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Wood anatomical analysis of *Alnus incana* and *Betula pendula* injured by a debris-flow event

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Summary Vessel chronologies in ring-porous species have been successfully employed in the past to extract the climate signal from tree rings. Environmental signals recorded in vessels of ring-porous species have also been used in previous studies to reconstruct discrete events of drought, flooding and insect defoliation. However, very little is known about the ability of diffuse-porous species to record environmental signals in their xylem cells. Moreover, time series of wood anatomical features have only rarely been used to reconstruct former geomorphic events. This study was therefore undertaken to characterize the wood anatomical response of diffuse-porous *Alnus incana* (L.) Moench and *Betula pendula* Roth to debris-flow-induced wounding. Tree microscopic response to wounding was assessed through the analysis of wood anatomical differences between injured rings formed in the debris-flow event year and uninjured rings formed in the previous year. The two ring types were examined close and opposite to the injury in order to determine whether wound effects on xylem cells decrease with increasing tangential distance from the injury. Image analysis was used to measure vessel parameters as well as fiber and parenchyma cell (FPC) parameters. The results of this study indicate that injured rings are characterized by smaller vessels as compared with uninjured rings. By contrast, FPC parameters were not found to significantly differ between injured and uninjured rings. Vessel and FPC parameters mainly remained constant with increasing tangential distance from the injury, except for a higher proportion of vessel lumen area opposite to the injury within *A. incana*. This study highlights the existence of anatomical tree-ring signatures—in the form of smaller vessels—related to past debris-flow activity and addresses a new methodological approach to date injuries inflicted on trees by geomorphic processes.

Keywords: broad-leaved tree, diffuse-porous wood, ecological wood anatomy, geomorphic process, natural wounding.

Introduction

Tree-ring series contain ecologically relevant information encoded in the form of ring-width variations, which reflect environmental influence on radial growth over time (Fritts 1976, Schweingruber 1996). For instance, Tardif and Bergeron (1993) observed that both climatic and hydrological fluctuations affected the radial growth of *Fraxinus nigra* Marsh. in floodplain forest stands. Series of dated tree rings hold additional environmental information archived in their cells. Ecological wood anatomy (sensu stricto; Baas and Miller 1985, Wimmer 2002) aims at extracting environmental signals from tree rings and is based on inter- and/or intra-annual variations in wood anatomical features along tree-ring series. Therefore, tree macroscopic and microscopic response to environmental factors can be evaluated in retrospect through the analysis of tree-ring width and tree-ring anatomy, respectively. The latter approach has, however, been less widely used. Nevertheless, the water-conducting cells of trees, especially the vessels of broad-leaved trees, have proved to be a valuable source of environmental information over the last few decades. In particular, ecological studies have explored the climate signal recorded in vessels of ring-porous species such as *Quercus* spp. (Eckstein and Frisse 1982, Woodcock 1989, García-González and Eckstein 2003, Tardif and Conciatori 2006), *Castanea sativa* Mill. (Fonti and García-González 2004) and *Tectona grandis* L. (Pumijumnong and Park 1999). Further ecological investigations have identified vessel anomalies in ring-porous species to reconstruct discrete events of drought (Corcuera et al. 2004, Eilmann et al. 2006), flooding (Yanosky 1983, Astrade and Bégin 1997, St George and Nielsen 2003) and insect defoliation (Huber 1993, Asshoff et al. 1999). Surprisingly, very few similar studies have been conducted with diffuse-porous species. Eckstein and Frisse (1982) and Sass and Eckstein (1995) found a close relationship between vessel size and seasonal climatic conditions within *Fagus sylvatica* L. Schume et al. (2004) demonstrated the influence of hydrological fluctuations on vessel size within *Populus* × *euroa-*

