

# Rockfall and snow avalanche impacts leave different anatomical signatures in tree rings of juvenile *Larix decidua*

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**Summary** Rockfall and snow avalanche events often cause injury to European larch (*Larix decidua* Mill.) trees, giving rise to the formation of callus tissue and tangential rows of traumatic resin ducts (TRDs). We analyzed and quantified anatomical reactions of juvenile trees injured before the start of the growing season by snow avalanches (15 trees, 324 cross sections) or rockfalls (18 trees, 270 cross sections). Traumatic resin ducts were observed in the growth ring formed following injury in 94.3% of the rockfall samples and 87.3% of the snow avalanche samples. Traumatic resin ducts were formed at the beginning of the new annual ring around wounds caused by rockfalls. In contrast, in trees injured by snow avalanches, TRDs were not formed until after the formation of several rows of early earlywood (EE) tracheids (mean  $\pm$  SD =  $4.19 \pm 2.56$  rows). The dimensions of the EE tracheids observed in the snow avalanche samples were greatly reduced in the tissues bordering the wound, with radial width reaching an average of only 50% and lumen cross-sectional area an average of only 46% of pre-event values. It is therefore possible to differentiate injuries due to past snow avalanches from injuries due to rockfall based on anatomical growth reactions in the tissues bordering scars.

**Keywords:** earlywood tracheids, European larch, growth ring, injury, rays, traumatic resin ducts, wood anatomy, wounding.

## Introduction

Effects of geomorphic processes such as rockfall and snow avalanches on trees have usually been investigated by static pulling tests in the field (e.g., Moore 2000, Peltola et al. 2000, Lundström et al. 2007, 2008) and by dynamic impact tests on wood samples in the laboratory (e.g., Sell 1987, Niemz 1993). More recently, analyses have focused on the mechanical resistance of intact trees to stem breakage or uprooting during rockfall impacts (Stokes et al. 2005, Dorren and Berger 2006, Lundström et al., unpublished results).

Dendrogeomorphology has been used to reconstruct past

geomorphic activity in trees (Stoffel and Bollschweiler 2008). Studies on rockfalls have aimed at the dating of events and the determination of event frequency, volume and spatial extent (Stoffel et al. 2005a, 2005b, Perret et al. 2006, Schneuwly and Stoffel 2008a, 2008b), whereas the analyses of trees injured by snow avalanches have primarily considered the frequency and spatial distribution of past activity (Patten and Knight 1994, Hebertson and Jenkins 2003, Stoffel et al. 2006, Butler and Sawyer 2008).

Despite the potential of wood anatomical analyses (Schweingruber 2001), observation of microscopic changes in cell structure resulting from geomorphic activity have rarely been applied in dendrogeomorphological studies. Exceptions include investigations of flooding events (e.g., Kozłowski 1997, St. George et al. 2002), landslides (e.g., Clague and Souther 1982, Fantucci and McCord 1995) and debris-flows (e.g., Bollschweiler et al. 2008). Anatomical changes induced by rockfall or snow avalanches have, in contrast, never been analyzed. Similarly and with the exception of the study by Stoffel et al. (2006) who assessed debris-flow and snow avalanche processes on a forested cone, previous investigations were conducted exclusively where only a single type of geomorphic process disturbed tree growth.

Several conifer species respond to injury with changes in cell structure, including the formation of callus tissue and tangential rows of traumatic resin ducts (TRDs; Bannan 1936, Lev-Yadun 2002, Stoffel and Perret 2006, Stoffel 2008). Bollschweiler et al. (2008) reported on the timing of the first appearance of TRDs after debris-flow impacts and on the axial and tangential extent of TRD around wounds, but they did not focus on the effect of impact events on other anatomical features such as cell or lumen dimensions of earlywood tracheids.

Our objective was to observe and characterize anatomical changes in earlywood tracheid structure, changes in the number of rays and the occurrence of TRDs in juvenile European larch (*Larix decidua* Mill.) trees injured by rockfall or snow avalanches. We report on results for 351 micro-sections prepared from 594 cross sections of 33 trees.

## Materials and methods

### Study sites and sampling

Anatomical changes resulting from snow avalanche or rockfall impacts were analyzed in 33 juvenile *L. decidua* trees felled at two sites within the Valais Alps, Switzerland.

The rockfall site, Täschgufer, is located northeast of the village of Täsch (46°4' N, 7°47' E, 1780–1900 m a.s.l.; Figure 1A) and is subject to frequent rockfall activity. Trees are continually removed by rockfalls, and the stand therefore remains predominantly young. Scars are frequently observed on tree stems and rockfall fragments hit individuals on an approximately decadal basis (Stoffel et al. 2005a). Based on scar positions and on-site observations, rockfall usually occurs outside the vegetation period (88%) in April or May (Stoffel et al. 2005b). Although rockfall occurs frequently, no snow avalanches have been witnessed on the slope. Figure 1B illustrates one of the 18 *L. decidua* trees felled for analysis.

Figure 1D shows a characteristic example of one of the 15 *L. decidua* trees selected at the snow avalanche site, Sitstafol, located in the Nanztal valley east of Visperterminen, where trees colonize a small cone close to the valley floor (46°14' N, 7°57' E, 1750–1810 m a.s.l.; Figure 1C). Adult trees are largely absent from the site, and the juvenile *L. decidua* trees growing on the fan show signs of multiple snow avalanche impacts in the form of scars, apex loss or tilted trunks. Dendrogeomorphological analysis of trees at this site indicate that snow avalanches occur on an almost yearly basis (Stoffel et al. 2007), but evidence of rockfall was absent.

