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Different forms of tension wood in alder and beech in relation to mechanical stress – preliminary results

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Introduction

In the context of changing magnitudes and frequencies of natural hazards such as debris flows or snow avalanches caused by the current climate change a detailed understanding of tree reactions on growth stresses induced through different geomorphological forces is desirable. Macroscopic changes in wood formation (growth variations in trees) as reaction to external impacts have often been used for dating catastrophic events. Frequently, conifers have been used in dendrogeomorphology for reconstructions of geomorphic processes while similar studies with broadleaf species are rather rare. However, broadleaf species often occur in mixed forests together with conifer trees and are sometimes the dominant species in lower elevations. Furthermore, broadleaf species possess a more complex wood anatomy and offer structural features for further analysis not found in coniferous wood. Hence, it is essential to also examine the reaction wood of broadleaf species in more detail in order to enable dendrogeomorphological studies in vegetation zones dominated by them. It is suggested here that the additional application of wood anatomical techniques can harvest supplementary information about type, size and intensity of past hazardous impacts on tree growth. Long-term growth experiments imitating typical impacts of different geomorphic events are being conducted and their wood anatomical reactions monitored in order to study the likely varying reactions to a range of mechanical stresses, and first results are presented.

Study sites and methods

Growth experiments with European beech (*Fagus sylvatica*) and European alder (*Alnus glutinosa*) were set up near Krattigen (7º 45' / 46º 38', 840m asl, Bernese Oberland) and near Posieux (7º 08' / 46º 45', 600m asl, Canton of Fribourg), respectively, at the end of the tree winter dormancy in March 2004 (Fig. 1)

Figure 1: Location of experimental plots: Krattigen (dot), Posieux (star)

The treated specimens at both sites were mainly young trees. In Krattigen the forest stand contains beech regrowth following storm damage and the stand of European alder in Posieux was planted for re-vegetation purposes approximately ten years ago. At both sites ten groups containing four trees each were set up applying different treatments listed in table 1.

Table 1: List of groups with different treatments (four trees per group)

T1	Stem bent to 80° from the vertical
T2	Stem bent to 45° from the vertical
T3	Stem bent increasingly in time starting from small angles up to 80°
T4	Stem bent to 80°, but with the apex remaining vertical
T5	Stem bent to 80°, with apex cut
T6	Stem bent to 80°, but with the bark & cambium partly removed from the upper side
T7	Stem bent to 80°, but with the bark & cambium partly removed from the lower side
T8	Stem bent to 80° and sideways
T9	Stem and root system tilted to 80° from the vertical, with roots partly destroyed
T10	Reference group

After the commencement of tree growth at the beginning of the vegetation period 2004 the pinning method (Mariaux 1967, Wolter 1968) was applied to all trees and repeated afterwards every fortnight. In addition, puncher samples (Forster *et al*. 2000) of the tension wood side of one tree per group were taken. Thin sections of the puncher samples were cut for further microscopy and digital photos were taken. Wood anatomical structures, that is, cell wall and lumen area of all cells and lumen area of vessels were recorded by digital imagery and analysed utilizing the software programs Adobe Photoshop Elements and WinCELL Pro 2005a.

Results and discussion

Figure 2 illustrates the differences between typical tension wood and normal growth in beech. The tension wood contains much denser fibre cell tissue with fewer and smaller vessels. Furthermore, it shows no vessels in the early part of the tree ring. Obviously, then priority was given to stabilisation of the tree rather than to its supply with nutrients and water. This stands in direct contrast to the results gained for the two coniferous species (spruce and larch) which were also treated in the experiment (Gärtner *et al.* in prep.). The first cell rows formed by the conifers were normal earlywood tracheids with thin cell walls and large lumen. Hence, it seems as if conifers follow a different strategy when responding to heavy mechanical impact, *e.g.*, geomorphic processes. While they seem to secure water conductance at the beginning of the growing period the broadleaf species first respond to the mechanical stress by forming reaction wood cells and then ensure sufficient water supply.

The visual impression is confirmed by the analysis results of the digital imagery. Both species display substantial differences between the treatment groups and the reference group (Fig. 3).