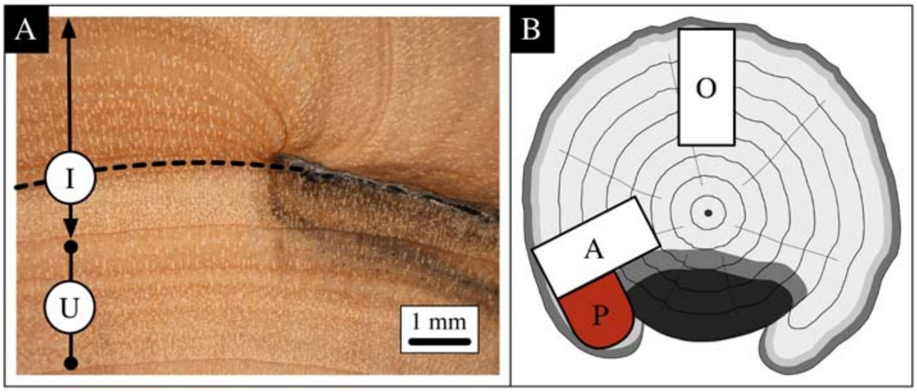

Figure 1. (A) Injured ring (I) and uninjured ring (U) close to the injury within *A. incana*. The injury was dated to early earlywood as shown by the dashed line, which indicates the radial position of the injury within the increment ring. (B) Location of the two radial segments investigated. Radius A is immediately adjacent to the injury, next to the callus pad (P) proceeding inward from the wound edge. Radius O is opposite to the injury, on the uninjured side of the sample. It should be specified that radial segments extracted from the callus pad and/or the decayed zone (darkened area) would have provided incomplete tree-ring records because wood is eroded and decayed following wounding. This figure appears in color in the online version of *Tree Physiology*.

mericana (Dode) Guinier. Moreover, environmental information on former geomorphic events has only rarely been retrieved from time series of wood anatomical features. Hitz et al. (2008) studied root anatomy of ring-porous *Fraxinus excelsior* L. to reconstruct erosion rates, whereas Ballesteros et al. (2010) investigated stem anatomy of diffuse-porous *Alnus glutinosa* L. and ring-porous *Fraxinus angustifolia* Vahl. and *Quercus pyrenaica* Willd. to reconstruct flash floods.

This study is the first ecological study to intensively test the ability of diffuse-porous species to register geomorphic events in their xylem cells. We examined the wood anatomical response of diffuse-porous *Alnus incana* (L.) Moench and *Betula pendula* Roth to debris-flow-induced wounding. Even though visible injuries on the stem surface of trees already attest to debris-flow activity, the analysis of anatomical tree-ring signatures caused by geomorphic processes is very promising. Indeed, the existence of such environmental signals in tree-ring series would allow internally hidden scars to be detected and dated, thus improving tree-ring reconstructions and complementing archival records on geomorphic activity. It would also encourage the use of minimally destructive sampling methods in order to date injuries, referring to the taking of cores with increment borers as opposed to the collection of cross-sections. Therefore, for the purpose of this research, we analyzed wood anatomical differences between injured rings formed in the debris-flow event year and uninjured rings formed in the previous year. This inter-annual comparison of wood anatomical features was realized close and opposite to the injury. Results were obtained from 56 sample rings (28 sample rings per species).

Material and methods

Study area

Trees were sampled on the lower terraces that border the Illgraben (Valais, Swiss Alps, 46°18′ N/7°38′ E, 755 m a.s.l.), which is considered one of the most active debris-flow torrents of the Alps, with several events per year (Rickenmann et al. 2001). The Illgraben fan is located on the southern slopes of the upper Rhone river valley opposite the town of Leuk and is partly covered by a large Scots pine (*Pinus sylvestris* L.) forest. Broad-leaved trees on the lower terraces form narrow and discontinuous strips of riparian vegetation predominantly composed of gray alder (*A. incana* (L.) Moench). Silver birch (*B. pendula* Roth), pubescent birch (*Betula pubescens* Ehrh.), aspen (*Populus tremula* L.), white poplar (*Populus alba* L.), black poplar (*Populus nigra* L.), gray poplar (*Populus* × *canescens* (Ait.) Sm.), goat willow (*Salix caprea* L.) and black elder (*Sambucus nigra* L.) are present as well.

Sample selection and sample ring examination

We collected cross-sections from trees with injuries exposed to the assumed flow direction of former debris flows. Average tree height was 4.32 m (σ = 1.36 m), and average base circumference was 27.00 cm (σ = 3.04 cm). Cross-sections from seven *A. incana* and seven *B. pendula* trees were chosen for wood anatomical analysis. All sample injuries were dated to the early earlywood of 2005 and were related to a large debris flow (140,000 m^3) that occurred and was registered in archival records on 28 May 2005 (Arbellay et al. 2010). We purposely worked with samples whose injury was attributed to the same period of the growing season because wound-induced variations in wood anatomical features could differ depending on the seasonal timing of wounding.

The methodological approach used in this study was derived from Sutton and Tardif (2005), who compared wood anatomical characteristics of *Populus tremuloides* Michx rings formed before and at the time of insect defoliation. The present study investigated wood anatomical differences between injured rings (I) formed in the debris-flow event year and uninjured rings (U) formed in the previous year (Figure 1A). The uninjured rings served as controls since their development was completed the year before the event. Each injured ring was thus paired with the previous year ring for comparison purposes.

