Traumatic resin ducts in *Larix decidua* stems impacted by debris flows

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Summary Following mechanical injury, stems of many conifers produce tangential rows of traumatic resin ducts (TRDs), the distribution of which has been used to date geomorphic events. However, little is known about how far TRD formation extends tangentially and axially from the point of injury or what the time course of TRD appearance is. We analyzed 28 injuries in eight Larix decidua Mill. tree stems resulting from debris flows in October 2000 and November 2004. Injuries occurred outside the period of cambial activity, and TRD formation occurred in the first layers of the growth ring formed in the year following that of injury. The axial extent of TRD formation averaged 74 cm and was greater above the injury than below it. At the height of the wound center, TRDs extended horizontally to a mean of 18% of the stem circumference excluding that portion where the cambium had been destroyed. In subsequent growth rings, TRDs, if present, were confined mainly to the height of the center of injury. Both the vertical and horizontal extent of TRD formation was related to the injury size. Within growth rings, the position of TRD formation changed with increasing distance from the wound progressing from early earlywood to later portions of the growth ring.

Keywords: axial extension, dendrogeomorphology, European larch, injury, onset of traumatic resin ducts, tangential extension.

Introduction

Debris flows on steep hillsides are fast-flowing mixtures of water, gas, soil and rock (Varnes 1978) that can cause tree stem abrasion, bending, burial or breakage. Growth responses to such impacts, which include compression wood formation (Clague and Souther 1982, Timell 1986, Braam et al. 1987, Fantucci and Sorriso-Valvo 1999), reduced growth (La-Marche 1968, Strunk 1997) and multiple leader formation (Butler and Malanson 1985, Mattheck 1996), have been used to date geomorphic events (e.g., Baumann and Kaiser 1999, May and Gresswell 2004, Stoffel et al. 2005*a*, Bollschweiler and Stoffel 2007).

In many conifers, mechanical damage to stems results in the

formation of tangential rows of traumatic resin ducts (TRDs; LePage and Bégin 1996, Stoffel and Perret 2006). In several studies, the presence and distribution of TRDs have been used to date past debris flows (Stoffel and Beniston 2006, Bollschweiler et al. 2007, Stoffel 2007). There is uncertainty, however, about the timing and the vertical and horizontal distribution of TRD formation following stem injury. This information is crucial for determining the appropriate sampling strategy for tree-ring analysis based on nondestructive increment core sampling.

Widely scattered resin ducts are a common feature in stems of trees of the genus *Larix* (Bannan 1936). In contrast, TRD formation in the developing secondary xylem is observed only after insect or fungal attack, fire damage or mechanical wounding (e.g., Thomson and Sifton 1925, Fahn et al. 1979, Nagy et al. 2000, Langenheim 2003, Hudgins et al. 2004). When a portion of the cambium has been destroyed, resin ducts normally form within the current growth ring in tangential series close to the wound and occasionally also in succeeding rings (Bannan 1936). The formation of TRDs represents a nonspecific defense response to injury that compartmentalizes the wood (Berryman 1972, Tippett et al. 1982, Shigo 1984).

A tree's response to wounding normally begins shortly after injury. If wounding occurs during the period of cambial activity, resin ducts differentiate in the developing secondary xylem within 4 to 28 days following injury (Nagy et al. 2000, Franceschi et al. 2002, Luchi et al. 2005). Fahn et al. (1979), who studied Cedrus libani A. Rich. trees growing in a Mediterranean climate in the Northern Hemisphere, observed that TRDs are always formed in the year of the disturbance if the wounding occurs between April and October. They also observed that wounding in November may occasionally lead to a brief resumption of cambial activity during which time a few short TRDs are formed. In contrast, TRDs were not formed until the following growing season if the disturbance occurred between December and March. Similarly, Bannan (1936) concluded that the characteristics and the amount of tissue formed in response to wounding vary with the circumstances of the injury. The most extensive development of ducts was observed following injury during the growing season. If injury occured during dormancy, TRD formation did not take place or occurred to only a limited extent in the next season's growth ring. Likewise, Franceschi et al. (2002) observed that TRD formation in *Picea abies* (L.) Karst. trees following methyl jasmonate treatment was much weaker when treatment occurred late in the growing season than when it occurred in spring.

