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Research paper

How fast do European conifers overgrow wounds inflicted by rockfall?

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The capacity of trees to recover from mechanical disturbance is of crucial importance for tree survival but has been primarily investigated in saplings using artificially induced wounds. In this study, mature *Larix decidua* Mill., *Picea abies* (L.) Karst. and *Abies alba* Mill. trees growing on alpine slopes that were wounded by naturally occurring rockfall were analyzed to determine their efficiency in overgrowing wounds. In total 43 *L. decidua*, *P. abies* and *A. alba* trees were sampled. First, 106 samples from 27 *L. decidua* and *P. abies* trees were analyzed to reconstruct yearly and overall overgrowth rates. Cross sections were taken at the maximum extension of the injury and overgrowth rates were determined on a yearly basis. Results clearly showed that *L. decidua* overgrew wounds more efficiently than *P. abies* with an average overgrowth rate of 19° and 11.8° per year, respectively. The higher on the stem the injury was located, the faster the wound was closed. Young and small trees overgrew wounds more efficiently than older or thicker trees. In contrast, no correlation was observed between injury size or increment before/after wounding and wound closure. Second, cross sections from 16 *L. decidua, P. abies* and *A. alba* (54 injuries) were used to assess closure rates at different heights around the injury. Overgrowth was generally smallest at the height of the maximum lateral extension of the injury and increased at the upper and lower end of the injury. The efficiency with which *L. decidua* closes wounds inflicted by rockfall makes this species highly adapted to sites with this type of mechanical disturbance.

Keywords: *Abies alba*, injury, *Larix decidua*, *Picea abies*, wound closure.

Introduction

The capacity of tree stems to recover from damage is critical for tree survival especially on sites with repeated wounding due to fire, herbivores, wind or mechanical impacts such as rockfall, debris flow or other geomorphic processes. Mechanical wounding exposes wood to infection by fungi and bacteria (Smith 2006) and may be fatal for a tree. To protect against this, a wound cambium is formed within the parenchymatous zone as a tangential extension of the undisturbed vascular cambium (Shigo 1986, Delvaux et al. 2010). The affected cambium at the edge of a wound reacts with the formation of callus tissue and normal wood to close the opened surface of the stem (Fisher 1981, Larson 1994, Liese and Dujesiefken 1996, Oven and Torelli 1999, Grünwald et al. 2002, Stobbe et al. 2002). The exposed surface is slowly covered by the centripetal growth of the cambium, which results in production of new wood and bark to eventually seal the wound site (Fisher 1981). A layer of lignified parenchyma cells forms tangentially from the callus at first, followed by a layer of short tracheids and a series of traumatic resin canals (Liese and Dujesiefken 1996, Oven and Torelli 1999).

Wound healing and responses of tree stems to damage depend on the extent of damage and the tissues involved, but this also varies among species. Depending on the depth of wounding, reactions can be restricted to the bark or initiated in the xylem. Injured trees with deep wounds, which is more commonly the case if injury is due to geomorphic processes, generally react with two primary responses to stem damage: (i) closing of wounds by tissues produced by the vascular cambium or (ii) re-differentiated xylem parenchyma cells (i.e., callus formation) and the compartmentalization of decay in the xylem (Romero et al. 2009).

The capacity of a tree to react to wounding and form boundary zones as well as compartmentalization barriers is crucial for avoiding infections and resisting the spread of wood decay (Pearce 1996). Rates of wound closure can differ greatly, varying with tree species, type and size of wound and growth rates of the tree (Neely 1970, 1988). According to Larson (1994) and Martin and Sydnor (1987), the rates of callus development and wound closure are influenced by many factors, the most important of which are tree vigor or rate of growth, season of wounding, location of the wound on the tree and intensity of pathogenic invasion.