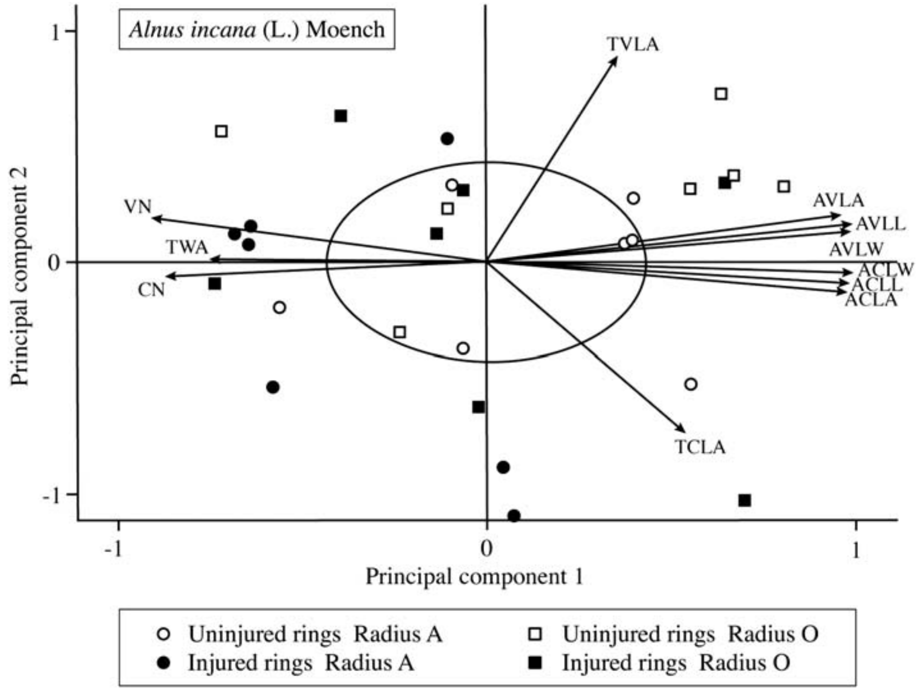

Figure 2. Principal component correlation biplot for *A. incana*. The 11 wood anatomical variables (arrows) are: total wall area (TWA), total cell lumen area (TCLA), average cell lumen area (ACLA), average cell lumen length (ACLL), average cell lumen width (ACLW), cell number (CN), total vessel lumen area (TVLA), average vessel lumen area (AVLA), average vessel lumen length (AVLL), average vessel lumen width (AVLW) and vessel number (VN). The equilibrium circle shows that all variables strongly contributed to the formation of both axes. The 28 sample rings are coded by ring type (black or white shapes) and radial location (round or square shapes).

Furthermore, each ring pair was studied close and opposite to the injury in order to determine whether wound effects on xylem cells decrease with increasing tangential distance from the injury. Radius A, immediately adjacent to the injury, is located next to the callus pad proceeding inward from the wound edge, whereas radius O, opposite to the injury, is located on the uninjured side of the sample (Figure 1B). In total, 28 sample rings within *A. incana* and 28 sample rings within *B. pendula* were analyzed.

Sample preparation

Cross-sections were sectioned with a chisel to obtain a small wood block (1–3 cm edges) for both radial segments. Thin sections were prepared following the procedures described in Schweingruber et al. (2006). Single working steps involved (i) cutting thin sections (15 μm) from the blocks using a Reichert sliding microtome; (ii) staining them with a 1% safranin and astrablue solution; and (iii) rinsing them with

Table 1. Two-way ANOVA result table for *A. incana*

	Uninjured rings (mean ± SD)	Injured rings (mean ± SD)	Change (%)	*P*	Radius A (mean ± SD)	Radius O (mean ± SD)	Change (%)	*P*
TWA (%)	60.61 ± 7.2	62.53 ± 6.23	+3	0.447	63.61 ± 4.84	59.53 ± 7.77	−6	0.113
TCLA (%)	18.76 ± 5.43	19.87 ± 6.74	+6	0.645	19.19 ± 5.64	19.44 ± 6.61	+1	0.918
ACLA (μm^2)	54.35 ± 33.14	31.37 ± 31.81	−42	0.076	37.03 ± 31.14	48.69 ± 36.76	+32	0.356
ACLL (μm)	7.46 ± 2.55	5.65 ± 2.89	−24	0.099	6.14 ± 2.76	6.98 ± 2.94	+14	0.434
ACLW (μm)	7.2 ± 2.97	4.92 ± 2.8	−32	0.047	5.54 ± 3.06	6.58 ± 3.09	+19	0.351
CN (mm^{-2})	3539.5 ± 3267.3	6231.64 ± 4493.23	+76	0.088	5502.79 ± 4407.75	4268.36 ± 3810.26	−22	0.422
TVLA (%)	20.63 ± 4.04	17.61 ± 5.5	−15	0.094	**17.2 ± 4.09**	**21.03 ± 5.18**	**+22**	**0.037**
AVLA (μm^2)	**732.89 ± 492.93**	**336.55 ± 371.67**	**−54**	**0.023**	402.97 ± 352.22	666.47 ± 551.6	+65	0.119
AVLL (μm)	**28.11 ± 11.12**	**18.91 ± 9.82**	**−33**	**0.028**	20.59 ± 9.36	26.43 ± 12.64	+28	0.152
AVLW (μm)	**27.25 ± 11.76**	**16.85 ± 9.7**	**−38**	**0.017**	19.32 ± 10.74	24.78 ± 12.62	+28	0.189
VN (mm^{-2})	283.57 ± 270.83	507.79 ± 373.21	+79	0.087	426.21 ± 355.71	365.14 ± 333.42	−14	0.632