At both study sites, trees were felled close to ground level with a handsaw and entire stems transported to the laboratory. For each tree, data recorded included (1) sketches and position of visible defects in tree morphology such as scars, broken crowns or branches, candelabra growth and tilted stems; (2) tree height (cm); (3) diameter at breast height (DBH); and (4) indications of damage to neighboring trees (Table 1).

### Sample preparation

In the laboratory, stem cross sections were prepared with a circular saw at points 5 to 8 cm apart along each stem. As shown in Table 1, 270 cross sections were sawn from the 18 trees from the rockfall site and 324 cross sections were taken from the 15 trees from the avalanche site. Thereafter, small cubes (6–8 mm edges) were prepared from the cross sections from which transverse micro-sections (15 µm) were cut with a Reichert sliding microtome equipped with wedge-shaped blades. In total, 158 micro-sections were prepared from the rockfall trees and 171 micro-sections from the snow avalanche trees. Sections were obtained from the tissues immediately adjacent to the wounds and prepared as described by Schweingruber (2001) and Schoch et al. (2004). Pictures (2088 × 1550 pixels, 150 dpi) were taken of the micro-sections with a digital microscope camera. Analysis of tracheids was made at 50× magnification to capture tree rings in groups of at least three or four.

### Qualitative assessment of TRD formation following impacts

To identify the seasonal onset of callus tissue and TRD forma-

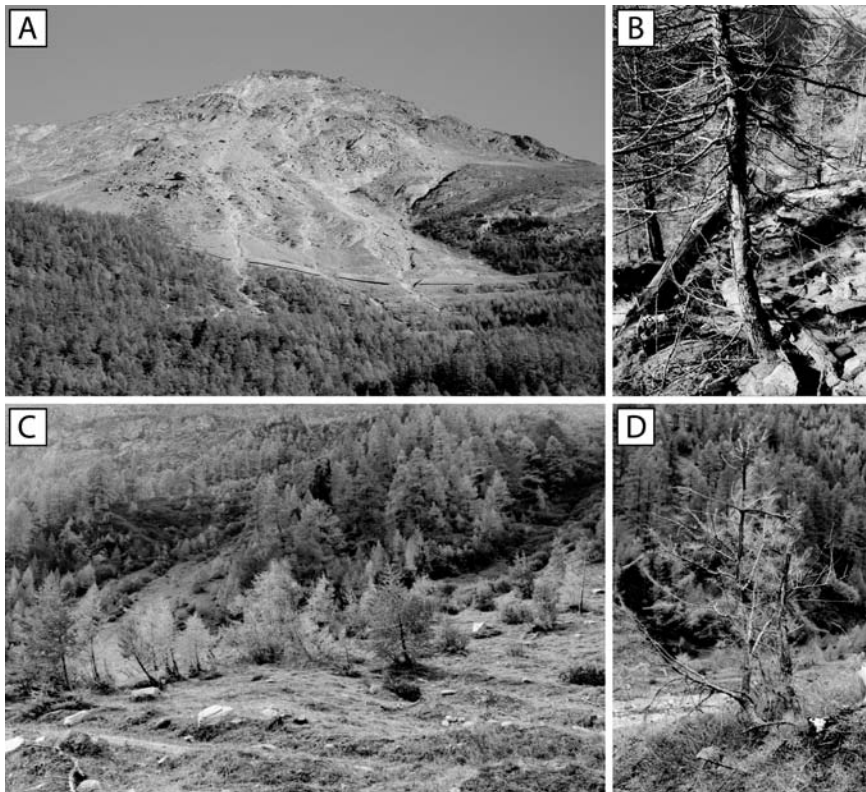


Figure 1. (A) The forest stand at Täschgufer is dominated by *Larix decidua* and (B) the predominantly young trees growing at the upper limit of the forest are regularly injured by rockfall activity. (C) Snow avalanches affect the Sitstafol cone on an almost yearly basis and leave multiple signs of activity in (D) the juvenile *L. decidua* trees.

tion, annual rings were subdivided as follows: the first formed cell layer (in which TRD production was expected to occur as a result of an injury during the dormant season), early (EE), middle (ME) and late (LE) earlywood, and early (EL) and late (LL) latewood (Figure 2). We noted the position of callus tissue, the first occurrence of TRDs after an impact and the position of TRDs later in the annual ring and in subsequent years. The tangential extent of TRD formation was qualitatively assessed on the cross sections to identify radial migration of TRDs to different portions of the annual ring with increasing distance from the wound, as described by Bollschweiler et al. (2008) for trees injured by debris flows.

#### Quantitative assessment of anatomical changes in tracheids

We analyzed the number of rows of earlywood tracheids before the onset of TRDs in all cross sections of all snow avalanche wounds and for those rockfall samples where wood-penetrating impacts occurred before the onset of the vegetation period. Similarly, the number of rays was assessed on the micro-sections and changes before and after an impact quantified. Generally, the number of rays was counted on a surface of 1 mm<sup>2</sup> in the LE cell layers of the year of impact and the preceding year.