Although many studies have focused on healing of wounds and on associated reactions, most have been conducted on the cellular level. Macroscopic studies on overgrow rates of wounds have generally been based on artificial wounding of young saplings under laboratory conditions (e.g., Rademacher et al. 1984, Schmitt and Liese 1990, Schmitt and Liese 1995, Schmitt et al. 1995, Lev-Yadun 2002, Stobbe et al. 2002). Broadleaved species have been investigated more frequently than conifers, and existing studies are limited to the work of Bangerter (1984) on the closure of longitudinal wounds in *Larix decidua* Mill. and *Picea abies* (L.) Karst. However, this study was based on 4-year-old saplings and wounds were induced artificially.

It is therefore the aim of the present study to investigate mature trees of three conifer species (*L. decidua*, *P. abies* and *Abies alba* Mill.) injured by rockfall on high-elevation sites in the Swiss and French Alps. First, overgrowth rates at the height of the maximum extension of the injury for *L. decidua* and *P. abies* were assessed and the factors influencing wound closure rates were determined and quantified. In a second step, closure rates at different heights around the injury were investigated to determine if wound closure rates depend on the vertical position relative to the injury.

Materials and methods

Trees were sampled from three different rockfall slopes in the Swiss and French Alps. Site conditions, such as slope angle and boulder size, did not differ considerably (see Schneuwly et al. 2009*a*, 2009*b*). Rockfall at all study locations mainly occurs outside the growing season, i.e., between October and May with highest activity in April and May (Schneuwly and Stoffel 2008).

Wound closure at the maximum extension of the injury

For the analysis of wound closure at the height of maximum extension of the injury, 43 severely injured trees with multiple rockfall injuries were sampled. Tree species, height and diameter at breast height (DBH) were recorded. All visible defects in morphology were noted and pictures of each tree were taken. The maximum extension, width, height and orientation of each injury were also noted and photographed. Finally, one cross section was sawn from each wound at its maximum lateral extension, resulting in a dataset of 106 injuries (81 *L. decidua*, 25 *P. abies*). The average tree diameter at the time when the rockfall inflicted the injury was 43.2 and 47.4 mm and the injury height was 92.6 and 68.4 cm for *L. decidua* and *P. abies*, respectively. Figure 1 shows the properties of sampled trees and injuries and provides details on the age and diameter of trees at the time of wounding, the annual increment before wounding and the height, width and size of sampled injuries.

In the laboratory, samples were first air-dried and polished with sandpaper (maximum 400 grit). The width and yearly overgrowth of each injury were assessed using binocular and transparent sheets with an on-printed ‘degree-grid’ (Figure 2). To facilitate comparison between stems of different sizes, overgrowth was measured in degrees where 360° represents the total stem circumference. The average injury width was 91.7° (*L. decidua*) and 95.2° (*P. abies*). The ring width of each sample was then measured on an average radius (i.e., excluding compression wood or callus tissue) using a LINTAB measuring device and TSAPWin software (Rinntech 2011). The average yearly increment before the injury was 4.2 mm *(L. decidua)* and 3.1 mm *(P. abies)*. The yearly increment in a specific year was then compared with the wound closure rate of the same year to test the correlation between yearly increment and wound closure.

The number of years to complete closure was counted for samples with closed wounds and interpolated from the yearly overgrowth rate and the size of the open wound for samples with open wounds. Finally, various parameters of tree growth and injury severity (height of the injury, diameter of the stem, age at the time of injury, overall yearly increment, yearly increment before/after wounding, and injury width, length and size) were correlated to wound closure rate using Pearson’s correlation coefficient.

Overgrowth rates at different heights around the injury

For the analysis of the overgrowth rates at different heights around the injury, 16 trees with multiple rockfall injuries were selected: six *L. decidua*, six *P. abies* and four *A. alba*. Species, height and diameter at DBH were recorded in the field for each tree. The maximum extension, width, height and orientation of each injury were also noted before the injury was photographed. The selected trees were then felled and cut into 820 stem