According to Bannan (1936), TRDs may extend several centimeters above and below a stem wound, although remaining narrowly confined in the horizontal dimension. Franceschi et al. (2002) observed that, in P. abies treated with methyl jasmonate, a ring of TRDs formed in the treated area, but was rarely more than 5 cm above the treated sector and never beyond 15 cm from the wound. Luchi et al. (2005) observed TRDs in Pinus nigra Arn. up to 12 cm from sites of inoculation with Diplodia scrobiculata or Spahaeropsis sapinea. Experiments with Pinus pinea L. show that decapitation significantly increases the number of TRDs to a distance of 10 cm below the point of stem severance (Lev-Yadun 2002). In contrast, there is little information on the tangential extension of TRD formation after wounding. It appears that the number and size of ducts decreases with distance from the wound (Fahn et al. 1979) and that their arrangement becomes more dispersed (Bannan 1936). Moore (1978) concluded that responses in broad-leaved trees can extend tangentially up to 20 cm from the impact site. Thus, there is, at present, only limited knowledge about the axial and tangential distribution of TRDs in tree stems after wounding. Furthermore, most studies have been on juvenile plants or based on treatments with hormones or fungi, or on decapitated trees.

In this study, we focused on the presence of TRD bordering wounds in adult *Larix decidua* Mill. trees injured by debris-flow events of known date, and sought to determine the vertical and horizontal extent of induced TRD formation and the time course of TRD appearance following injury. We analyzed 182 stem discs from eight *L. decidua* trees with a total of 28 injuries.

Materials and methods

Study site

The study site (46°11′ N, 8°05′ E) is located 8 km south of

the Simplon Pass (Valais Alps, Switzerland). The forest stand is situated at 1220 m a.s.l. on a fluvial terrace and is primarily composed of European larch (*L. decidua*). Vegetation is influenced by debris flows and flooding in the Feergraben and Laggina creeks that traverse the terrace. Between October 14 and 15, 2000, intense precipitation in the Valais Alps caused debris-flow events in the Feergraben, when trees were impacted during the transport of large amounts of solid material. Another debris flow, on November 2, 2004, caused further damage. The debris included boulders up to 0.5 m in diameter.

Phenological data at the study site were obtained in 1976, when growth of *L. decidua* started around May 16, latewood formation commenced on July 17 and growth ceased on October 9 (Müller 1980). It can thus be assumed that earlywood formation at this site lasts from around mid-May to mid-July and that latewood tracheids develop between mid-July and early to mid-October. The cambium is inactive between mid-October and mid-May. Mean annual temperature at the study site is about 5 °C, and mean annual rainfall totals 1216 mm (MeteoSwiss 2007).

Field collection and sample preparation

Formation and extension of TRDs after wounding was observed in eight *L. decidua* trees visibly damaged by either the 2000 or the 2004 debris flows or both. Tree characteristics are given in Table 1. The bases of some trees growing in the levees of the creeks were buried by material originating from previous debris flows. To permit analysis of all injuries, such partially buried stems were excavated before the trees were felled. Stem injuries were located by height above the root collar, and their vertical and horizontal extent of the injuries recorded. Trees were then cut into segments about 10 cm long, with the first cross section taken at the root collar. Additional sections were taken around the upper and lower boundaries of the wounds.

In the laboratory, stem sections were dried and polished with 400-grit sandpaper, and the tree rings counted. To investigate changes in the position of TRDs within the growth rings, sections for microscopic examination were prepared from some samples, as described by Clark (1981) and Schweingruber (1978).

Table 1. Descriptive parameters of the *Larix decidua* trees chosen for analysis. The height of trees is relative to the present-day ground line. Abbreviation: DBH, diameter at breast height; and *L*, vertical extent of injury.

Tree	Age (years)	DBH (cm)	Height (m)	Injuries (no.)	Event years	Samples (no.)	$L(\mathrm{cm})$
A	48	19.5	14	4	2000, 2004	18	258
В	54	9	15	3	2000, 2004	30	324
С	54	7	14	3	2000	18	200
D	42	6	6.5	5	2000, 2004	27	234
Е	44	15	14	2	2000	16	249
F	42	12	5	5	2000, 2004	24	273
G	41	5	14	5	2000	30	287
Н	48	13	12	1	2000	19	268
Mean	46.63	10.81	11.81	3.50		22.75	261.63
Total				28		182	

Analytical procedures

To identify the location of TRDs, growth rings were subdivided according to time of formation as follows: the first formed cell layer (in which TRD formation usually occurs as the result of an injury during the dormant season) (d), early (ee), middle (me) and late earlywood (le), and early (el) and late (ll) latewood (Figure 1A). We noted the first occurrence of TRDs after an impact as well as the position of TRDs in subsequent years.