Dimensions of EE tracheids were measured with the automated image analysis program WinCell Pro Version 5.6c (Régent Instruments 2008) with a precision of 1 µm. We measured the radial length and tangential width of EE tracheids for (1) the year preceding and (2) the year following the impact and (3) EE tracheid rows present before the onset of TRDs in the annual ring where wounding occurred. In a subsequent step, the lumen width of EE tracheids was assessed on a surface of about 0.5 mm<sup>2</sup>, with error margins of 50 µm<sup>2</sup> (i.e., intercellular interstices) for the lower and 1300 µm<sup>2</sup> for the upper limit (i.e., several tracheids with poorly discernible cell walls). Analyses were performed on eight snow avalanche samples and three rockfall samples where wounding occurred outside the vegetation period.

## Results

### Callus and TRD formation following wounding

Chaotic callus and TRDs are the most common growth fea-

Table 1. Overview of the rockfall and snow avalanche datasets used for analysis. Abbreviation: DBH, diameter at breast height.

Trees	Age <sup>1</sup>	Height (cm)	DBH (cm)	Stem discs	Micro-sections	Scars
<i>Rockfall trees</i>						
18	37	380	7	270	180	180
<i>Avalanche trees</i>						
15	29	325	8	324	171	212
<i>Total</i>						
33	–	–	–	594	351	392

<sup>1</sup> Assessed at the stem base.

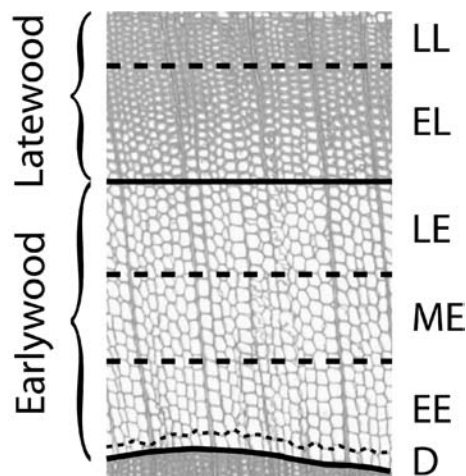


Figure 2. Subdivision of *Larix decidua* tree rings according to the time of formation: the first formed cell layer in which tangential rows of traumatic resin duct (TRD) formation usually occurs as the result of injury during the dormant season (D), early (EE), middle (ME) and late (LE) earlywood, and early (EL) and late (LL) latewood.

tures observed in tissues that are axially and tangentially located around stem wounds in *Larix decidua*. Although chaotic callus always formed on both sides of the wounds, TRDs were occasionally missing from the tissue bordering the impacts.

Traumatic resin ducts were formed in 149 (94.3%) of the 158 rockfall samples following injury outside the vegetation period and were observed following the impact for a mean ( $\pm$  SD) period of  $2.31 \pm 1.22$  years. In a few samples, TRDs were even observed 5 years after the event (5.4%), but most frequently, their occurrence was restricted to the first 3 years after rockfall wounding (Table 2).

The percentage of samples with TRDs following snow avalanche impacts (87.3%) was slightly less than for the rockfall samples (94.3%) (Table 2). Resin ducts were, on average, present for  $1.62 \pm 0.78$  years after a snow avalanche impact

Table 2. Presence of tangential rows of traumatic resin ducts (TRDs) in the years following impacts in rockfall and snow avalanche trees injured before the onset of the local vegetation period.

TRDs	Rockfall		Snow avalanche	
	n	%	n	%
Present around wound	149	94.3	185	87.3
Absent around wound	9	5.7	27	12.7
Only present in year of event	9	6.0	16	8.6
Event year + 1 year	47	31.5	54	29.2
Event year + 2 years	36	24.2	101	54.6
Event year + 3 years	32	21.5	12	6.5
Event year + 4 years	17	11.4	2	1.1
Event year + 5 years	8	5.4	0	0.0
Total	149	100	185	100
Mean (years)	2.31		1.62	
Standard deviation (years)	1.22		0.78	

and were most frequently observed only in the year of wounding and in the subsequent annual ring (29.2%) or in the two annual rings (54.6%) following wounding. No TRDs were observed more than three years after a snow avalanche impact.

The rockfall (Figure 3) and snow avalanche (Figure 4) samples differed in the first occurrence of callus tissue and TRDs following an impact. Although callus formation always started at the beginning of the new annual ring in both datasets (Figure 4), TRD formation was systematically delayed in the annual rings of trees injured by snow avalanches. This lag between the dormant period when wounding occurred and the onset of callus and TRD formation is evident in Table 3, as resin ducts were formed only in EE (96.8%) or ME (3.2%). In the rockfall samples, in contrast, no earlywood tracheids were observed between the end of the previous growth ring and the formation of TRDs in 98% of samples, and only three wounds were identified where TRDs were formed after one row of EE tracheids formed in the tissues adjoining the wound.

The number of EE tracheid rows preceding TRDs averaged  $0 \pm 0.2$  rows in the rockfall samples, and no sample had more than one layer of EE tracheids (Figure 3). In the snow ava-

lanche samples, in contrast, 1–15 EE (and ME) tracheid rows (mean:  $4.19 \pm 2.56$  rows) were observed in the increment ring formed following impact (Figure 4).