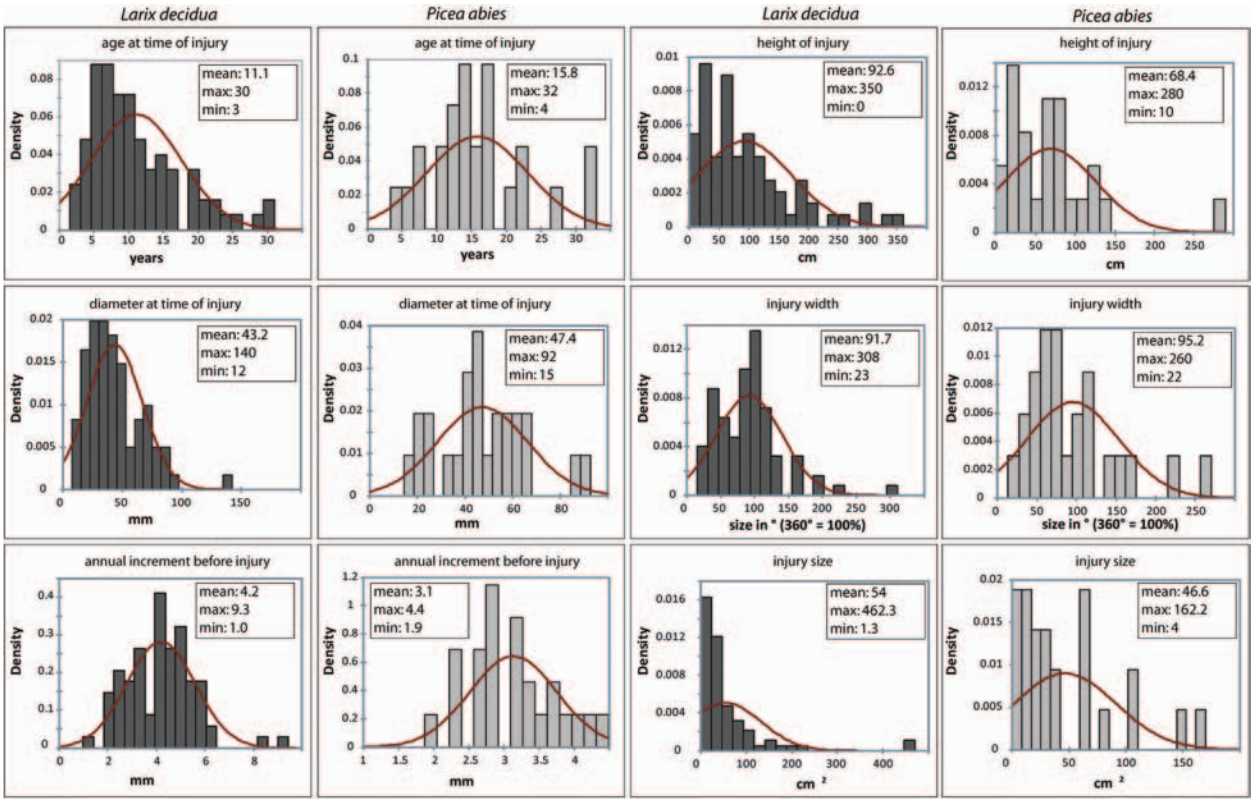

Figure 1. Characteristics of analyzed trees and samples presented as density distributions.

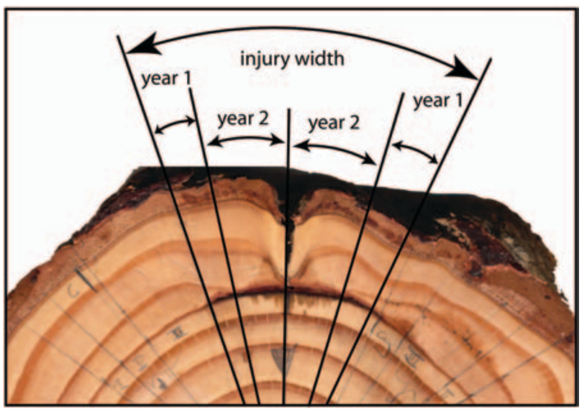

Figure 2. Schematic view of the calculation of wound closure per year. In this case, the tree was injured three years before the sampling and the wound was closed after 2 years. Closure rates include overgrowth on both sides of the wound as indicated here for year 1 and year 2. Tree-ring widths were measured along a radius with no growth anomalies.

sections of 0.1-m length in the laboratory; they were air-dried and sanded using paper up to 400 grit. While the mean tree diameters of *L. decidua* and *P. abies* were similar (18.7 and 23.7 cm, respectively), those of *A. alba* trees were considerably larger (43.1 cm). The average tree ages were 30.4 (*L. decidua*), 20.0 (*P. abies*) and 43.0 (*A. alba*) years (Table 1; Schneuwly et al. 2009*b*).