Mean, standard deviation (SD), wood anatomical change and *P*-value (*P*) for each of the 11 wood anatomical variables: total wall area (TWA), total cell lumen area (TCLA), average cell lumen area (ACLA), average cell lumen length (ACLL), average cell lumen width (ACLW), cell number (CN), total vessel lumen area (TVLA), average vessel lumen area (AVLA), average vessel lumen length (AVLL), average vessel lumen width (AVLW) and vessel number (VN). The interaction term was removed from the table because of non-significance for all variables. Significant results ($P < 0.05$) appear in bold.

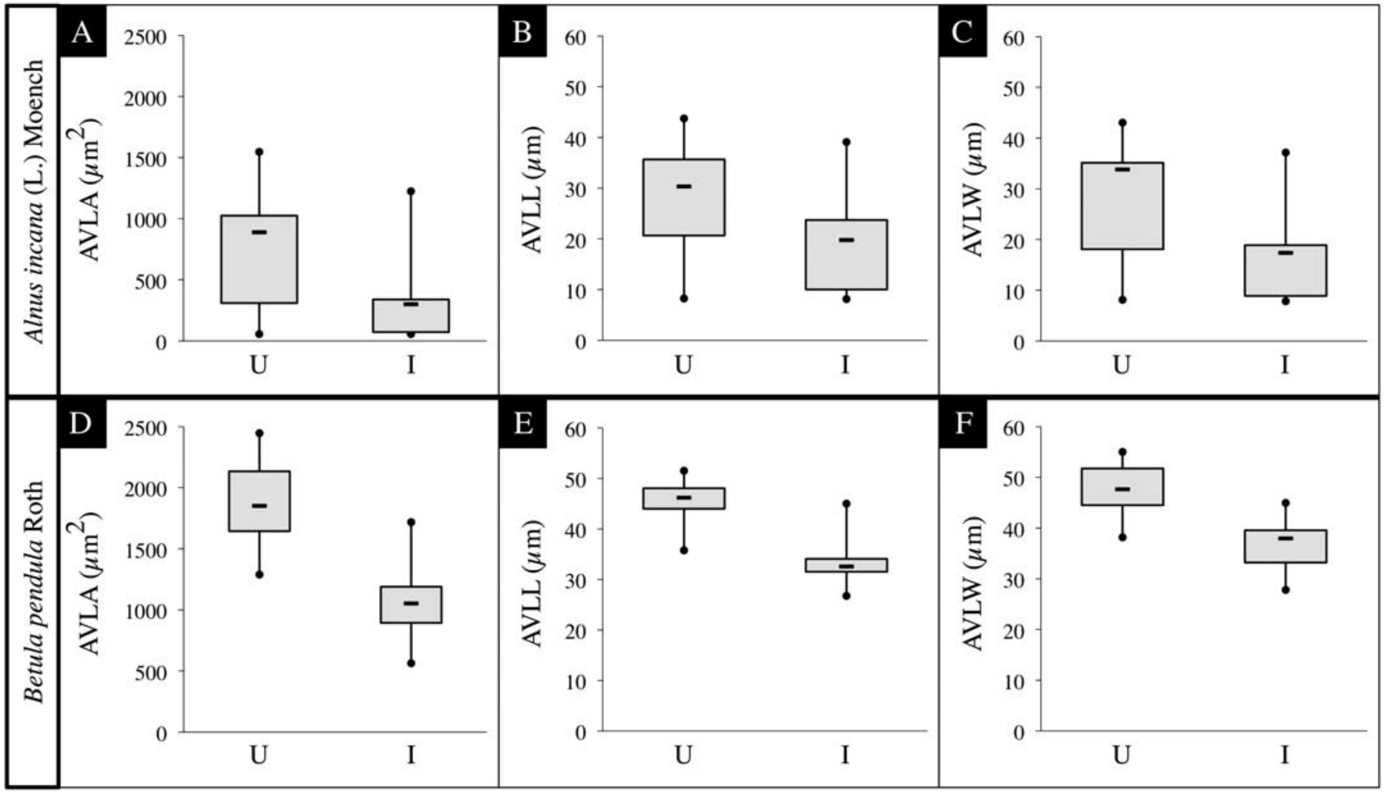

Figure 3. Wound-induced decrease in vessel parameters within *A. incana* and *B. pendula*. Vessels of injured rings (I) formed in the debris-flow event year were compared with those of uninjured rings (U) formed in the previous year. (A–C) Average vessel lumen area (AVLA), average vessel lumen length (AVLL) and average vessel lumen width (AVLW) significantly ($P < 0.05$) decreased within injured rings of *A. incana*. (D–F) The same three vessel size parameters highly significantly ($P < 0.001$) decreased within injured rings of *B. pendula*.

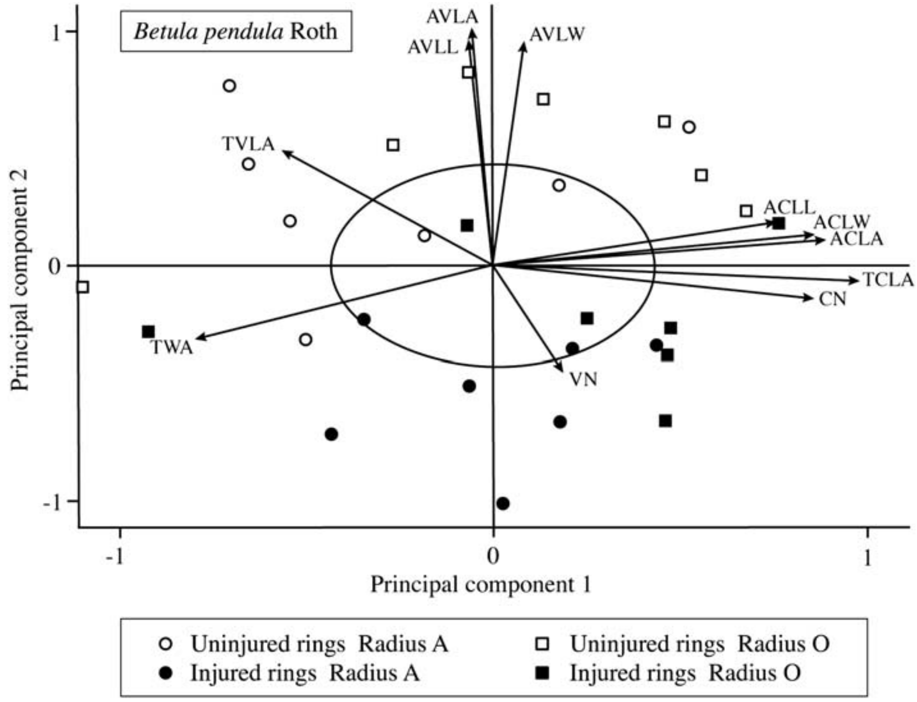

Figure 4. Principal component correlation biplot for *B. pendula*. The 11 wood anatomical variables (arrows) and the 28 sample rings (shapes) are represented. For more explanations, see caption of Figure 2.

