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Dating of snow avalanches by means of wound-induced vessel anomalies in sub-arctic *Betula pubescens*

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Dendrogeomorphic research has long relied on scarred trees to reconstruct the frequency of mass-movement processes. Injuries have mostly been dated macroscopically by counting the tree rings formed after wounding. Tree-ring anatomical anomalies induced by cambial injury, in contrast, have only recently been recognized as proxy records of past events. We investigated 12 sub-arctic downy birch (*Betula pubescens* Ehrh.) trees scarred by snow avalanches in Norway and Iceland. Earlywood vessel lumina were measured for each tree in the xylem tissue bordering the scars. Seven successive rings were examined, namely two control rings laid down prior to wounding and five rings in the wound xylem. We provide evidence that snow-avalanche-induced wounding resulted in atypically narrow earlywood vessels over at least two years. Our data demonstrate that wound-associated vessel anomalies represent tangible markers of mass-movement processes, and as such make a viable tool for reconstructing past events. Similar dendrogeomorphic studies based on tree-ring anatomy can be readily conducted with other mass-movement processes, as well as with other broad-leaved tree species. Ultimately, this new approach will foster increment coring over more invasive sampling techniques.

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The wounding of trees by mass-movement processes or forest fires occurs when conveyed material or heat abrades the bark and destroys part of the underlying cambium (Stoffel & Bollschweiler 2008). As a consequence, tree growth is locally disrupted, leading to the formation of a wound callus (Larson 1994; Fink 1999). The importance of tree injuries for dendrogeomorphic research has been emphasized repeatedly, from benchmark works (Sigafoos 1964; Alestalo 1971; Shroder 1980; Stoffel *et al*. 2010) to recent studies on snow avalanches (Muntán *et al*. 2009; Corona *et al*. 2012), rockfalls (Stoffel *et al*. 2005; Schneuwly & Stoffel 2008a, b), debris flows (Arbellay *et al*. 2010a; Schneuwly-Bollschweiler & Stoffel 2012), floods (Zielonka *et al*. 2008; Ballesteros *et al*. 2011a,b) and forest fires (McClain *et al*. 2010; Stambaugh *et al*. 2011). The dating of scars to the year by counting the number of tree rings formed after wounding, and to the season by observing the radial position of the injury within the tree ring allows the timing, frequency and spatial extent of events to be inferred (Stoffel *et al*. 2008).

Fonti *et al*. (2010) recently highlighted the growing interest of dendro-ecologists in investigating tree-ring anatomy to explore how environmental factors mould the xylem of trees. Moreover, anatomical changes in wood structure resulting from natural wounding have been successfully exploited for retrospective injury detection over the last few years. Scars in *Larix decidua* Mill. and *Picea abies* (L.) Karst. trees have been dated with tangential rows of traumatic resin ducts caused by mass-movement processes (Bollschweiler *et al*. 2008; Stoffel 2008; Schneuwly *et al*. 2009a,b). Stoffel & Hitz (2008) reported that the lumen size of earlywood tracheids was greatly reduced in *L. decidua* following wounding. As for broad-leaved trees, the formation of more and narrower earlywood vessels after cambial injury has been documented in dendrogeomorphic studies of both diffuse- and ring-porous species (Ballesteros *et al*. 2010; Bigio *et al*. 2010; Arbellay *et al*. 2010b, 2012a,b; Kames *et al*. 2011). Arbellay *et al*. (2012b) also observed the initiation of more and larger rays in *Fraxinus excelsior* L. as a response to mechanical damage.

The practical use of tree-ring anatomy in dendrogeomorphology forms the framework of this study, in which snow-avalanche scars on sub-arctic downy birch (*Betula pubescens* Ehrh.) stems were analysed for earlywood vessel anomalies in the wound xylem. This work aims to assess the robustness of using the annual variability in vessel lumen size as a tool for dating injuries and reconstructing past snow-avalanche events. The coupling of this new approach with increment coring is addressed.