The radial location of TRD formation sometimes migrated with increasing distance from the wound. Such a shift was observed in 31% of rockfall samples and 36% of snow avalanche samples. In the rockfall samples, the radial migration was toward later formed cell layers in the ring (Figure 5A), whereas in 10% of the snow avalanche samples, the migration was in the opposite direction, with the number of EE tracheids between the growth ring boundary of the previous ring and the first TRDs decreasing with increasing tangential distance from the wound (Figure 5B).

#### *Formation of rays around impacts*

Rockfall and snow avalanche impacts caused changes in the number of rays in the samples. There was no significant difference in the number of rays between the sample types. The number of rays in the late earlywood (LE) layers increased by more than 40% in the year of the impact compared with the year preceding it (Table 4). In the rockfall samples, the number

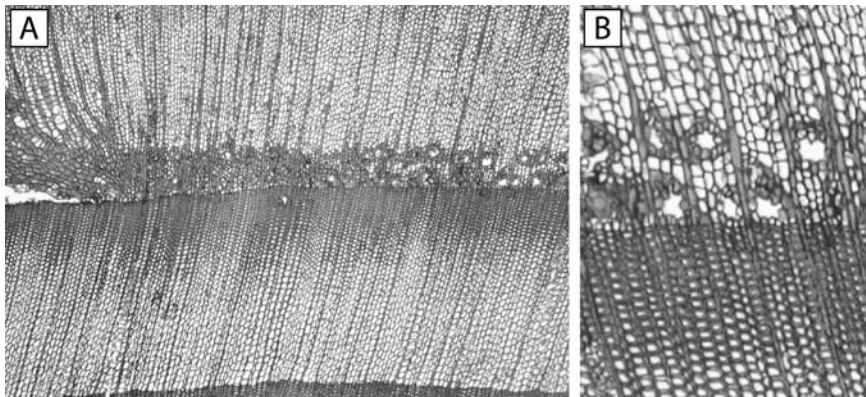


Figure 3. First occurrence of callus tissue and tangential rows of traumatic resin ducts (TRDs) after rockfall-induced wounding before the start of the local vegetation period. Note the formation of callus tissue and TRDs at the beginning of the new growth ring.

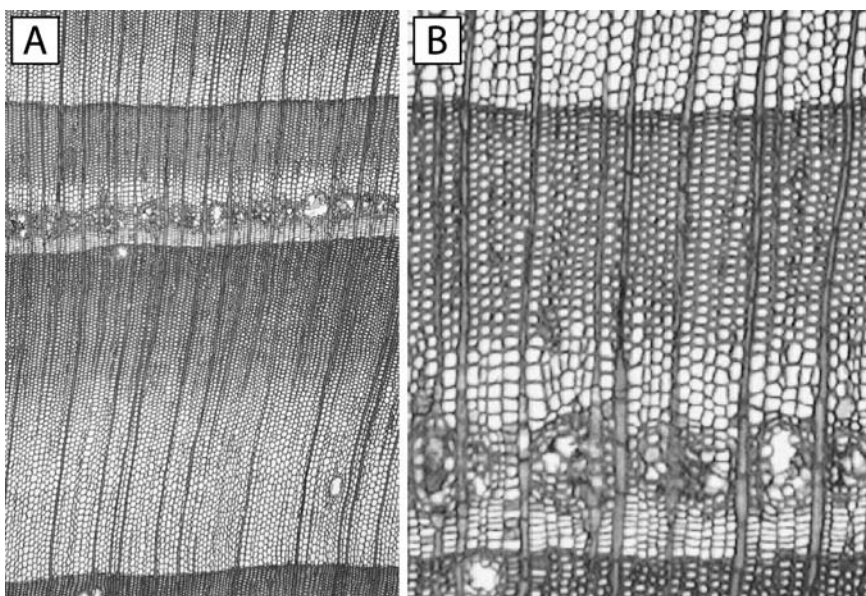


Figure 4. First occurrence of tangential rows of traumatic resin ducts (TRDs) following snow avalanche-induced wounding during the dormant period. Note the delayed occurrence of TRDs and the presence of flattened EE tracheids.

Table 3. Onset of callus tissue formation and production of tangential rows of traumatic resin ducts (TRDs) as a reaction to wounding during the dormant season. Abbreviations: D, first formed cell layer; EE, early earlywood; and ME, middle earlywood.

Callus and TRD formation	Rockfall							Snow avalanche								
	D	%	EE	%	ME	%	Tot	%	D	%	EE	%	ME	%	Tot	%
First callus tissue formation	158	100	0	0	0	0	158	100	212	100	0	0	0	0	212	100
First TRD formation	145	98	3	2	0	0	148	100	0	0	179	96.8	6	3.2	185	100

of rays increased from  $11 \pm 2.0$  to  $16 \pm 3.0 \text{ mm}^{-2}$ , whereas in the snow avalanche samples, the number of rays increased from  $10 \pm 2.2$  to  $15 \pm 2.7 \text{ mm}^{-2}$ . In both datasets, we observed that many additional rays were absent at the beginning of the new annual ring, but emerged in the ME or LE tracheid layers in the year of wounding.

#### Anatomical changes in earlywood tracheids

We focused on variations in the radial and tangential widths and the lumen cross-sectional area of individual tracheids in the EE rows in the annual ring formed in the year preceding and in the annual ring formed in the year following wounding as well as on changes in the EE rows formed before TRDs in the year of impact (event year).

