our data that TRD formation is the most prominent growth feature in *L. decidua* and *P. abies* after the rockfall impact. In the first ring that was formed after the impact, TRDs were observed in all samples. These findings corroborate those of Stoffel and Hitz (2008), who identified tangential TRDs in 94% of their rockfall

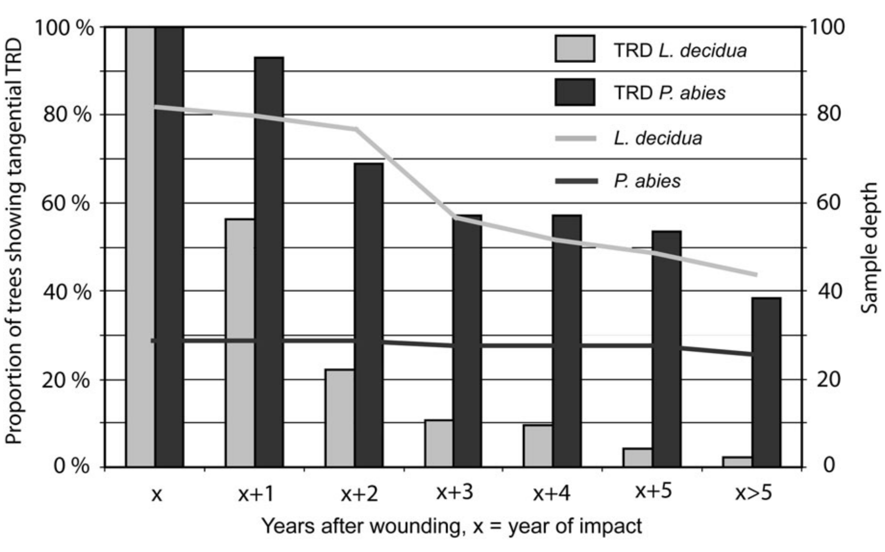

Figure 6. Persistence of TRD formation in the years following wounding in *L. decidua* (light gray) and *P. abies* (dark gray). The year of the impact is indicated with '*x*'. The gray lines indicate the number of samples per species; the decline for *L. decidua* between $x+2$ and $x+3$ can be explained by the large number of injuries in 2004.

samples. The tangential spread of TRDs is important, and ducts were found in 34% (*L. decidua*) and 36.4% (*P. abies*) of the circumference that was remaining vital after the impact (Figure 3). In contrast to the important tangential spread of TRDs, callus tissue was present on only 4.2% (*L. decidua*) and 3.6% (*P. abies*) of the functional tissue. These findings match the results of Bannan (1936), who mentioned that TRDs are present over 'considerable distances' in case of severe injuries. Our results are also in good agreement with the data obtained by Bollschweiler et al. (2008), who observed TRD formation in 19% of the vital circumference of *L. decidua* after debris-flow events. The differences in the tangential extent between the study by Bollschweiler et al. (2008) and this study are probably the result of the different nature of the wounding process. It is known that different geomorphic processes influence the tree response; for example, snow avalanche impacts do not cause the same reactions as rockfall injuries (Stoffel and Hitz 2008). The abrading action of debris flows can be compared with that of snow avalanches and they both induce a long-lasting and intense impact. In contrast, the energy transfer between a falling rock and a tree is transferred in only a fraction of a second, i.e., between 2 and 6×10^{-3} s (Rutz 1999) and energy is, moreover, concentrated at a single point on the tree's stem.

Our results also support the finding of Bannan (1936) that the intensity of a tree's response to a disturbance depends on the seasonality of the injuring event. We observed that the influence of seasonality was more obvious for callus tissue than for TRD formation. Callus tissue was formed much more frequently in trees during the growth period (42.3%) than during the dormant period (18.8%). In contrast, the difference was less obvious for TRD formation which showed a proportional increase from 32.7% to 40.7%.