Study sites

Fieldwork was conducted in two sub-arctic valleys frequently affected by snow-avalanche activity (Fig. 1A). The Erdalen valley (61°51′N, 7°09′E, 500 to 1900 m

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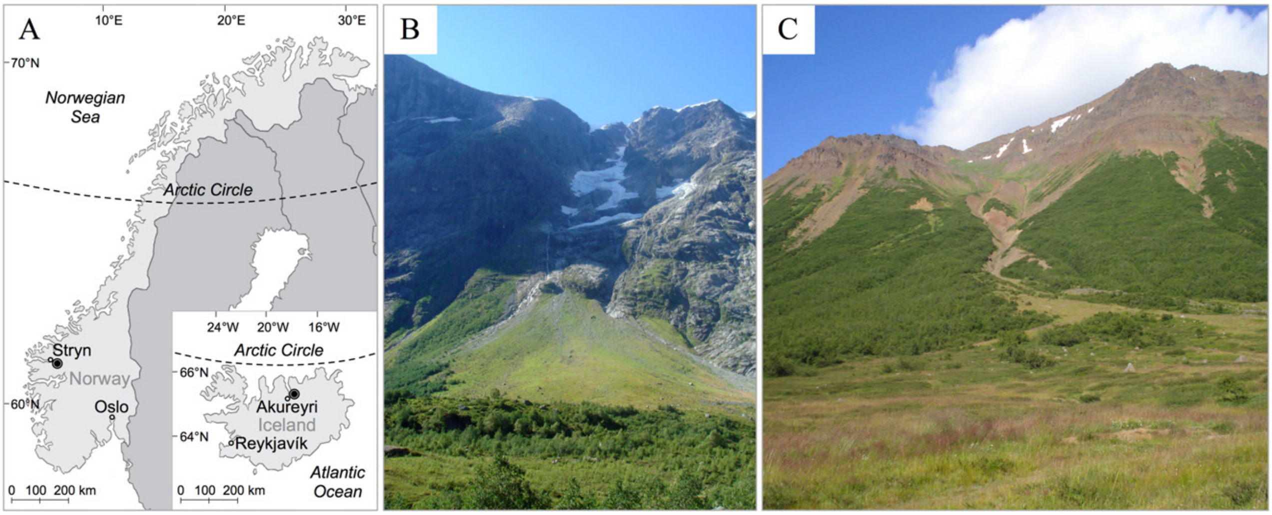

Fig. 1. A. Location of the two study sites in southwestern Norway and in northern Iceland. B. Trees in Erdalen, harvested in an avalanche path on the southern slopes of the valley. C. Trees in Dalsmynni, sampled on the Skarð avalanche cone. This figure is available in colour at http://www.boreas.dk.

a.s.l.) is located in the inner Nordfjord of western Norway about 23 km east of Stryn (208 m a.s.l.). It is a steep U-shaped and glacier-fed tributary valley connected to the Jostedalsbreen ice field. Mean January and July temperatures in Stryn are –1.2 and 15.1°C, respectively. The total annual precipitation is 1650 mm (NMI 2012).

The Dalsmynni valley (65°53′N, 17°58′W, 160 to 1000 m a.s.l.) is situated in northern Iceland about 22 km north of Akureyri (21 m a.s.l.). It is also a U-shaped valley, characterized by steep rockwalls and well-developed colluvial cones. The climate in Akureyri shows a total annual precipitation of 510 mm, and mean January and July temperatures of –0.4 and 11.4°C, respectively (IMO 2012).

Both valleys are predominantly vegetated with downy birch (*Betula pubescens* Ehrh.), which in Norway constitutes the forest limit and in Iceland is the sole tree species that forms extensive natural forests or woodlands (Aas & Faarlund 2001).