water, alcohols and xylol. The thin sections were then mounted on microscope slides with coverslips using Canada balsam. They were finally put on a plate, firmly secured with a small magnet and placed in an oven at 60 °C for 12 h.

Image analysis

Sample ring images (2088 × 1550 pixels, 150 dpi) were taken at ×50 magnification using a Leica compound microscope equipped with a digital camera linked to a computer. In the case of large growth rings, several images were captured and then merged. The analyzed area in each sample ring was ~0.5 mm^2 in size and encompassed the entire ring width. Care was taken to avoid capturing areas with (i) broken or largely distorted vessels; (ii) tension wood, which has fewer and smaller vessels, more and thicker-walled fibers and fewer rays than normal wood (Scurfield 1973); and (iii) aggregate rays in *A. incana* (Schoch et al. 2004) in order not to distort results with an excessively high number of parenchyma cells.

WinCELL Pro V 2004a software (Régent Instruments Inc. 2004) was used to measure 11 wood anatomical variables: total wall area, total cell lumen area, average cell lumen area, average cell lumen length, average cell lumen width, cell number, total vessel lumen area, average vessel lumen area, average vessel lumen length, average vessel lumen width and vessel number. It is important to note that the term ‘cell’ stands for fibers and parenchyma cells, which apart from the ‘cell’ parameters will be referred to as fibers and parenchyma cells (FPC) throughout the rest of the article.