To determine the axial extent of TRDs formed after an impact, samples above and below each injury were examined. In addition, the total axial extent of the TRDs was assessed. This represents the total distance between the upper- and the lowermost cross-sections with TRDs and includes the length of the injury (Figure 2).

The tangential extent of TRD formation was assessed at the height of the center of each injury (H_c) by measuring the distance between the wound boundary and the farthest point at which TRDs occurred. This distance is given as a percentage of the ring circumference at H_c , excluding that portion where the cambium had been destroyed (Figure 1B). The maximal tangential extent of TRDs in samples from above and below the injury was also determined. We recorded the tangential extent of TRD formation at distances of 10, 30, 50 and 70 cm above the top as well as 10, 30 and 50 cm below the bottom of each injury. We focused mainly on the first year after injury (i.e., 2001 and 2005), but tree rings of all subsequent years with TRDs were also analyzed. In the succeeding years, we concentrated on assessment of tangential distribution at H_c .

Pearson product-moment correlations (r) were calculated for the factors influencing the formation and extension of TRDs. We also present and discuss linear regressions between both the the axial and tangential extent of TRD formation and various injury parameters.

Results

TRD position within annual growth rings

Analysis of 182 cross sections from eight trees led to the identification of 28 injuries: 23 the result of debris flows in October 2000; and five the result of debris flows in November 2004 (Table 2). In 25 cases, damaged trees formed at least one tangential row of TRDs. In the remaining three cases, no TRDs were formed in tissue adjacent to the injury.

Wounding occurred in mid-October 2000 and in early November 2004, which was, in both cases, after cambial activity had ceased. Traumatic resin duct formation in response to injury occurred during the following growing season. In 23 of 25 cross sections located at H_c , TRDs were observed in either the first (17 cases) or the next four cell layers (6 cases) of the new growth ring (Table 3). In one case, TRD formation occurred in the latewood of the growth ring formed in the year after injury, and in another case, TRD formation occurred in the early-wood formed in the second year after injury.

Although, the first formed TRDs were usually located in the first cell layers of the new growth ring, in approximately half of all cases, the location of TRD formation migrated, with increasing horizontal and vertical distance from the site of injury, to the middle or late earlywood or the latewood (Figure 3). In five stems, multiple rows of ducts were formed within a single growth ring.

Axial extent of TRDs

In the first year after disturbance, total axial extent of TRDs reached up to 320 cm and had a mean vertical extent of 78 cm (Table 3). Extent above the top and below the bottom of the injury averaged 43 and 14 cm, respectively, although in four cases, TRDs occurred neither above nor below the injury boundaries. In seven cases, TRDs formed at and above the



direction of impact



y = area of TRD left of the injury (70° = 22%)

Figure 1. (A) Subdivision of Larix decidua tree rings according to the time of formation: the first formed cell layer in which TRD formation usually occurs as the result of injury during the dormant season (d), early (ee), middle (me) and late (le) earlywood as well as early (el) and late (ll) latewood. (B) The relative tangential extent of traumatic resin ducts (TRDs) at the wound height takes account of the area available for resin duct formation and the absence of cambial activity in the injured segment. The portion of the ring with cambial activity thus represents 100% of the surface where TRDs can theoretically form.



Figure 2. Schematic view of a *Larix decidua* stem with an open wound (No. D-03) and traumatic resin ducts (TRD) bordering the injury. In this example, the axial extension of TRD above the injury amounts to 14 cm.

injury, but not below it, and in four cases, TRDs formed below the injury but not above it. Downward propagation of TRDs was sometimes limited by the root collar.

In the growth rings formed in the second and subsequent year after injury, TRD formation was limited axially mainly to the vicinity of the wound. In the second and fifth growth ring formed after injury, TRDs were observed beyond the axial limits of the injury in only seven and four cases, respectively.

Tangential extent of TRDs

In the case of 25 impact injuries resulting in TRD formation, the TRDs formed at H_c were distributed tangentially over a mean of 19% of the stem circumference, excluding that portion where the cambium had been destroyed, and extending in one case to more than half the circumference of the tree (Table 4).

Figure 4 shows the variation with height in the tangential distribution of TRDs. Tangentially, TRDs were most widely distributed at H_c , decreasing to 5% of the stem circumference with viable cambium 50 cm above H_c and to less than 1% at 50 cm below H_c .

In subsequent years, the tangential distribution of TRDs decreased to a median value of about 10% and a maximum of 50% of the undamaged stem circumference at H_c . In about one third of the wounds, TRDs were evident in only those segments of the secondary xylem overgrowing the wound.