Methods

Fieldwork and laboratory work

Seven wounded *B. pubescens* trees were harvested in an avalanche path on the southern slopes of the Erdalen valley (Fig. 1B), while five wounded individuals of the same tree species were sampled on the Skarð avalanche cone in the Dalsmynni valley (Fig. 1C). All trees selected displayed one single scar on the stem, caused by snow-avalanche activity during the winter of 2004/2005 in Norway and during the winter of 2006/2007 in Iceland (Fig. 2; Table 1). One cross-section per tree was taken at the mid-length of the injury. The 12 cross-sections were sectioned with a chisel to obtain a small wood block (2×1.5×1.5 cm) of the xylem tissue directly next to the injury. After dating the rings, 15-μm-thick transverse sections of the wood blocks were cut using a Reichert sliding microtome. The micro-sections were stained with a 1% safranin and astrablue solution, rinsed with water, alcohol and xylol, and permanently mounted on microscope slides using Canada balsam.

Wood anatomical analysis

Earlywood vessels were studied in seven successive rings for each tree (84 rings in total): the injury ring (Ir 1) formed during the growing season following wounding, two control rings (Cr 1 and Cr 2) laid down previously, and four post-injury rings (Pr 1, Pr 2, Pr 3 and Pr 4) formed subsequently (Fig. 3A). Anatomical measurements of the cells were taken from images of the micro-sections captured at 50× magnification with a digital camera mounted on a light microscope. The software WinCELL (Régent Instruments Inc 2012) was used to measure the lumen area of vessels (Fig. 3B). Tree rings in diffuse-porous species consist almost entirely of earlywood, whereas latewood is confined to a very narrow terminal zone mostly made of ground tissue (Schoch *et al.* 2004). We thus followed the recommendation by Arbellay *et al.* (2012a) for an adequate sample of earlywood vessels to be measured (number and intra-ring location of cells). A total of 50 cells were analysed in each ring (4200 cells in total), where early earlywood vessels – conduits from the first half of the earlywood – were favoured. We selected cells located closest to the injury in Ir 1 and proceeded with

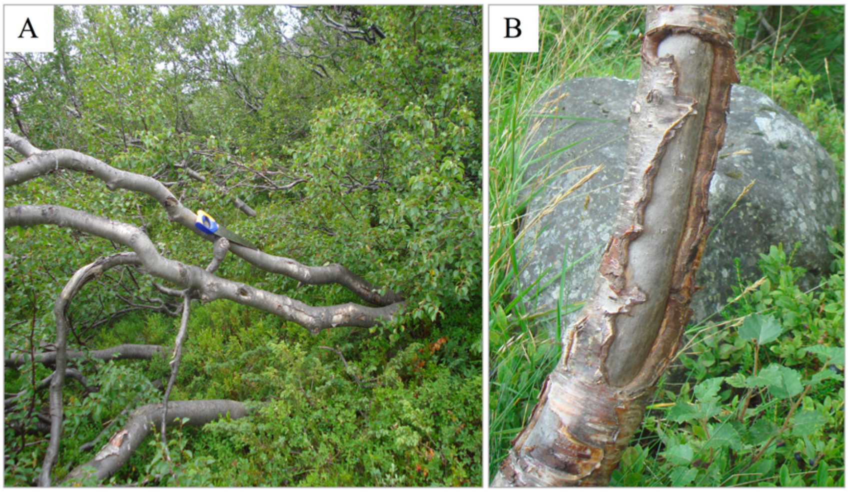

Fig. 2. A. Illustration of how snow avalanches have caused trees to lean towards the direction of the snow flow and have often left elongated scars on the stem. B. This tree, displaying one single scar on the stem, was sampled for wood anatomical analysis. This figure is available in colour at http://www.boreas.dk.

the measurement of cells in the other rings by observing a radial strip of equal tangential position, reminding that of an increment core.

Statistical analysis

The average vessel lumen area (AVLA) in each ring was depicted in box plots, and one-way ANOVA was used to determine whether there were significant ($p<0.05$) changes in AVLA between rings. First, the two control rings were compared in order to establish Cr 2 as a suitable control. Second, the five rings of the wound xylem were each compared with Cr 2 to evaluate tree recovery from cambial injury. In addition, this last procedure was also performed for each individual tree using the non-averaged lumen area of the 50 vessels analysed.