Statistical analysis

Principal component analysis (PCA) was performed separately for *A. incana* and *B. pendula*. Both input matrices included 11 wood anatomical variables and 28 sample rings. PCA was calculated using a correlation matrix so that all variables contributed equally to the separation of the objects (sample rings) in the reduced space (Legendre and Legendre 1998). Two-way analysis of variance (ANOVA) was also performed separately for both species. The 11 wood anatomical variables were used to determine the effects of ring type (injured rings or uninjured rings) and radial location (radius A or radius O) as well as the interaction term (ring type versus radial location).

Results

Statistical analysis for A. incana

PCA synthesized the data from the 11 wood anatomical variables into a set of axes. Only the first two axes, or principal components (PCs), are shown in the PC correlation biplot (Figure 2). They represented, respectively, 72.9% and 12.7% of the total variance for a cumulative total of 85.6%. It can be seen in Figure 2 that the 14 injured rings were mainly concentrated within the negative portion of PC-1. Average vessel lumen area, average vessel lumen length, average vessel lumen width, average cell lumen area, average cell lumen length and average cell lumen width were positively inter-correlated as indicated by the narrow angles among their vectors (Figure 2). The projection of the 28 objects along the axis created by these

Table 2. Two-way ANOVA result table for *B. pendula*

	Uninjured rings (mean ± SD)	Injured rings (mean ± SD)	Change (%)	*P*	Radius A (mean ± SD)	Radius O (mean ± SD)	Change (%)	*P*
TWA (%)	59.8 ± 7.16	60.79 ± 5.27	+2	0.668	62.56 ± 6.3	58.04 ± 5.37	−7	0.059
TCLA (%)	22.66 ± 8.46	25.78 ± 7.47	+14	0.314	22.45 ± 7.51	25.99 ± 8.33	+16	0.255
ACLA (μm^2)	63.77 ± 12.84	69.78 ± 11.25	+9	0.192	62.95 ± 9.99	70.6 ± 13.4	+12	0.101
ACLL (μm)	7.79 ± 0.89	8.03 ± 0.81	+3	0.447	7.62 ± 0.75	8.21 ± 0.85	+8	0.071
ACLW (μm)	8.88 ± 1.19	9.09 ± 0.99	+2	0.626	8.69 ± 0.86	9.28 ± 1.23	+7	0.165
CN (mm^{-2})	1894.86 ± 664.45	2092.14 ± $733.04	+10	0.479	1962.5 ± 526.02	2024.5 ± 849.13	+3	0.823
TVLA (%)	**17.53 ± 4.92**	**13.42 ± 4.7**	**−24**	**0.039**	14.99 ± 4.97	15.97 ± 5.49	+7	0.608
AVLA (μm^2)	**1872.32 ± 340.48**	**1082.83 ± 285.38**	**−42**	**< 0.001**	1399.51 ± 533.84	1555.65 ± 484.64	+11	0.198
AVLL (μm)	**45.37 ± 4.57**	**33.46 ± 4.46**	**−26**	**< 0.001**	38.53 ± 7.89	40.31 ± 7.3	+5	0.308
AVLW (μm)	**47.33 ± 5.37**	**36.89 ± 5.2**	**−22**	**< 0.001**	40.72 ± 8.06	43.51 ± 6.73	+7	0.172
VN (mm^{-2})	47.43 ± 15.63	58.36 ± 18.23	+23	0.101	57 ± 18.53	48.79 ± 16.16	−14	0.213

Mean, standard deviation (SD), wood anatomical change and *P*-value (*P*) for each of the 11 wood anatomical variables. For more explanations, see caption of Table 1. The interaction term was removed from the table because of non-significance for all variables. Significant results ($P < 0.05$) appear in bold.

vectors reveals that injured rings have lower values than uninjured rings for these variables. The related ANOVA results were not significant for the three FPC parameters (Table 1). By contrast, the three vessel parameters significantly ($P < 0.05$) decreased within injured rings (Table 1, Figure 3A–C). Average vessel lumen area decreased by 54%, average vessel lumen length by 33% and average vessel lumen width by 38%. The PC correlation biplot also shows that injured rings have higher values than uninjured rings for total wall area, vessel number and cell number (Figure 2). However, the ANOVA results were not found to be significant for these variables (Table 1). Moreover, the PC correlation biplot displays no clear distinction between sample rings of radius A and sample rings of radius O (Figure 2). Surprisingly, total vessel lumen area was found to significantly differ between the two radial locations, although no further significant changes in vessel and FPC parameters were observed (Table 1).