Traumatic resin ducts were formed for a mean period of 2.6 years (SD \pm 1.8) after injury, with no TRDs being formed after the first year following injury in eight cases, whereas, in the remaining 17 cases, they were formed in each of the subsequent four years.

Discussion

We analyzed 182 stem discs from eight *Larix decidua* trees injured by debris flows in October 2000 or November 2004, or both, i.e., after the end of the local growing period. Traumatic resin ducts were observed in the growth ring formed in the year following injury in the case of 25 of the 28 injuries, which is in agreement with observations of Bannan (1936), Fahn et al. (1979) and Cruickshank et al. (2006).

In almost one third of the samples taken at the center of the injury, TRD formation extended radially across a number of cell layers within a single tree ring. The location of TRD formation migrated radially to later formed cell layers with increasing distance from the wound. Changes in the radial position of ducts with distance from the center of the injury were described by Bannan (1936), but this observations concerned only changes in position relative to the upper and lower boundaries of the wound. Such variation in position of TRD formation is consistent with dependence on a slowly propagating signal. Krekling et al. (2004) stated that, in Norway spruce, the signal propagates about 2.5 cm day⁻¹ in the axial direction. In our samples, we found no significant influence of injury size, length, width or height on the migration of the site of TRD formation.

We observed a mean total axial extension of TRDs of over 78 cm, with ducts present 43 cm above and 14 cm below the zone of injury (Table 3). Previous studies report axial extensions ranging from 5 cm (Franceschi et al. 2002) to 10 cm (Lev-Yadun 2002) or 12 cm (Luchi et al. 2005). Fahn et al. (1979) showed that TRDs form over greater distances above wounds than below wounds. In these other studies, trees reacted to an artificial stimulus in the form of hormones or decapitation. Therefore, the much larger axial spread of TRDs

(see Figu Radial po	x_{a} (10), w_{R} , relative width of injury carculated as shown in Figure 15, Area, the wound surface carculated from internal width and length; x_{a} (10), w_{R} , relative width of injury is relative to the upslope position (0°); and SD, standard deviation.											
Injury	L (cm)	%L	H _{LB} (cm)	H _{center} (cm)	H _{UB} (cm)	W _{OS} (cm)	W _{IS} (cm)	W _R (%)	Area (cm ²)	Radial position (°)	Year	
A-01	12	0.9	13	19	25	2	3	4.5	41	330	2004	
A-02	25	1.8	62	74	87	2	2	3	47	280	2000	
A-03	15	1.1	77	84	92	1	2	1	9	160	2000	
A-04	14	1	96	103	110	9	6	11	97	220	2000	
B-01	16	1.1	5	13	21	4	6	8	48	350	2000	
B-02	58	3.9	58	87	116	11	15	24	437	130	2000	
B-03	5	0.3	164	166	169	1	2	3	4	275	2004	
C-01	18	1.3	36	45	54	6	9	25	113	100	2000	
C-02	32	2.3	76	92	108	3	4	11	77	110	2000	
C-03	7	0.5	138	141	145	1	1	3	5	20	2000	
D-01	21	3.2	52	62	73	4	5.5	29	115	330	2000	
D-02	8	1.2	76	80	84	3.5	4	19	29	200	2000	
D-03	24	3.7	102	114	126	3	4	18	68	320	2000	
D-04	4	0.6	11	13	15	2	4	18	18	340	2004	
D-05	7	1.1	51	54	58	2.5	3	11	17	350	2004	
E-01	44	3.1	20	42	64	9	7	10	235	290	2000	
E-02	32	2.3	86	102	118	6	8	8	129	350	2000	
F-01	20	4	19	29	39	1	2	3	25	350	2000	
F-02	13	2.6	108	114	121	5	9	19	93	230	2000	
F-03	27	5.4	114	127	141	7	8	20	204	50	2000	
F-04	4	0.8	43	45	47	2	2	3	5	330	2004	
F-05	61	12.2	157	187	218	6	9	18	414	20	2000	
G-01	29	2.1	0	15	29	5	8	38	208	60	2000	
G-02	21	1.5	89	99	110	3	5	22	73	100	2000	
G-03	6	0.4	97	100	103	2	3	11	10	210	2000	
G-04	72	5.1	117	153	189	2	2.5	14	158	340	2000	
G-05	6	0.4	130	133	136	2	3	14	13	170	2000	
H-01	18	1.5	162	171	180	3	4	10	68	160	2000	
Mean	22	2.8	77	88	99	4	5	14	99			
Min	4	0.4	0	13	15	1	1	1	4			
Max	72	12	164	187	218	11	15	38	437			
SD	18	2	49	50	53	3	3	9	113			