Quantification of changes in the snow avalanche samples was based on eight micro-sections and on the measurement of 12,619 EE tracheids. Results are presented in Table 5 and in the boxplots in Figure 6. Wounding of *L. decidua* led to a reduction of almost 50% in radial widths of EE tracheids formed before the first appearance of TRDs in the event year (Figures 4 and 6A) compared with those formed in the year preceding impact. In the year following the impact, the radial widths of EE tracheids increased to a mean value of  $19 \mu\text{m}$ , which was 77% of the value measured before wounding. The tangential widths of EE tracheids were also reduced as a result of wounding, but the reduction averaged only 15% (Figure 6B).

The changes in radial and tangential widths of EE tracheids of trees impacted by snow avalanches caused a reduction in lumen cross-sectional area to only  $46 \pm 15\%$  of the value measured in the year preceding the event (Figures 4 and 6C). In the growth ring formed in the year succeeding the impact, lumen cross-sectional area generally remained smaller, with a reduction equal to  $35 \pm 15\%$  of that measured in the ring formed be-

fore wounding.

In the rockfall trees, where wounding occurred before the start of the vegetation period, EE tracheids were not normally present before TRD formation in the tissues adjacent to the injury. Away from the point of impact, where EE tracheids were formed in the year of wounding before TRD formation, there was a 27% reduction in radial width of EE tracheids of rockfall samples relative to the width of EE tracheids formed the previous year. Changes in the tangential widths of EE tracheids as a result of wounding were insignificant in the year of wounding. We observed a slight reduction in EE tracheid lumen cross-sectional area in the event year ( $-19\%$ ), but it was much less pronounced compared with that in the snow avalanche samples, and EE tracheids reached pre-event dimensions in the growth ring formed in the year following a snow avalanche event.

#### Discussion

We analyzed 324 cross sections from 15 *Larix decidua* trees injured by snow avalanche and 270 cross sections from 18 *L. decidua* trees scarred by rockfall events and assessed anatomical changes in tree growth following wounding. Tangential rows of TRDs were observed in the growth ring formed during the vegetation period following injury in 94.3% of rockfall samples and 87.3% of snow avalanche samples, which is in agreement with observations by Bannan (1936), Cruickshank et al. (2006) and Bollschweiler et al. (2008). Besides chaotic callus tissue bordering 100% of the rockfall and snow avalanche wounds, TRDs were the most common feature observed in the tissues bordering scars in the tangential and axial directions.

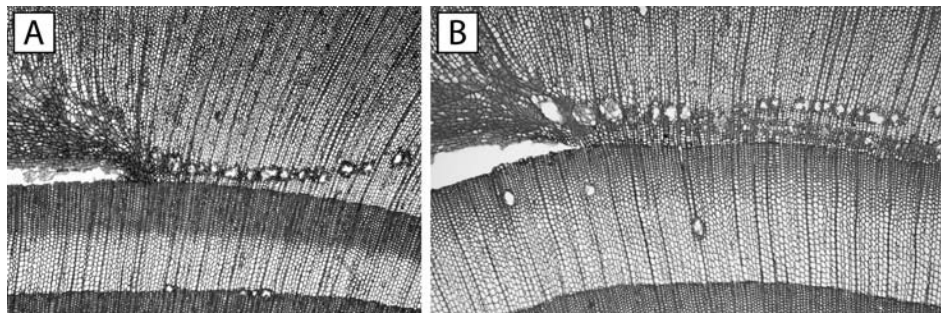


Figure 5. (A) Radial migration of tangential rows of traumatic resin ducts (TRDs) toward later formed cell layers of the annual ring are often observed in rockfall and snow avalanche samples with increasing tangential distance from the wound. (B) In 10% of snow avalanche samples, radial migration results in fewer EE tracheids between the boundary of the previous ring and the first TRDs with increasing tangential distance from the wound.

The number of rays formed in the late earlywood (LE) layers increased by more than 40% in the year of the impact compared with the year preceding it. This finding is in agreement with data from Lev-Yadun and Aloni (1992, 1993, 1995), who reported significant changes in the numbers, sizes or shapes of rays in several conifer and broad-leaved species including *Ailanthus altissima* (Mill.) Swingle, *Melia azedarach* L. and *Pinus halepensis* Mill.

In a majority of samples, multiple series of TRDs were formed over several growing seasons after wounding. In the rockfall trees, TRDs were present in an average of  $2.31 \pm 1.22$  growth rings after the event, whereas they were found in an average of only  $1.62 \pm 0.78$  rings after wounding in snow avalanche trees. These multiple series belong to the same initial event and, according to Franceschi et al. (2002), result from the continuous production of signaling agents.

After an injury, resin production in conifers starts within only a few days, and axial ducts normally emerge from the developing secondary xylem within less than 3 weeks (cf. Ingemarsson and Bollmark 1997, Ruel et al. 1998, Fink 1999, Martin et al. 2002, McKay et al. 2003, Luchi et al. 2005). We observed that TRDs occurred immediately at the beginning of the new annual ring around rockfall wounds occurring during the dormant period, thus confirming the findings of the above studies. In trees injured by snow avalanches, however, we detected a delay in TRD formation. Although snow avalanche impacts occurred during the dormant period and callus tissue was present at the beginning of the new growth ring, TRDs emerged in the new growth ring only after several rows of EE tracheids (mean =  $4.19 \pm 2.56$  rows) had formed. In addition, the tangential extent of TRDs was less in trees injured by snow avalanches than in trees injured by rockfall.