Table 1. Descriptive parameters and further information on the two sets of sub-arctic *B. pubescens* trees. SCBH = stem circumference at breast height.

	Norwegian trees	Icelandic trees
n	7	5
Age (years) mean±SD	31.29±6.32	30.25±12.53
SCBH (cm) mean±SD	22.27±5.43	9.13±2.84
Snow avalanche	Winter 2004/2005	Winter 2006/2007
Field campaign	Summer 2010	Summer 2011

Results

The average age of the *B. pubescens* trees was 31.29±6.32 years in Norway and 30.25±12.53 years in Iceland, while the average stem circumference at

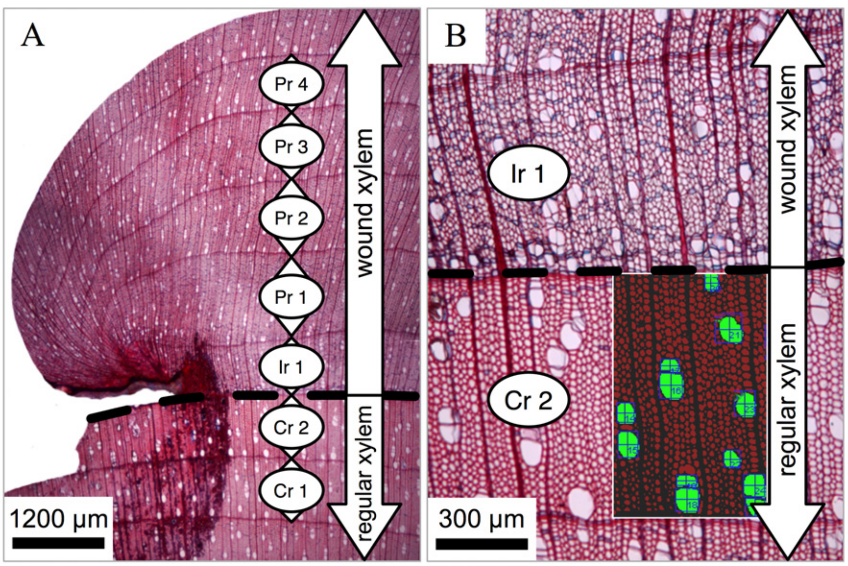

Fig. 3. Micro-sections of *B. pubescens* showing the wood prior to and after cambial injury. The dashed line indicates the position of the cambium at the time of wounding and allows the distinction between regular xylem and wound xylem. Ring types: Cr = control ring; Ir = injury ring; Pr = post-injury ring. A. This tree was scarred during the winter of 2004/2005 and sampled in summer 2010. B. Enlarged view of the wood directly next to the injury. Colour legend of the displayed window: green = vessels; maroon = fibres and axial parenchyma cells; black = cell walls and rays. This figure is available in colour at http://www.boreas.dk.