Table 2. Characteristics of the 28 injuries identified in eight *Larix decidua* trees. Column headings: *L*, vertical extent of injury; %*L*, *L* as a percent of total stem length; H_{LB} , H_{center} and H_{UB} , height from root collar to the lower boundary, the center and the upper boundary of the stem injury, respectively; W_{OS} , injury width measured on the stem surface; W_{IS} , injury width measured in the horizontal plane across the surface of the wound (see Figure 1B); W_R , relative width of injury calculated as shown in Figure 1B; Area, the wound surface calculated from internal width and length; Radial position, position of injury is relative to the upslope position (0°); and SD, standard deviation.

that we observed might be explained by the difference in stimulus and the high impact energies involved. During debris flows, trees may be struck violently by rocks and boulders and severely shaken (Dorren and Berger 2006, Stoffel 2007). Debris flows also cause deeper wounds than the artificial impacts that have been induced in laboratory experiments (Moore 1978).

Total axial extent of TRDs seemed to be influenced by injury size (Table 5), because the largest total axial extension of TRDs as well as the largest maximum extension above the area of impact were associated with the largest injuries. This observation is consistent with the findings of Fahn et al. (1979), who reported a correlation between wound size and number of TRDs. In our study, the axial extent of TRDs below the injury was independent of injury area, length or width (Pearson product-moment correlations of < 0.3).

In the first tree ring formed after an impact, tangential extent of TRDs at H_c varied greatly among samples. Although no TRDs were observed in 10% of the samples, 50% of the total circumference of the tree ring showed TRDs in other samples. The tangential extent of TRDs in the first year following injury showed a significant correlation with injury size (Table 5). Furthermore, the tangential spread of TRDs was more closely correlated with the length of an injury than its width (r = 0.40 and < 0.01, respectively).

Linear regressions (Figures 5A and 5B) indicated a relationship between the axial extent of TRD formation and injury size (area and length). Similarly, it appears that the tangential and axial extents of TRD formation are positively correlated (Figure 5C). Injury width did not influence the tangential extent of TRD formation (Figure 5D).

The occurrence of TRDs in the tree rings following injury was restricted by the time elapsed between the injury event in October 2000 (23 injuries) or November 2004 (5 injuries) and the felling of the trees in August 2005. From the cross sections showing wounds as a result of the October 2000 event, we observed that in more than two thirds of the cases (16 injuries) TRDs were formed in all years following the injury. Therefore,

Table 3. Axial extent of traumatic resin ducts (TRDs) in growth rings formed 1 to 5 years after injury for all injuries analyzed in eight *Larix decidua* trees (A–H). Abbreviations: SA, surface area of the injury; *L*, vertical extent of injury; H_c , height from the root collar to the center of injury; d, dormant period; ee, early earlywood; ll, late latewood; hi+, axial extension of TRDs above the top of the injury; hi–, axial extension of TRDs below the bottom of the injury; and SD, standard deviation.