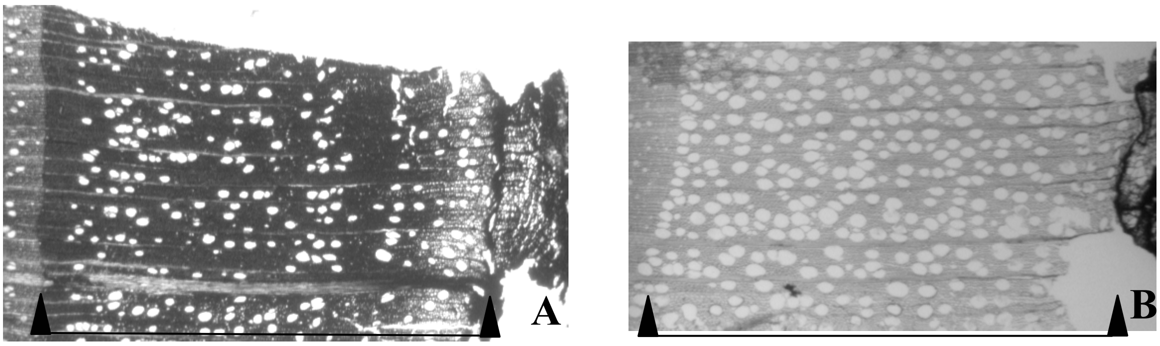

Figure 2: Light microscopy photos of microsections cut from a tilted beech (A) and an untreated reference tree (B) at site Krattigen; tree-ring width indicated by lines between arrows (mag.: 25x)

In alder, the largest percentage of cell-wall material are found in groups T1 and T9 in contrast to the smallest values in groups T2 and T6 and in the reference group. In beech, groups T1 and T7 exhibit the largest cell wall area percentages while the reference group and T3 have the smallest values. This shows that generally the treatments were successful in inducing tension wood in both species and that the quality of the tension wood varied between the groups due to the special treatments, *e.g.*, cutting off the apex or partial removal of the cambium. The data reveal a differentiation into tension wood classes caused by the different treatments. Severe mechanical stress appears to result in more cell wall material, *e.g.*, in groups T1 to T3 of alder the decreasing mechanical stress is paralleled by a diminishing amount of cell wall material. In both species, the more intensive treatments in T1 result in denser tension wood compared to group T3 with less mechanical stress present.

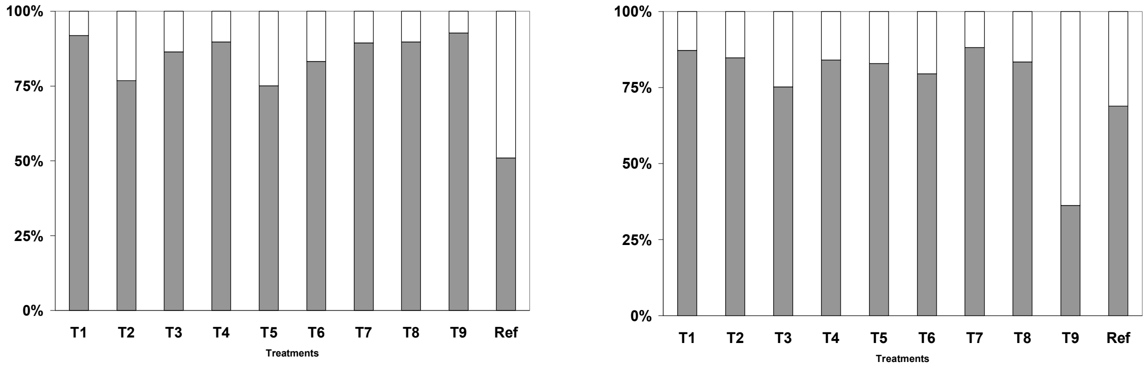

Figure 3: Percentage area covered by cell wall (grey) and cell lumen (white) per treatment (T1-9 & reference group) for alder (left) and beech (right)

The percentage area covered by cell wall material for both species is larger in T7 than in T6. In both treatment groups the trees were bent to 80° from the vertical. However, the difference between both groups is that in T6 bark and cambium were partly removed from the upper part of the stem above the bend while in T7 they were stripped off from the lower side below the bend. This result indicates that the reaction wood induction is controlled more from the upper part of trees because the removed tissue from the upper side probably hindered relatively stronger the flow of hormones and other substances responsible for stimulating the production of tension wood than did the removed tissue from the lower part.