The importance of TRD formation depends on different variables including tree age (Thomson and Sifton 1925, Bannan 1936) and injury size (Fahn et al. 1979, Bollschweiler et al. 2008).We tested the dependence of TRD formation in trees injured by rockfall on tree age and injury width, along with other variables such as DBH at the time of the impact as well as the annual DBH increment rate. For all variables, both tree species reacted in a comparable way. As shown in Figure 7A, we confirmed that TRD formation depends on injury width. The larger the wound, the more tangential TRD can be expected. This result contrasts with that of Bollschweiler et al. (2008) who had found no significant correlation between injury width and tangential spread of TRD. We believe that this discrepancy between studies is associated with the nature of the disturbance, because injury size is presumably not a reliable indicator of the degree of the disturbance. As can be seen from Figure 7B, TRD formation is also influenced by the age of the tree at the time of wounding. Younger trees form fewer TRDs than older trees. These findings are consistent with those of Thomson and Sifton (1925) and Bannan (1936). Similarly, DBH at the time of injury affects tangential TRD extension; bigger trees are stiffer and less flexible and therefore show a stronger reaction (Figure 7C). This result is not surprising, because tree age and DBH are not independent variables; older trees are normally bigger than younger trees. Finally, annual DBH increment of a tree before injury did not influence TRD formation (Figure 7D).

The intra-annual shift of TRDs with increasing tangential distance from the injury has been reported in earlier studies. Bollschweiler et al. (2008) had reported a shift in one-third of their *L. decidua* samples following debris-flow activity. Stoffel and Hitz (2008) had confirmed these findings on *L. decidua* trees injured by snow avalanches and rockfalls, mentioning a shift in 36% of the snow avalanche samples and 31% of the rockfall samples. Such variations in the intra-annual position of TRDs are the result of a slowly propagating chemical signal in the tree after wounding. Krekling et al. (2004) had reported that this signal propagates about 2.5 cm day^{-1} in the axial direction in *P. abies*. In this study, 87.4% of the injuries showed an intra-annual shift with increasing distance from the wound, but the reason for this high proportion is unknown.

Tree reactions following rockfall impacts were similar in our study species. For example, there was less difference between the species in the tangential extension of callus tissue and TRDs, in the intra-seasonal shift of TRDs, or in the effects of tree age and injury width on TRD formation. There was a major difference between the species, however, in the persistence of TRD formation in the years following wounding. We found that the proportion of *L. decidua* trees showing TRDs was reduced by about 50% every additional year following wounding (Table 6). In contrast, the proportion of *P. abies* trees showing TRDs followed a more or less linear function. Five years after wounding, more than half of the *P. abies* samples still formed TRDs. A possible explanation for this diverging behavior of the species is a different resistance to mechanical impact. It seemed that injury to a *L. decidua* tree resulted in less stress than injury to a *P. abies* tree. A reason for this resilience might be that the relatively thick bark of *L. decidua* is able to absorb a certain amount of energy. Alternatively, because *L. decidua* is a pioneer plant that is able to grow under difficult conditions, toleration of mechanical stress and accelerated healing might account for its high resistivity compared with *P. abies*.

The high proportion of trees having TRDs in the first ring that was formed after wounding is in agreement with the results of other studies (Table 6). No matter what geomorphic process caused the injury, at least 87.3% of the investigated samples presented TRDs as a response to wounding. However, TRD formation persisted for longer in *L. decidua* trees that were damaged by debris flows compared with trees injured by rockfall or snow avalanche activity.