We demonstrated that the location of TRD formation sometimes migrated radially to later formed cell layers with increasing distance from the wound. Changes in the radial position of ducts with distance from the injury have been described previously by Bannan (1936), but his observations concerned only changes in position relative to the upper and lower boundaries of the wound. Bollschweiler et al. (2008) and Schneuwly and Stoffel (2008a, 2008b), in contrast, report radial migration of ducts at the mid-point between the upper and lower wound boundaries, as observed in our study. Such variation in the position of TRD formation is consistent with its dependence on a slowly propagating hormonal signal. Krekling et al. (2004) state that, in *Picea abies* (L.) Karst., this signal propagates

Table 4. Mean, maximum and minimum number of rays observed in the late earlywood (LE) cell layers in the year preceding the impact and in the event year and their percent change between years.

Rays	Rockfall			Snow avalanche		
	Before	Event year	%	Before	Event year	%
Mean	11	16	42	10	15	47
Max	15	23	80	14	21	100
Min	9	14	24	7	9	18
SD	2.0	3.0	16.5	2.2	2.7	22.8

about  $2.5 \text{ cm day}^{-1}$  in the axial direction. There are, however, no data on the rate of signal propagation in *L. decidua*. We do not know of any study reporting centrifugal migration of TRDs with increasing distance from the wound, although we

Table 5. Absolute (Abs) and relative (%) changes in radial and tangential widths and lumen cross-sectional area of early earlywood (EE) tracheids in the year of impact as well as in the growth ring preceding (-1) and succeeding (+1) wounding. Maximum values are in bold, and minimum values are italicized.

Avalanche	-1		Event year		+1	
	Abs		Abs	%	Abs	%
<i>Lumen cross-sectional area (<math>\mu\text{m}^2</math>)</i>						
1	<b>502</b>		138	27	292	58
2	284		147	52	179	63
3	297		103	35	207	70
4	287		146	51	164	57
5	408		<b>273</b>	67	–	–
6	323		209	65	<b>300</b>	93
7	310		121	39	<i>159</i>	51
8	296		87	29	–	–
Mean	338		153	46	217	65
SD	77		61	15	64	15
<i>Tracheid radial width (<math>\mu\text{m}</math>)</i>						
1	<b>34</b>		12	37	<b>25</b>	76
2	22		13	61	18	81
3	23		9	38	18	76
4	21		11	54	<i>14</i>	68
5	27		<b>20</b>	73	–	–
6	25		18	71	24	96
7	26		14	53	17	67
8	26		10	40	–	–
Mean	25		13	53	19	77
SD	4		4	14	4	11
<i>Tracheid tangential width (<math>\mu\text{m}</math>)</i>						
1	<b>18</b>		13	75	14	78
2	16		13	85	12	78
3	15		14	93	14	90
4	16		15	92	14	82
5	<b>18</b>		<b>16</b>	91	–	–
6	15		14	92	<b>15</b>	100
7	<i>14</i>		<i>11</i>	78	<i>11</i>	78
8	<i>14</i>		<i>11</i>	77	–	–
Mean	16		13	85	13	84
SD	2		2	8	1	9
<i>Growth ring width (<math>\mu\text{m}</math>)</i>						
1	2390		1310	55	1170	49
2	2160		950	44	760	35
3	1440		740	51	1270	88
4	1620		660	41	1340	83
5	770		1990	258	–	–
6	2420		2590	107	2910	120
7	2100		1390	66	1930	92
8	870		1040	120	–	–
Mean	1720		1330	93	1560	78
SD	65		66	73	76	31

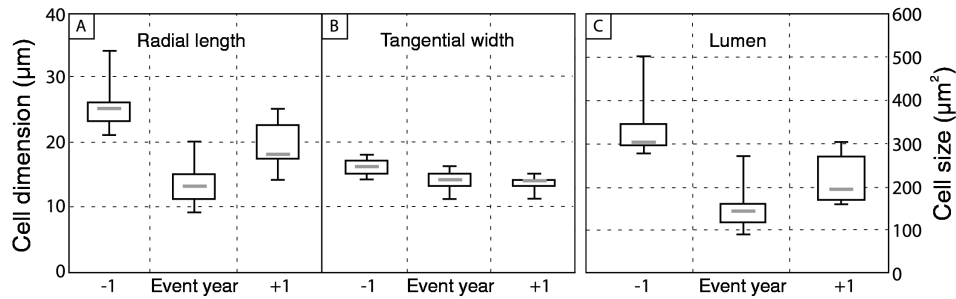


Figure 6. Changes in the (A) radial length, (B) tangential width and (C) lumen of EE tracheids as a result of snow avalanche-induced wounding in *Larix decidua*. Cells formed in the growth ring of wounding (*event year*) are compared with those of the increment ring formed before (*-1*) and after (*+1*) the injuring event.

observed this phenomenon in the tissues bordering about 10% of the snow avalanche injuries.

The impacts affected the radial widths and lumen cross-sectional areas of subsequently formed EE tracheids, but had less effect on their tangential widths. Changes were most evident in the EE tracheids formed between the growth boundary of the pre-event ring and the first occurrence of TRDs in snow avalanche trees, with widths reduced by almost 50% and lumen cross-sectional areas reduced by more than 50%. In the rockfall trees, EE tracheid dimensions were less affected by wounding and only detected at distances > 1 cm from the wound. Fahh et al. (1979) and Fahh and Zamski (1970) report on “tracheids of the late type” in *Cedrus libani* A. Rich. and “traumatic tracheids” in *Pinus halepensis* as a result of wounding, by which they were most likely referring to the presence of narrower and flattened EE tracheids as observed in our study.