Injury	SA	L	$H_{\rm c}$	Location of TRD onset	Axial extent of TRDs (cm)										
	(cm^2)	(cm)	(cm)		Year 1			Year	2	Year 3		Year 4		Year 5	
					Total	hi+	hi-	hi+	hi-	hi+	hi-	hi+	hi-	hi+	hi–
A-01	41	12	19	d	161	149	0	0	0	0	0	0	0	0	0
A-02	47	25	74	d	79	37	17	0	0	0	0	0	0	0	0
A-03	9	15	84	d	130	91	24	0	0	0	0	0	0	0	0
A-04	97	14	103	d	139	84	41	0	0	0	0	0	0	0	0
B-01	48	16	13	ee	49	24	9	0	0	0	9	0	9	0	0
B-02	437	58	87	d	320	230	32	24	13	24	13	24	13	24	13
B-03	4	5	166	ee	5	0	0	0	0	0	0	0	0	0	0
C-01	113	18	45	ee	63	16	29	0	0	0	0	0	0	0	0
C-02	77	32	92	ee	54	11	11	0	0	0	0	0	0	0	0
C-03	5	7	141	_	0	0	0	0	0	0	0	0	0	0	0
D-01	115	21	62	ee	51	0	30	0	42	0	0	0	0	0	0
D-02	29	8	80	ee	8	0	0	0	0	0	0	0	0	0	0
D-03	68	24	114	ee	42	10	8	0	8	0	8	0	0	0	0
D-04	18	4	13	_	0	0	0	0	0	0	0	0	0	0	0
D-05	17	7	54	_	0	0	0	0	0	0	0	0	0	0	0
E-01	235	44	42	ee	261	202	15	0	0	0	0	0	0	0	0
E-02	129	32	102	d	167	135	0	0	0	0	0	0	0	0	0
F-01	25	20	29	d	81	19	42	0	0	0	0	0	0	0	0
F-02	93	13	114	d	63	50	0	12	0	12	0	12	0	12	0
F-03	204	27	127	d	80	0	53	13	12	25	12	25	12	25	12
F-04	5	4	45	11	65	19	42	0	0	0	0	0	0	0	0
F-05	414	61	187	d	125	64	0	24	0	24	0	24	0	24	0
G-01	208	29	15	d	41	12	0	0	0	0	0	0	0	0	0
G-02	73	21	99	d	40	19	0	0	0	0	0	0	0	0	0
G-03	10	6	100	d	17	11	0	0	0	0	0	0	0	0	0
G-04	158	72	153	d	78	0	6	0	0	0	0	0	0	0	0
G-05	13	6	133	d	13	0	7	0	0	0	0	0	0	0	0
H-01	68	18	171	d	63	20	25	20	0	0	0	0	0	0	0
Mean	99	22	88		78	43	14	3	3	3	2	3	1	3	1
Min	4	4	13		0	0	0	0	0	0	0	0	0	0	0
Max	72	72	187		320	230	53	24	42	25	13	25	13	25	13
SD	113	18	50		77	63	17	8	8	8	4	8	4	8	3



Figure 3. A wounded *Larix decidua* stem, showing the formation of traumatic resin ducts (TRDs) at (A) the beginning of the new tree ring or (B) within the first five cell layers. (C) Multiple rows of TRDs formed in the years following wounding in October 2000. (D) Tangential migration of TRDs within the tree ring.

Table 4. Tangential extent of traumatic resin duct (TRD) formation (% of circumference with undamaged cambium) at the height of the center of injury (H_c) in growth rings formed 1 to 5 years after injury for all injuries analyzed in the eight *Larix decidua* trees. For Year 1, TRD extent is also given for the indicated vertical distances (cm) above the top (+) and below the bottom (–) of the injury. Abbreviations: SA, surface area of injury; and *L*, vertical length of injury.

Injury	SA	L (cm)	H _c (cm)	Tangential extent of TRDs											
	(cm ²)			Year 1				Year 2	Year 3	Year 4	Year 5				
				At $H_{\rm c}$	+10	+30	+50	+70	-10	-30	-50				
A-01	41	12	19	47	39	31	25	17	0	0	0	0	0	0	0
A-02	47	25	74	6	11	6	0	0	11	6	0	9	3	6	0
A-03	9	15	84	18	11	6	6	6	8	0	0	11	3	3	6
A-04	97	14	103	19	14	14	6	0	6	0	0	8	5	3	11
B-01	48	16	13	33	31	47	6	0	0	0	0	8	15	5	5
B-02	437	58	87	56	28	8	6	6	44	3	0	31	26	37	33
B-03	4	5	166	6	0	0	0	0	0	0	0	0	0	0	0
C-01	113	18	45	19	3	0	0	0	33	19	0	19	9	28	13
C-02	77	32	92	3	3	0	0	0	14	0	0	14	8	11	9
C-03	5	7	141	0	0	0	0	0	0	0	0	3	3	3	3
D-01	115	21	62	22	0	0	0	0	28	22	0	25	23	47	27
D-02	29	8	80	7	0	0	0	0	0	0	0	15	0	0	0
D-03	68	24	114	22	17	0	0	0	17	0	0	22	34	19	14
D-04	18	4	13	0	0	0	0	0	0	0	0	24	0	0	0
D-05	17	7	54	0	0	0	0	0	0	0	0	0	0	0	0
E-01	235	44	42	13	42	17	17	17	3	0	0	20	8	5	5
E-02	129	32	102	39	22	22	25	31	0	0	0	8	20	5	9
F-01	25	20	29	31	11	0	0	0	19	6	6	0	0	0	0
F-02	93	13	114	21	22	17	14	0	0	0	0	19	22	12	10
F-03	204	27	127	25	36	0	0	0	44	25	28	17	10	12	3
F-05	4	45	46	14	0	0	0	6	0	0	0	0	0	0	
F-05	414	61	187	36	58	17	19	0	0	0	0	22	25	15	14
G-01	208	29	15	16	31	0	0	0	0	0	0	4	0	4	0
G-02	73	21	99	7	31	0	0	0	0	0	0	7	18	14	0
G-03	10	6	100	6	17	0	0	0	0	0	0	0	0	0	0
G-04	158	72	153	24	0	0	0	0	14	0	0	39	27	13	6
G-05	13	6	133	6	0	0	0	0	17	0	0	0	0	0	0
H-01	68	18	171	17	19	18	17	3	14	13	0	2	6	9	3
Mean	99	22	88	19	16	7	5	3	10	3	1	12	9	9	6
Min	4	4	13	0	0	0	0	0	0	0	0	0	0	0	0
Max	72	72	187	47	58	31	25	31	44	25	28	39	34	47	33
SD	113	18	50	15	16	12	8	7	13	7	5	11	11	12	8