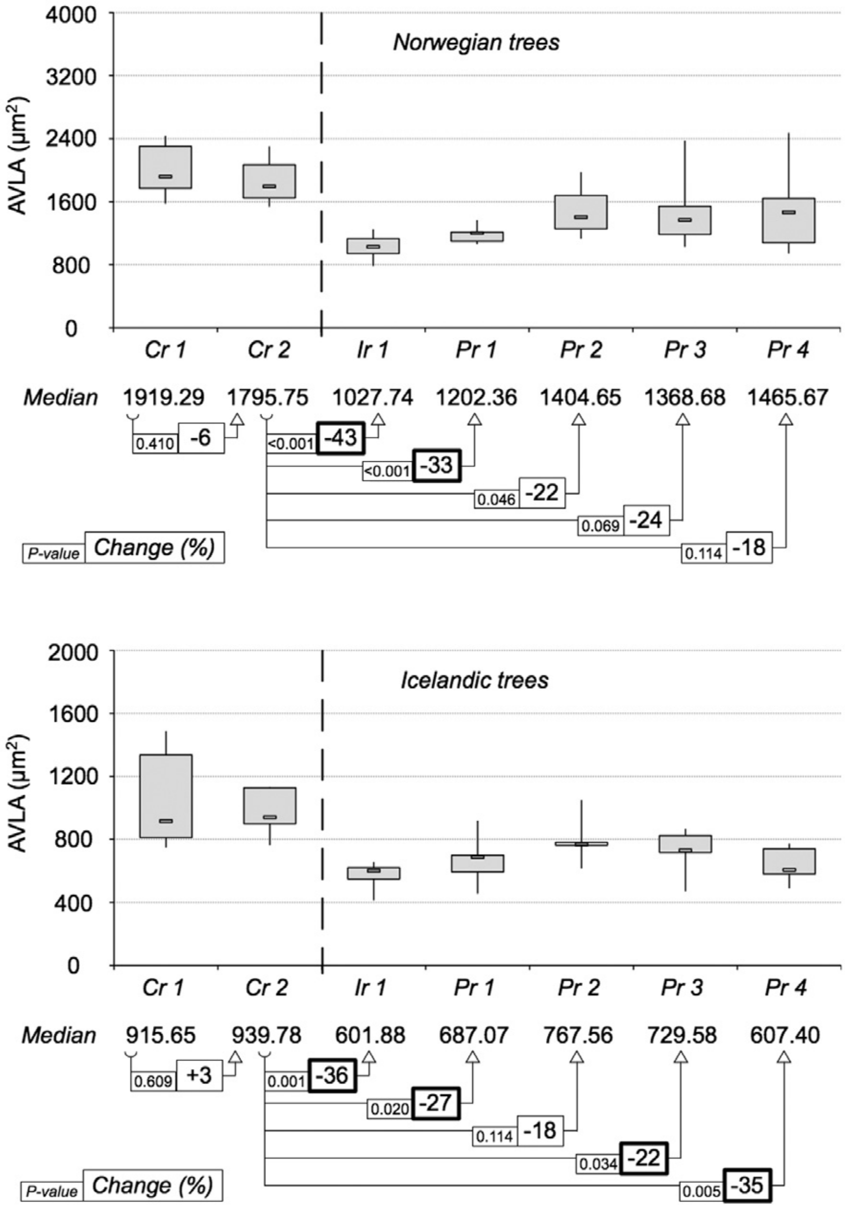

Fig. 4. Box plots depicting how trees adjusted to cambial injury (dashed line) after five years. Changes (%) in average vessel lumen area (AVLA) between rings are given along with one-way ANOVA results. Significant results are thick-framed. Ring types: Cr = control ring; Ir = injury ring; Pr = post-injury ring.

breast height was 22.27±5.43 and 9.13±2.84 cm, respectively (Table 1). AVLA in the Norwegian trees was about twice as large as in the Icelandic trees, with pre-wounding values ranging from 1535 to 2436 μm^2 in the former and from 748 to 1489 μm^2 in the latter (Fig. 4). Neither set of trees showed a significant change in AVLA between the two control rings (Cr 1 and Cr 2). They displayed, however, some significant ($p<0.05$) to very highly significant ($p<0.001$) changes in AVLA between Cr 2 and the five rings formed after wounding (Ir 1, Pr 1, Pr 2, Pr 3 and Pr 4). The box plots in Fig. 4 illustrate how in both sets of trees the lumen size of earlywood vessels was significantly reduced in the first two rings of the wound xylem (Ir 1 and Pr 1), with the strongest decrease in the injury ring. The conduits were, on average, narrower by 43% (Ir 1) and 33% (Pr 1) in the Norwegian trees, and by 36% (Ir 1) and 27% (Pr 1) in the Icelandic trees. In the third ring (Pr 2), vessel narrowing was less important and no longer statistically significant (Fig. 4). However, the temporal extent of the signal differed between the two study sites. In Norway, AVLA in Pr 3 and in Pr 4 was as large as in Pr 2 and therefore failed to be statistically significant. In Iceland, in contrast, AVLA was again significantly reduced by 22% in Pr 3 and by 35% in Pr 4 (Fig. 4). The magnitude of vessel narrowing in Pr 4 was consequently as high as in Ir 1.