Our data provide evidence that juvenile *L. decidua* reacts to rockfall and snow avalanche events in different ways and with a slight difference in timing. As a result, it is possible to differentiate the causes of past injuries by anatomical investigations of the tissues bordering scars. The cause of these differences is unknown. Although an abrupt reduction in EE tracheid cross-sectional area was observed in the snow avalanche trees from the beginning of the new growth ring, resin duct formation was delayed. Based on local growth data (Müller 1980), the duration of this delay must have been at least several days and possibly a few weeks. We observed a centrifugal migration of TRDs at a distance from the wound in some snow avalanche samples.

The reason for the difference in anatomical response to rockfall and snow avalanche impacts is unknown. Rockfall impacts are highly localized and energy absorption occurs rapidly, whereas snow avalanches impact much of the tree stem, with events lasting from several seconds to several minutes. The anatomical differences between rockfall and snow avalanche scars may therefore result from differences in the intensity and duration of the two types of event. However, it is possible that, through an effect on stem temperature, the persistence of avalanche snow around the stem base affects wound ethylene and jasmonate production and processes of cell differentiation, thereby producing a characteristic wound response.

Similar to flooding, avalanche snow around the tree persisting into the vegetation period may markedly affect soil and stem tissue aeration and thereby influence vascular differenti-

ation (Kozłowski 1997, Yamamoto et al. 1987).

In conclusion, we found that juvenile *Larix decidua* trees exhibited different anatomical reactions following dormant season injury by rockfalls and snow avalanches. These findings will allow analysis of event frequencies of snow avalanches and rockfall on complex multi-process sites where tree rings could not be used for the assessment of hazards and risks so far.

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#### References

- Bannan, M.W. 1936. Axial resin ducts in the secondary wood of the Abietineae. *New Phytol.* 35:11–46.
- Bollschweiler, M., M. Stoffel, D.M. Schneuwly and K. Bourqui. 2008. Traumatic resin ducts in *Larix decidua* impacted by debris flows. *Tree Physiol.* 28:255–263.
- Butler, D.R. and C.F. Sawyer. 2008. Dendrogeomorphology and high-magnitude snow avalanches: a review and case study. *Nat. Hazards Earth Syst. Sci.* 8:303–309.
- Clague, J.J. and J.G. Souther. 1982. The Dusty Creek landslide on Mount Cayley, British Columbia. *Can. J. Earth Sci.* 19:524–539.
- Cruickshank, M.G., D. Lejour and D.J. Morrison. 2006. Traumatic resin canals as markers of infection events in Douglas-fir roots infected with *Armillaria* root disease. *For. Pathol.* 36:372–384.
- Dorren, L.K.A. and F. Berger. 2006. Stem breakage of trees and energy dissipation during rockfall impacts. *Tree Physiol.* 26:63–71.
- Fahh, A. and E. Zamski. 1970. The influence of pressure, wind, wounding and growth substances on the rate of resin duct formation in *Pinus halepensis* wood. *Israel J. Bot.* 19:429–446.
- Fahh, 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.
- Fantucci, R. and A. McCord. 1995. Reconstruction of landslide dynamic with dendrochronological methods. *Dendrochronologia* 13: 43–58.
- Fink, S. 1999. Pathological and regenerative plant anatomy. *Encyclopedia of wood anatomy XIV*. Gebrüder Borntraeger, Berlin, Stuttgart, 1095 p.