Figure 4. Tangential extent of traumatic resin ducts (TRDs) at different heights in the stem of *Larix decidua* trees. The extent is greatest at the height of the center of the injury (H_c) and decreases above (+) and below (–).

it was impossible to determine for how many years after injury new TRDs are formed.

Our observations on the axial and tangential distribution of TRDs following stem injury have a direct bearing on sampling strategies for dendrogeomorphological studies. Because treering analysis in protection forests is normally limited to the extraction of increment cores, positioning of cores around the wound is critical. Our results indicate that immediately above the injury, TRDs are present over a large portion of the stem circumference, and are, therefore, easily detected. However, TRD formation above H_c may be delayed relative to that at H_c . Given that the onset of TRD formation higher up in the stem starts only in late earlywood or even latewood cell layers of the tree ring formed in the year following the impact event (e.g., 2001), the disturbance would have been misdated and attributed to a non-existent summer 2001 debris flow. Thus, it appears preferable to extract cores from either side of the injury,

Table 5. Pearson product-moment correlation coefficients for the injury parameters (area, length, width) and the vertical as well as axial extensions of traumatic resin ducts (TRDs) (n = 28) in cross sections of *Larix decidua* stems.

Parameter	Description	Parameter										
		1	2	3	4	5	6	7	8	9	10	
1	Injury area		0.82	0.50	0.75	0.68	0.54	0.12	0.49	0.50	0.65	
2	Injury length	0.82		0.27	0.75	0.59	0.41	0.08	0.40	0.55	0.65	
3	Injury width	0.50	0.27		0.26	-0.02	-0.11	-0.19	0.00	0.30	0.54	
4	Injury as % of stem length	0.75	0.75	0.26		0.32	0.14	0.15	0.38	0.38	0.54	
5	TRD distribution, vertical total	0.68	0.59	-0.02	0.32		0.95	0.08	0.40	0.55	0.65	
6	TRD distribution, vertical above	0.54	0.41	-0.11	0.14	0.95		0.14	0.56	0.25	0.25	
7	TRD distribution, vertical below	0.12	0.08	-0.19	0.15	0.08	0.14		0.35	0.07	0.05	
8	TRD distribution, tangential 1 year center of injury	0.49	0.40	0.00	0.38	0.40	0.56	0.35		0.14	0.37	
9	Number of years in which TRDs formed	0.50	0.55	0.30	0.38	0.55	0.25	0.07	0.14		0.66	
10	TRDs in following years	0.65	0.65	0.54	0.54	0.65	0.25	0.05	0.37	0.66		



Figure 5. Linear regressions for: (A) axial extent of traumatic resin ducts (TRDs) and injury size; (B) axial extension of TRDs and injury length; (C) axial extent of TRDs and tangential extent of TRDs; (D) tangential extent of TRDs and injury width in a *Larix decidua* stem.

where the delay in TRD formation with distance from the wound is more limited.

Even in this case, however, absolute dating precision cannot be guaranteed, as the tangential spread of TRDs was greater in the fourth year than in the year following the October 2000 event in eight cross sections. Thus, if an increment core had been extracted where TRDs were formed in the fourth but not the first year after injury, the injury would have been misdated. For these reasons, at least two cores should be extracted from different locations as close to the wound as possible and data from several trees should be compared.

The information obtained in this study raises new questions about the dating of past geomorphic events. In particular, it remains to be determined when TRD formation is initiated after wounding by debris flows occurring during the growth period.

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References

- Bannan, M.W. 1936. Vertical resin ducts in the secondary wood of the Abietineae. New Phytol. 35:11–46.
- Baumann, F. and K.F. Kaiser. 1999. The Multetta debris fan, Eastern Swiss Alps: a 500-year debris flow chronology. Arct. Antarct. Alp. Res. 31:128–134.