Our observations on the tangential distribution of TRDs in rockfall trees show the potential of nondestructive sampling methods for dendrogeomorphic studies. After detailed

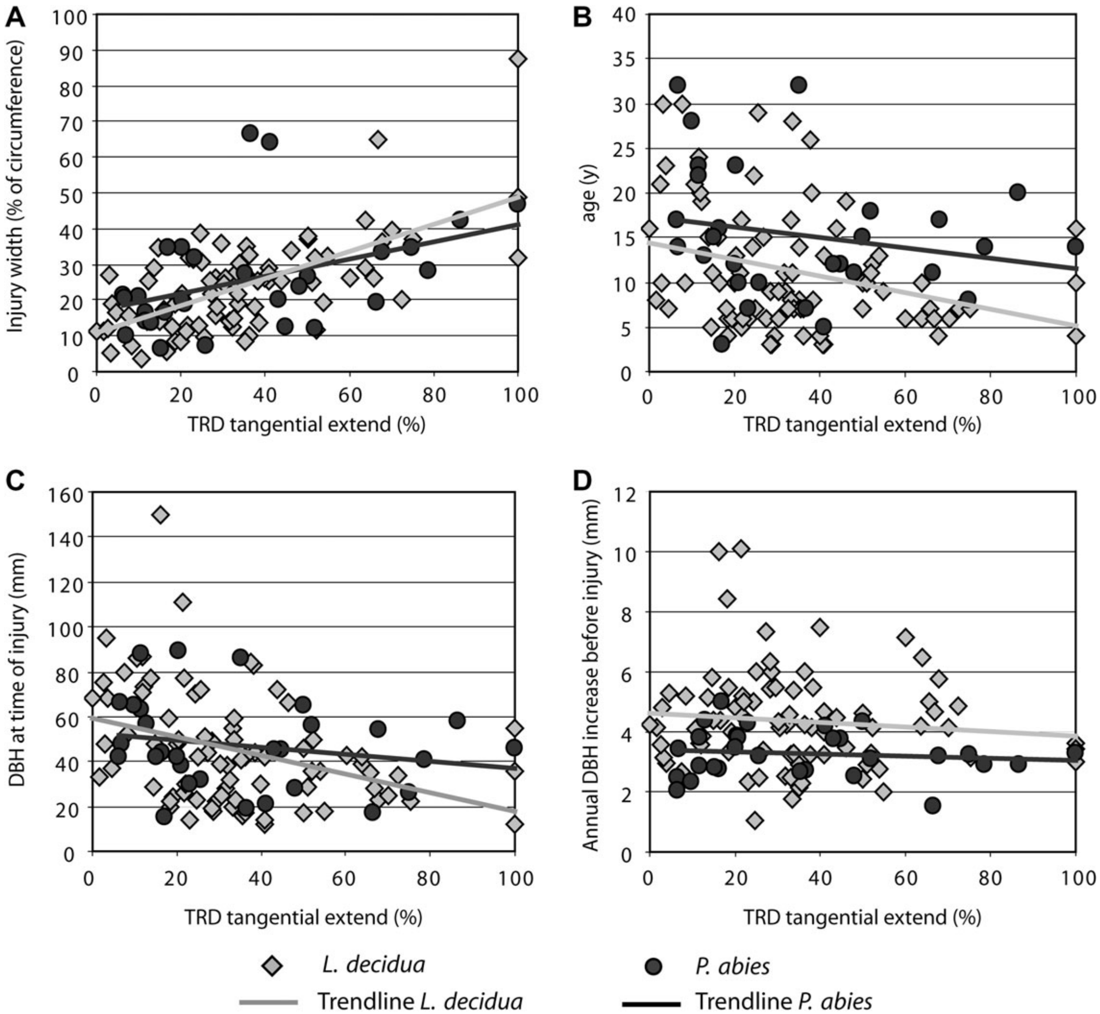

Figure 7. Dependence of TRD formation on (A) injury width; (B) tree age at the time of wounding; (C) DBH at the time of wounding; and (D) annual DBH increment rate before wounding, each with trendlines for *L. decidua* (gray) and *P. abies* (black).

Table 6. Long-term appearance of tangential TRDs in *L. decidua* and *P. abies* following injury. Comparison of formation of tangential TRDs after wounding. Abbreviation: x, year of wounding.