As regards the individual tree response to cambial injury (Fig. 5), Ir 1 of all trees experienced a very highly significant ($p<0.001$) decrease in vessel lumen size,

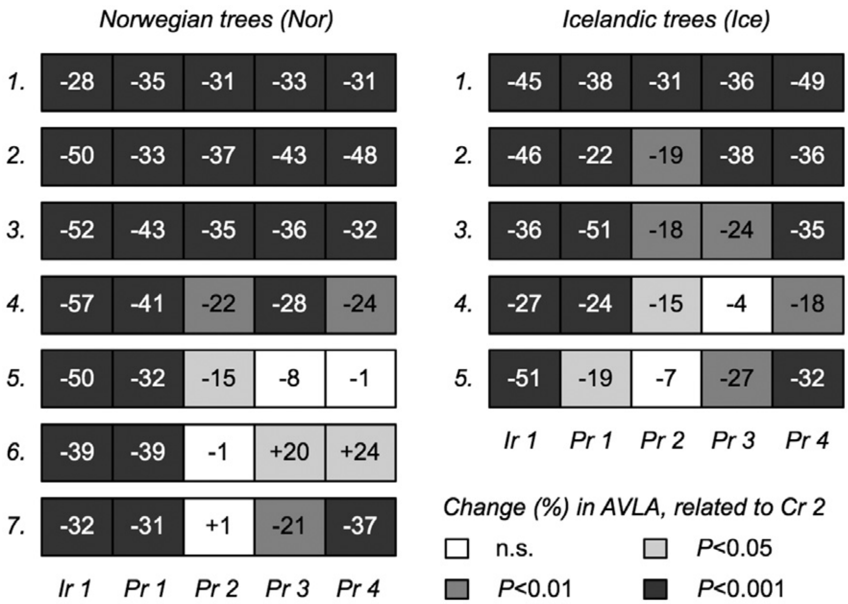

Fig. 5. Analysis of individual tree response to cambial injury. Changes (%) in average vessel lumen area (AVLA), related to Cr 2, were tested for significance with one-way ANOVA. Ring types: Cr = control ring; Ir = injury ring; Pr = post-injury ring.

ranging from 28 to 57% in the Norwegian trees and from 27 to 51% in the Icelandic trees. A similar reaction was observed in Pr 1 and was also found to be very highly significant (p<0.001) in all trees (expect for Ice 5), ranging from 31 to 43% in Norway and from 22 to 51% in Iceland. Individuals then developed different responses to the disturbance in the last three rings examined (Fig. 5). While some continued to show a statistically significant decrease in vessel lumen size, others displayed AVLA values close to pre-wounding values in Pr 2 (Nor 6, Nor 7 and Ice 5), Pr 3 (Nor 5 and Ice 4) and Pr 4 (Nor 5). One individual (Nor 6) even exhibited AVLA values greater than pre-wounding values in Pr 3 and Pr 4. On the contrary, in some cases vessel narrowing was again statistically significant in Pr 3 (Nor 7 and Ice 5) and Pr 4 (Nor 7, Ice 4 and Ice 5).

Discussion

Earlywood vessel anomalies in the wound xylem

The lumen size of earlywood vessels of sub-arctic *B. pubescens* trees was significantly reduced in the two years following cambial injury, with the strongest decrease in the first year. Moreover, investigations conducted for each individual tree meet these findings. Previous work on the wood anatomy of injured broad-leaved trees has reported a similar decrease in vessel lumen size in the first ring formed after wounding (Ballesteros *et al.* 2010; Bigio *et al.* 2010; Arbellay *et al.* 2010b, 2012a,b; Kames *et al.* 2011). As for the second ring, a prompt recovery in vessel lumen size has been observed in *Fagus*, *Fraxinus* and *Quercus* (Rademacher *et al.* 1984; Ballesteros *et al.* 2010; Arbellay *et al.* 2012b), whereas wood had not returned to normal by two years after wounding in *Acer* and *Betula* (Rademacher *et al.* 1984).