- Berryman, A.A. 1972. Resistance of conifers to invasion by bark beetle–fungus associations. Bioscience 22:598–602.
- Bollschweiler, M. and M. Stoffel. 2007. Debris flows on forested cones—reconstruction and comparison of frequencies in two catchments in Val Ferret, Switzerland. Nat. Hazards Earth Syst. Sci. 7:207–218.
- Bollschweiler, M., M. Stoffel, M. Ehmisch and M. Monbaron. 2007. Reconstructing spatio-temporal patterns of debris-flow activity using dendrogeomorphological methods. Geomorphology 87: 337–351.
- 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.
- Butler, D.R. and G.P. Malanson. 1985. A history of high-magnitude snow avalanches, southern Glacier National Park, Montana, USA. Mt. Res. Dev. 5:175–182.
- Clague, J.J. and J.G. Souther. 1982. The Dusty Creek landslide on Mount Caylay, British Columbia. Can. J. Earth Sci. 19:524–539.
- Clark, G. 1981. Staining procedures. Williams and Wilkins, Baltimore and London, 512 p.
- 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.
- 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.
- Fantucci, R. and M. Sorriso-Valvo. 1999. Dendrogeomorphological analysis of a slope near Lago, Calabria (Italy). Geomorphology 30:165–174.
- 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.
- 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.
- LaMarche, V.C. 1968. An 800-year history of stream erosion as indicated by botanical evidence. U.S. Geol. Surv. Prof. Paper 550D, pp 83–86.
- Langenheim, J.H. 2003. Plant resins: chemistry, evolution, ecology and ethnobotany. Timber Press, Portland, OR, 612 p.
- 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.
- 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.
- 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.

- Martin, D., D. Tholl, J. Gershenzon and J. Bohlmann. 2002. Methyl jasmonate induces traumatic resin ducts, terpenoid resin biosynthesis and terpenoid accumulation in developing xylem of Norway spruce stems. Plant Physiol. 129:1003–1018.
- Mattheck, G.C. 1996. Trees—the mechanical design. Springer-Verlag, Berlin, 121 p.
- May, C.L. and R.E. Gresswell. 2004. Spatial and temporal patterns of debris-flow deposition in the Oregon Coast Range, USA. Geomorphology 57:135–149.
- 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.
- MeteoSwiss. 2007. Federal Office of Meteorology and Climatology, MeteoSwiss (www. meteoschweiz.ch).
- 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 Bundes-Versuchsanstalt 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. 87:320–313.
- Schweingruber, F.H. 1978. Mikroskopische Holzanatomie. Flück, Teufen, Switzerland, 226 p.
- Shigo, A.L. 1984. Compartimentalization: a conceptual framework for understanding how trees grow and defend themselves. Annu. Rev. Phytopathol. 22:189–214.
- Stoffel, M. 2007. Dating past geomorphic activity with tangential rows of traumatic resin ducts. Dendrochronologia. In press.
- Stoffel, M. and M. Beniston. 2006. On the incidence of debris flows from the early Little Ice Age to a future greenhouse climate: a case study from the Swiss Alps. Geophys. Res. Lett. 33:L16404.
- Stoffel, M. and S. Perret. 2006. Reconstructing past rockfall activity with tree rings: some methodological considerations. Dendrochronologia 24:1–15.
- Stoffel, M., I. Lièvre, D. Conus, M.A. Grichting, H. Raetzo, H.W. Gärtner and M. Monbaron. 2005a. 400 years of debris flow activity and triggering weather conditions: Ritigraben, Valais, Switzerland. Arct. Antarct. Alp. Res. 37:387–395.
- Stoffel, M., I. Lièvre, M. Monbaron and S. Perret. 2005b. Seasonal timing of rockfall activity on a forested slope at Täschgufer (Swiss Alps)—a dendrochronological approach. Z. Geomorphol. 49: 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 Biol. Sci. 214:63–111.
- Timell, T.E. 1986. Compression wood in gymnosperms. Springer-Verlag, Berlin, 2150 p.
- Tippett, J.T., A.L. Bogle and A.L. Shigo. 1982. Response of balsam fir and hemlock roots to injuries. For. Pathol. 12:357–364.
- Varnes, D.J. 1978. Slope movement types and processes. *In* Landslides, Analysis and Control. Eds. R.L. Schuster and R.J. Krizek. Transportation Research Board of the U.S. National Academy of Sciences, Special Report, Washington, 176:11–33.