Statistical analysis for B. pendula

PCA resulted in a set of axes formed by weighting each of the 11 wood anatomical variables appropriately. The first two axes are presented in the PC correlation biplot (Figure 4) and accounted for, respectively, 41.7% and 29.7% of the total variance for a cumulative total of 71.4%. The 14 injured rings, occupying primarily the negative portion of PC-2, were clearly separated from the 14 uninjured rings (Figure 4). They are shown to have more vessels but lower values than uninjured rings for average vessel lumen area, average vessel lumen length and average vessel lumen width. The ANOVA results were not significant for vessel

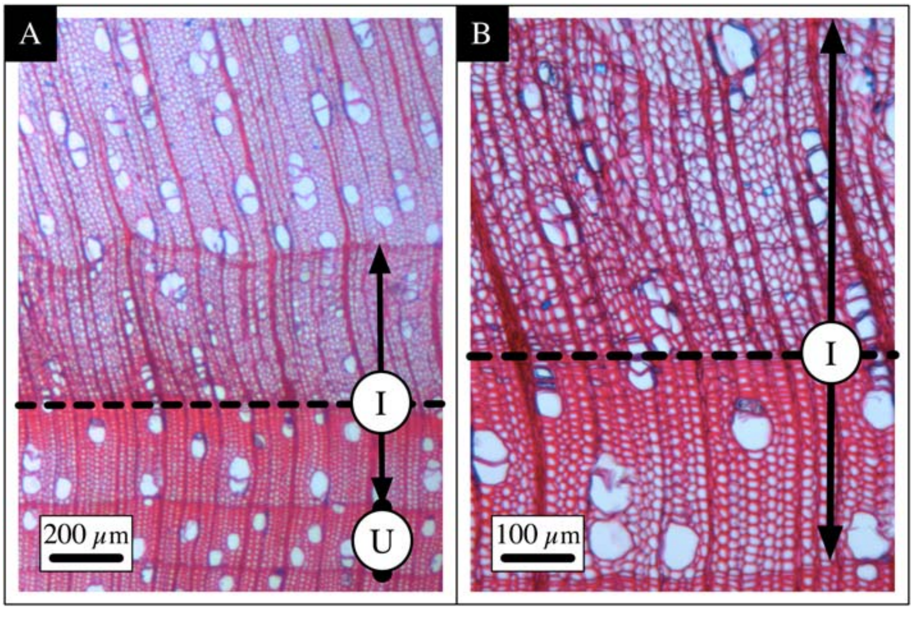

Figure 5. (A) Injured ring (I) and uninjured ring (U) close to the injury within *B. pendula*. The dashed line indicates the radial position of the injury within the increment ring. Following the early earlywood injury, smaller vessels and more radial parenchyma cells were formed. (B) Closer view of the injured ring (I) within *B. pendula*. This figure appears in color in the online version of *Tree Physiology*.

number contrary to the three vessel size parameters, which highly significantly ($P < 0.001$) decreased within injured rings (Table 2, Figure 3D–F). Average vessel lumen area decreased by 42%, average vessel lumen length by 26% and average vessel lumen width by 22%. In addition, it can be seen in Table 2 that total vessel lumen area was significantly lower in injured rings as compared with uninjured rings. However, when comparing FPC parameters between the two ring types, no significant differences were observed. Furthermore, as for *A. incana*, the PC correlation biplot displays no clear distinction between sample rings of radius A and sample rings of radius O (Figure 4). Accordingly, no significant changes in vessel and FPC parameters were found between the two radial locations (Table 2).

Sample ring visual inspection

In addition to the inter-annual variation in vessel size that could be statistically detected between injured and uninjured rings of *A. incana* and *B. pendula*, visual inspection of the injured rings revealed an intra-annual variation in vessel size. It can be clearly seen in Figure 5 that radial files of normal cells were produced until mechanical injury took place and that smaller vessels were subsequently formed within the increment ring. Moreover, even though no significant changes in FPC parameters were statistically found between injured and uninjured rings of *A. incana* and *B. pendula*, both species showed an increase in radial parenchyma cells following wounding (Figure 5) as pre-existing rays became larger and new rays were formed.

Discussion

Alnus incana and *B. pendula* showed the same wood anatomical response to mechanical injury inflicted by the debris flow of 28 May 2005. Injured rings formed in the debris-flow event year were characterized by smaller vessels as compared with uninjured rings formed in the previous year. By contrast, FPC parameters were not found to significantly differ between injured and uninjured rings. Vessel and FPC parameters were not observed to significantly vary between radius A and radius O, except for a higher proportion of vessel lumen area opposite to the injury (radius O) within *A. incana*.