TRDs	*L. deciduas*[a]	*P. abies*[a]	*L. decidua*[b]	*L. decidua*[b]	*L. decidua*[c]
	Rockfall (%)	Rockfall (%)	Rockfall (%)	Avalanche (%)	Debris flow (%)
x	100	100	94.3	87.3	89.3
$x + 1$	56.3	93.1	88.6	79.7	75
$x + 2$	22.1	69	58.9	54.2	64.3
$x + 3$	10.5	57.1	36.1	6.6	67.9
$x + 4$	9.6	57.1	15.8	0.9	57.1
$x + 5$	4.1	53.6	5.1	0	–
$x > 5$	2.3	38.5	–	–	–

Source: [a] Present study. [b] Stoffel and Hitz (2008). [c] Bollschweiler et al. (2008).

analyses of 111 rockfall wounds we can state that: (1) all samples produced TRDs next to the injuries and (2) the first appearance of TRDs was in the year of the injury or at the beginning of the new growing season when wounding occurred during the dormant season. We conclude that a reliable intra-annual dating of events is only possible if entire cross sections are analyzed. A careful sampling strategy based solely on increment cores with TRD as the marker allows rockfall injuries to be dated with a yearly precision.

In conclusion, our results clearly demonstrate the high potential of TRD analysis in dating past rockfall events. Nondestructive coring methods allow analysis of rockfall frequencies and can be used for the assessment of hazard and risks. This study also revealed a very high complexity of TRD formation after collision and identified some of the key factors that influence TRD formation. However, more research is needed to fully decode all aspects of TRD formation in trees.

Acknowledgments

The authors thank Lautaro Correa for his assistance in the field and Oliver Hitz for his helpful comments on wood anatomy. The authors express their appreciation to the local administration and the forest warden, Urs Andenmatten, who allowed them to work in the forest stand and gave permission to fell the experimental trees.

References

Bannan, M.W. 1936. Vertical resin ducts in the secondary wood of the Abietineae. New Phytol. 35:11–46.

Berger, F., C. Quetel and L.K.A. Dorren. 2002. Forest: a natural protection mean against rockfall but with which efficiency? The objectives and methodology of the ROCKFOR project. Intrapraevent 2002 Band 2:815–826.

Bollschweiler, M. 2007. Spatial and temporal occurrence of past debris flows in the Valais Alps – results from tree-ring analysis. GeoFocus 20:182.

Bollschweiler, M., M. Stoffel, D.M. Schneuwly and K. Bourqui. 2008. Traumatic resin ducts in *Larix decidua* stems impacted by debris flows. Tree Physiol. 28:255–263.

Braam, R.R., E.E.J. Weiss and P.A. Burrough. 1987. Spatial and temporal analysis of mass movement using dendrochronology. CATENA 14:573–584.

Clark, G. 1981. Staining procedures. Williams and Wilkins, Baltimore and London, 512 p.

Fahn, A., E. Werker and P. Ben-Tzur. 1979. Seasonal effects of wounding and growth substances on development of traumatic resin ducts in Cedrus libani. New Phytol. 82:537–544.

Franceschi, V.R., T. Krekling and E. Christiansen. 2002. Application of methyl jasmonate on *Picea abies* (Pinaceae) stems induces defense-related responses in phloem and xylem. Am. J. Bot. 89:578–586.

Friedman, J.M., K.R. Vincent and P.B. Shafroth. 2005. Dating floodplain sediments using tree-ring response to burial. Earth Surf. Process. Landforms 30:1077–1091.

Hudgins, J.W., E. Christiansen and V.R. Franceschi. 2004. Induction of anatomical based defense responses in stems of diverse conifers by methyl jasmonate: a phylogenetic perspective. Tree Physiol. 24:251–264.

Krekling, T., V.R. Franceschi, P. Krokene and H. Solheim. 2004. Differential anatomical response of Norway spruce stem tissues to sterile and fungus infected inoculations. Trees 18:1–9.

LePage, H. and Y. Bégin. 1996. Tree-ring dating of extreme water level events at Lake Bienville, Subarctic Québec, Canada. Arct. Alp. Res. 28:77–84.