In this study, and for the first time, the wound xylem was analysed for earlywood vessel anomalies over five years, and annual variability in vessel lumen size was quantified. Over the long term, the response of *B. pubescens* to cambial injury was found to differ substantially from tree to tree, a fact that is not apparent in the box-plot results. Individual tree plots revealed that trees either persisted in forming narrower earlywood vessels over at least five years after wounding or presented signs of recovery in the third to fifth year after the disturbance. Intriguingly, vessel narrowing significantly resumed in some of the latter trees.

Environmental forcing on vessel lumen size

The earlywood vessel anomalies identified in the first two rings of the wound xylem undoubtedly originated from wound effects on the hydraulic architecture of *B. pubescens*, which is consistent with the observations of Rademacher *et al.* (1984) for *Betula alleghaniensis* Britt. The anomalies that were sometimes detected in earlywood vessels of the subsequent rings, in contrast, should be interpreted with caution. It is possible that wound effects may be persistent, as demonstrated by Lowerts *et al.* (1986), who stated that in *Liriodendron tulipifera* L. the anatomy of the wound xylem gradually approached that of regular xylem with years, but failed to return to normal by four years after wounding. Nevertheless, we believe that with increasing radial distance from the injury other environmental influences may intertwine with persisting or fading wound effects. Halldorsson & Sverrisson (1997) cited early summer frosts and insect attacks as factors affecting wood formation of birch in Iceland. Furthermore, climatic influences are also manifested in vessel lumen size (Sass & Eckstein 1995; García-González & Eckstein 2003; Tardif & Conciatori 2006; Fonti *et al.* 2007), which is indeed apparent between the Norwegian and the Icelandic trees of this study. Both sets of trees are of similar age, but the Icelandic trees display much narrower vessels, certainly owing to the much cooler and dryer climate in Akureyri (Baas & Schweingruber 1987).

Implications for dendrogeomorphic research

In sub-arctic *B. pubescens* trees the first two rings formed after snow-avalanche-induced wounding furnished consistent evidence that was definitively wound-associated. The formation of atypically narrow earlywood vessels as a result of mechanical damage can be used in tree-ring series of increment cores for dating injuries and reconstructing past events. It should allow the accurate dating of visible injuries and, although usually thought compromised via increment coring, the possible dating of internally hidden injuries. It is strongly recommended to sample and analyse the xylem tissue directly next to the injury visible on the stem (Arbellay *et al.* 2012a,b). However, it is important to note that, even by means of vessel anomalies, events that occurred at short intervals are still likely to be difficult to differentiate on increment cores. Despite this drawback, the existence of tree-ring anatomical anomalies induced by cambial injury motivates the trade of the destructive extraction of disks and wedges for the minimally invasive sampling of increment cores, a move that is encouraged by the ongoing development of sample preparation techniques (Fonti *et al.* 2009) and image analysis systems (von Arx & Dietz 2005; Régent Instruments Inc 2012).

Conclusions

This study demonstrates that injuries can be dated microscopically by means of wound-induced vessel anomalies, which appeared in a very short time after the disturbance, showing that altered wood anatomical features can serve as proxy records of past events with at least annual resolution. Nevertheless, future dendrogeomorphic investigations based on tree-ring anatomy from wounded broad-leaved trees should analyse vessel anomalies in conjunction with ray anomalies to ensure proper dating of injuries. Ray anomalies can be easily assessed by visual inspection of the rings and would further attest to cambial injury, given that environmental influences other than wound effects may be manifested in vessel size. Furthermore, considering the inherent variability in individual tree response to cambial injury, future studies should rely on an increased number of trees to document past events with acceptable confidence.

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