This study reports on wound-induced formation of smaller vessels within naturally injured broad-leaved trees. This tree microscopic response to wounding has so far only been highlighted in studies based on artificial wounding (Rier and Shigo 1972, Sharon 1973, Bauch et al. 1980, Rademacher et al. 1984, Kuroda and Shimaji 1985, Lev-Yadun and Aloni 1993, Stobbe et al. 2002). Furthermore, we noticed that the formation of smaller vessels in response to mechanical injury could be detected inter-annually as well as intra-annually (Figure 5). Normal growth was interrupted during the growing season and was immediately supplanted by callus formation. Grünwald et al. (2002) stated that callus formation in broad-leaved trees started as early as 10 days after wounding. Moreover, environmental factors (in this case mechanical injury) are known to be operative on the formation of a particular vessel over a few weeks during the ontogeny of that vessel (Sass and Eckstein 1995, Eckstein 2004, Fonti et al. 2010).

We think that wound-induced formation of smaller vessels can be primarily accounted for by hormonal regulation. On the one hand, auxin is considered a major factor controlling xylem differentiation (Aloni 1987). We therefore presume that mechanical injury obstructed the normal basipetal flow of auxin within the impacted xylem and consequently increased auxin concentration along the wound edges, which became constriction areas (after Aloni and Zimmermann 1984). Increased auxin concentration triggered faster vessel differentiation within the constriction areas, resulting in the formation of smaller vessels (Aloni and Zimmermann 1983). On the other hand, ethylene is produced following wounding (Imaseki 1985) and is already described as a major signal in the initiation and differentiation of rays (Lev-Yadun and Aloni 1992). Thus, it is possible that ethylene might have influenced vessel differentiation as well.

We also interpret reduction in vessel size following wounding as a trade-off between xylem safety and hydraulic efficiency. Narrow vessels are indeed considered safer due to a lower risk of embolism and cavitation but hydraulically less efficient according to the Hagen–Poiseuille law (Zimmermann 1983, Tyree and Ewers 1991). We believe that the trees examined, which were all injured during the growing season, primarily allocated energy for compartmentalization (sensu Liese and Dujesiefken 1989) as well as regeneration and wound healing processes (Fink 1999). Besides, it is known that wounding during the growing season leads to more effective compartmentalization (Dujesiefken et al. 1991) and faster wound closure (Neely 1988) than in the dormant season.

In contrast to vessel parameters, no significant changes in FPC parameters were observed between injured and uninjured rings. This result has to be interpreted with caution since fibers and parenchyma cells were not distinguished in this study. We hypothesize that inter- and intra-annual variations in both cell types might have occurred and possibly counterbalanced each other. Wound wood is indeed known to contain more axial parenchyma cells than regular wood, whereas fibers are either fewer or in unchanged quantity (Sharon 1973, Bauch et al. 1980, Rademacher et al. 1984, Stobbe et al. 2002). In addition, sample ring visual inspection revealed an increase in ray size and number (Figure 5), which concurs with earlier findings on the effect of wounding (Lev-Yadun and Aloni 1992, Lev-Yadun and Aloni 1993). Vessel and FPC parameters mainly remained constant with increasing tangential distance from the injury, except for a higher proportion of vessel lumen area opposite to the injury (radius O) within *A. incana*. This is the only evidence supporting that injured trees may try to compensate reduction in vessel size by increasing their vessel number, which results in a higher proportion of vessel lumen area. Otherwise, based on the findings of this study, we can assume that tree microscopic response to wounding was marked around the entire tree circumference at impact height. Consequently, no particular sampling location would be specifically required—except for the callus pad and the decayed zone—for the wound-induced vessel anomalies to be detected.

Conclusion

Xylem cells of diffuse-porous species proved to be a valuable source of environmental information on past debris-flow activity. The most sensitive—and easy to measure—wood anatomical feature to mechanical injury was vessel size, which can be used as a basis for the reconstruction of various geomorphic events. However, it is necessary to first identify in the field the geomorphic process responsible for disturbances on trees. Furthermore, inter- and intra-annual variations in vessel size were observed, providing annual and seasonal resolutions, respectively. Similar studies should be conducted with further broad-leaved tree species because analysis of tree-ring anatomy benefits from a higher temporal resolution as compared to analysis of tree-ring width. Time elapsed between environmental events and the formation of anatomical tree-ring signatures is shortened, which allows the dating of events to be unequivocally inferred from tree rings. Nevertheless, ecological wood anatomy should more intensively investigate the relationships between wood anatomical features and tree-ring width in the light of environmental factors. Another pertinent issue tackled by this study is that the existence of anatomical tree-ring signatures caused by geomorphic processes should allow the dating of visible as well as internally hidden injuries and encourage the use of minimally destructive sampling methods in order to date injuries. Taking cores with increment borers and analyzing them for wound-induced vessel anomalies is certainly an excellent alternative to preserve forest ecosystems.

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