Luchi, N., R. Ma, P. Capretti and P. Bonello. 2005. Systemic induction of traumatic resin ducts and resin flow in Austrian pine by wounding and inoculation with *Sphaeropsis sapinea* and *Diplodia scrobiculata*. Planta 221:75–84.

Mattheck, G.C. 1996. Trees – the mechanical design. Springer-Verlag, Berlin, 121 p.

Moore, K.W. 1978. Barrier-zone formation in wounded stems of sweetgum. Can. J. For. Res. 8:389–397.

Müller, H.N. 1980. Jahrringwachstum und Klimafaktoren: Beziehungen zwischen Jahrringwachstum von Nadelbaumarten und Klimafaktoren an verschiedenen Standorten im Gebiet des Simplonpasses (Wallis, Schweiz). Veröffentlichungen Forstliche Bundesversuchsanstalt Wien 25, Agrarverlag, Wien, 81 p.

Nagy, N.E., V.R. Franceschi, H. Solheim, T. Krekling and E. Christiansen. 2000. Wound-induced traumatic resin duct formation in stems of Norway spruce (Pinaceae): anatomy and cytochemical traits. Am. J. Bot. 87:313–320.

Rutz, J. 1999. Block-Anprall auf Stahlbetonwände aus Steinschlägen, Lawinen, Murgängen und Überschwemmungen Gebäudeversicherungsanstalt des Kantons. St. Gallen, Sankt Gallen, Switzerland (in German).

Schneuwly, D.M. and M. Stoffel. 2008*a*. Tree-ring based reconstruction of the seasonal timing, major events and origin of rockfall on a case-study slope in the Swiss Alps. Nat. Hazards Earth Syst. Sci. 8:203–211.

Schneuwly, D.M. and M. Stoffel. 2008*b*. Spatial analysis of rockfall activity, bounce heights and geomorphic changes over the last 50 years – a case study using dendrogeomorphology. Geomorphology 102:522–531.

Schweingruber, F.H. 1978. Mikroskopische Holzanatomie. Flück, Teufen, Switzerland, 226 p.

Schweingruber, F.H. 1996. Tree Rings and Environment. Dendroecology, Paul Haupt, Bern, Switzerland, 188 p.

Schweingruber, F.H. 2001. Dendroökologische Holzanatomie. Paul Haupt, Bern, Switzerland, 472 p (in German).

Shigo, A.L. 1984. Compartmentalization: a conceptual framework for understanding how trees grow and defend themselves. Annu. Rev. Phytopathol. 22:189–214.

SMI (Swiss Meteorological Institute). 2008. Annals of the Swiss Meteorological Institute, daily precipitation sums and summarized rainfall, 1987–2007, Zurich.

Stoffel, M. 2008. Dating past geomorphic processes with tangential rows of traumatic resin ducts. Dendrochronologia 26:53–60.

Stoffel, M. and O.M. Hitz. 2008. Rockfall and snow avalanche impacts leave different anatomical signatures in tree rings of juvenile *Larix decidua*. Tree Physiol. 28:1713–1720.

Stoffel, M. and S. Perret. 2006. Reconstructing past rockfall activity with tree rings: some methodological considerations. Dendrochronologia 24:1–15.

Stoffel, M., I. Lièvre, M. Monbaron and S. Perret. 2005. Seasonal timing of rockfall activity on a forested slope at Täschgufer (Valais, Swiss Alps) – a dendrochronological approach. Zeitschrift für Geomorphologie 49(1):89–106.

Strunk, H. 1997. Dating of geomorphological processes using dendrogeomorphological methods. CATENA 31:137–151.

Thomson, R.B. and H.B. Sifton. 1925. Resin canals in the Canadian spruce (*Picea canadensis* (Mill.) B.S.P.). Philos. Trans. R. Soc. Lond. B 214:63–111.

Timell, T.E. 1986. Compression wood in gymnosperms. Springer-Verlag, Berlin, 2150 p.