The cell wall percentages of both species in T4 are smaller than in T1 but larger than in T5. This suggests that the intensity of the tension wood formation was weakened considerably in T5 when the apex was cut. In contrast, the apex remaining vertical in group T4 appeared to have less influence on the severity of the tension wood. The result implies that different conditions of an apex during a tree's reaction to mechanical stress can lead to dissimilar types of tension wood comparable to the differentiation in tension wood intensity due to the severity of the mechanical stress found in groups T1 to T3. The finding might also support the above result that tension wood formation is mainly controlled by the upper part of a tree. However, the very low cell wall percentages of beech in group T9 would suggest that the root system might be more important for the control of tension wood formation in beech than it is in Alder. In treatment T9 the root systems of the trees were partly destroyed and hence tension wood control by the roots might have been weakened in beech. The results suggest that the factor cell wall percentage can be used as an indicator of reaction wood intensity. However, attention needs to be paid when trees have not only been tilted or bent but also damaged in which case the intensity of the tension wood is likely to be altered.

Table 2: Analysis of variance (ANOVA) of vessel area for alder and beech

Species	***F***	***P-value***	***F crit***
Alder	18.99924	2.41E-25	1.954952
Beech	10.40234	8.39E-13	1.970619

(If F > F crit, then variances between groups are larger than within groups, small P-values indicate high significance of results)

The wood anatomical feature vessel area seems to have been affected by the different treatments as well. The analysis of variance (Tab. 2) shows that the vessel area differs more between than within the treatment and reference groups. This suggests that the treatments were successful in inducing different vessel sizes embedded in changed densities of fibre cell tissue.

For a better comparison of the vessel-area variations between the treatment groups, box-whisker plots were created (Fig. 4). The vessel areas in both species declined significantly in group T1. However, they decreased less when the apex, as one of the main locations for a tree's ability to respond to gravitational forces (Strasburger *et al.* 2002), was cut (T5). This is comparable to the altered percentage area covered by cell wall material in this group shown in figure 3. In both species a progression from small to relatively large vessel areas in groups T1 to T3 is discernible indicating that tension wood can be classified in intensity classes with changed fibre cell and vessel features resulting from mechanical impacts of varying strength.

In alder, treatment T6 resulted in significantly smaller vessel areas compared to those measured in T7, but in beech the vessel areas in the two groups do not differ distinctly. This might suggest that in alder both fibre cell and vessel formation are hindered by the removed tissue from above the impact zone while in beech the opposite seems to be true.

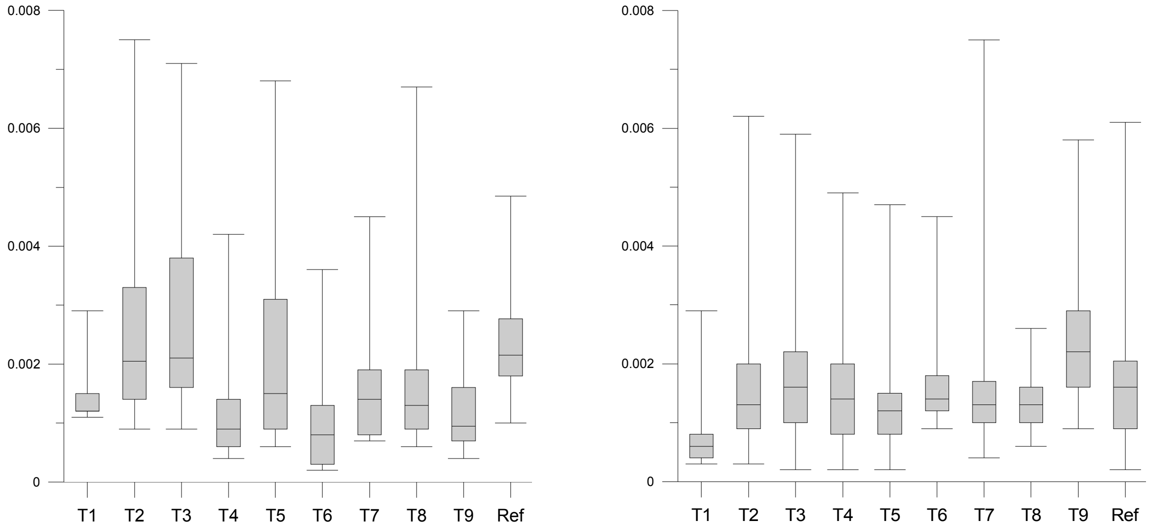

Figure 4: Vessel area per treatment (T1-9 & reference group) for alder (left) and beech (right)

When the root system is partly cut off in beech the species seems to produce less clear reaction wood, i.e., the cell lumen to wall ratio and the vessel area decrease less than in normal tension wood. However, before more reliable conclusions can be drawn all samples of the experiment need to be analysed.

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