- 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.
- Hebertson, E.G. and M.J. Jenkins. 2003. Historic climate factors associated with major avalanche years on the Wasatch Plateau, Utah. *Cold Reg. Sci. Technol.* 37:315–332.
- Ingemarsson, B.S.M. and M. Bollmark. 1997. Ethylene production and 1-aminocyclopropane-1-carboxylic acid turnover in *Picea abies* hypocotyls after wounding. *J. Plant Physiol.* 151:711–715.
- Kozłowski, T.T. 1997. Responses of woody plants to flooding and salinity. *Tree Physiol. Monograph* 1:1–29.
- 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.
- Lev-Yadun, S. 2002. The distance to which wound effects influence the structure of secondary xylem of decapitated *Pinus pinea*. *J. Plant Growth Regul.* 21:191–196.
- Lev-Yadun, S. and R. Aloni. 1992. The role of wounding in the differentiation of vascular rays. *Int. J. Plant Sci.* 153:348–357.
- Lev-Yadun, S. and R. Aloni. 1993. Effect of wounding on the relations between vascular rays and vessels in *Melia azedarach* L. *New Phytol.* 124:339–344.
- Lev-Yadun, S. and R. Aloni. 1995. Differentiation of the ray system in woody plants. *Bot. Rev.* 61:45–88.
- Luchi, N., R. Ma, P. Capretti and P. Bonello. 2005. Systematic 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.
- Lundström, T., U. Heiz, M. Stoffel and V. Stöckli. 2007. Fresh-wood bending: linking the mechanical and growth properties of a Norway spruce stem. *Tree Physiol.* 27:1229–1241.
- Lundström, T., M. Stoffel and V. Stöckli. 2008. Fresh-stem bending of fir and spruce. *Tree Physiol.* 28:355–366.
- Martin, D., D. Tholl, J. Gershenzon and J. Bohlmann. 2002. Methyl jasmonate induces traumatic resin ducts, terpenoids resin biosynthesis, and terpenoids accumulation in developing xylem of Norway spruce stems. *Plant Physiol.* 129:1003–1018.
- McKay, S.A.B., W.L. Hunter, K.A. Godard, S.X. Wang, D.M. Martin, J. Bohlmann and A.L. Plant. 2003. Insect attack and wounding induce traumatic resin duct development and gene expression of (–)-pinene synthase in Sitka spruce. *Plant Physiol.* 133:368–378.
- Moore, J.R. 2000. Differences in maximum bending moments of *Pinus radiata* trees grown on a range of soil types. *For. Ecol. Manage.* 135:63–71.
- 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 Bundes-Versuchsanstalt Wien 25, Agrarverlag, Wien, 81 p.
- Niemz, P. 1993. Physik des Holzes und der Holzwerkstoffe. DRW-Verlag, Stuttgart, 243 p.
- Patten, R.S. and D.H. Knight. 1994. Snow avalanches and vegetation pattern in cascade canyon, Grand Teton National Park, Wyoming, USA. *Arct. Alp. Res.* 26:35–41.
- Peltola, H., S. Kellomäki, A. Hassinen and M. Granader. 2000. Mechanical stability of Scots pine, Norway spruce and birch: an analysis of tree-pulling experiments in Finland. *For. Ecol. Manage.* 135:143–153.
- Perret, S., M. Stoffel and H. Kienholz. 2006. Spatial and temporal rockfall activity in a forest stand in the Swiss Prealps—a dendrogeomorphological case study. *Geomorphology* 74:219–231.
- Régent Instruments. 2008. <http://www.regentinstruments.com/> (accessed March 4, 2008).
- Ruel, J.J., M.P. Ayres and P.L. Lorio. 1998. Loblolly pine responds to mechanical wounding with increased resin flow. *Can. J. For. Res.* 28:596–602.
- Schneuwly, D.M. and M. Stoffel. 2008a. Tree-ring based reconstruction of the seasonal timing, major events and origin of rockfall on a case-study slope in the Swiss Alps. *Nat. Hazard Earth Syst. Sci.* 8:203–211.
- Schneuwly, D.M. and M. Stoffel. 2008b. Changes in spatio-temporal patterns of rockfall activity on a forested slope—a case study using dendrogeomorphology. *Geomorphology*. In press.
- Schoch, W., I. Heller, F.H. Schweingruber and F. Kienast. 2004. Wood anatomy of central European species. Online version: <http://www.woodanatomy.ch> (accessed March 4, 2008).
- Schweingruber, F.H. 2001. Dendroökologische Holzanatomie. Anatomische Grundlagen der Dendrochronologie. Paul Haupt Verlag, Bern, Stuttgart, Wien, 471 p.
- Sell, J. 1987. Eigenschaften und Kenngrößen von Holzarten. Baufachverlag AG, Zürich, 80 p.
- St. George, S., E. Nielsen, F. Conciatori and J. Tardif. 2002. Trends in *Quercus macrocarpa* vessel areas and their implications for tree-ring paleoflood studies. *Tree-Ring Res.* 58:3–10.
- Stoffel, M. 2008. Dating past geomorphic activity with tangential rows of traumatic resin ducts. *Dendrochronologia* 26:53–60.
- Stoffel, M. and M. Bollschweiler. 2008. Tree-ring analysis in natural hazards research—an overview. *Nat. Hazards Earth Syst. Sci.* 8:187–202.
- Stoffel, M. and S. Perret. 2006. Reconstructing past rockfall activity with tree rings: some methodological considerations. *Dendrochronologia* 24:1–15.
- Stoffel, M., D. Schneuwly, M. Bollschweiler, I. Lièvre, R. Delaloye, M. Myint and M. Monbaron. 2005a. Analyzing rockfall activity (1600–2002) in a protection forest—a case study using dendrogeomorphology. *Geomorphology* 68:224–241.
- Stoffel, M., I. Lièvre, M. Monbaron and S. Perret. 2005b. Seasonal timing of rockfall activity on a forested slope at Täschgufer (Valais, Swiss Alps)—a dendrochronological approach. *Z. Geomorphol.* 49:89–106.
- Stoffel, M., M. Bollschweiler and G.R. Hassler. 2006. Differentiating past events on a cone influenced by debris-flow and snow avalanche activity—a dendrogeomorphological approach. *Earth Surf. Process. Landf.* 31:1424–1437.
- Stoffel, M., M. Bollschweiler, G.R. Hassler and M. Monbaron. 2007. Reconstitution de dendrogeomorphologie de la dynamique spatio-temporelle des avalanches dans le Nanttal et le Lötschental. *Bull. Murith.* 125:89–97.
- Stokes, A., F. Salin, A.D. Kokutse et al. 2005. Mechanical resistance of different tree species to rockfall in the French Alps. *Plant Soil* 103:155–164.
- Yamamoto, F., T.T. Kozłowski and K.E. Wolter. 1987. Effect of flooding on growth, stem anatomy, and ethylene production of *Pinus halepensis* seedlings. *Can. J. For. Res.* 17:69–79.