Total overgrowth rates (i.e., average overgrowth since the beginning of callus formation and cambial activity after the wounding) were used for the comparison of samples from different heights.

Results

Closure rate at the height of the maximum extension of the injury

Analysis of the 106 samples taken at the maximum extension of the injury showed that *L. decidua* overgrew wounds inflicted by rockfall faster than *P. abies,* as seen in Figure 3. *L. decidua* showed an average yearly closure rate of 19° (SD: 11.1°) and *P. abies* a rate of 11.8° (SD: 7.9°), which corresponds to an average of 6 and 4.3 mm per year, respectively. Of the total injury width, *L. decidua* closed 27% per year on average while *P. abies* only overgrew 17%. Differences in closure rates were statistically significant between the two species (95% confidence interval) based on Student's *t*-test and the non-parametric Mann–Whitney test. Accordingly, and as seen in Figure 4, the time to complete wound closure was shorter in *L. decidua* (average of 7.4 years) than in *P. abies* (average of 12.3 years). In *L. decidua*, 63% of the wounds were closed within 6 years, while this was only the case in 40% of the *P. abies* samples even though the injury size in *L. decidua* was slightly larger than in *P. abies.*

Table 1. Characteristics of the sampled trees for the analysis of overgrowth rates at different positions around the injury.

	Number of trees	Diameter (cm)		Age (years)		Number of wounds	Wound heights (cm)	
		Mean	SD	Mean	SD		Mean	SD
L. decidua	6	18.7	24.9	30.4	17.1	26	91.2	92.8
P. abies	6	23.7	23	20	9.1	20	93	91.6
A. alba	4	43.1	53.5	43	12.9	8	55	64.6
Total	16	24.2	39.3	28.4	15.8	54	86.5	88.3

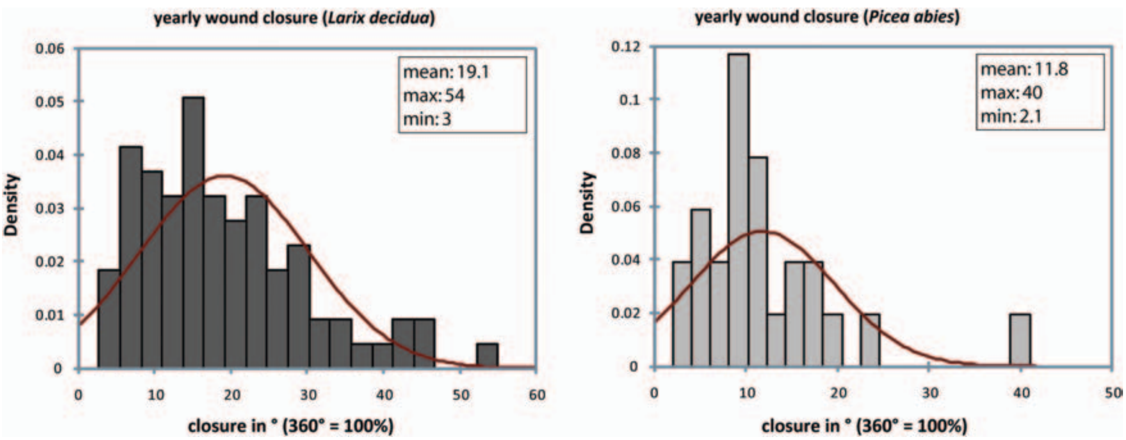

Figure 3. Wound closure in *L. decidua* and *P. abies* presented as density distributions. *L. decidua* shows higher closure rates than *P. abies*.

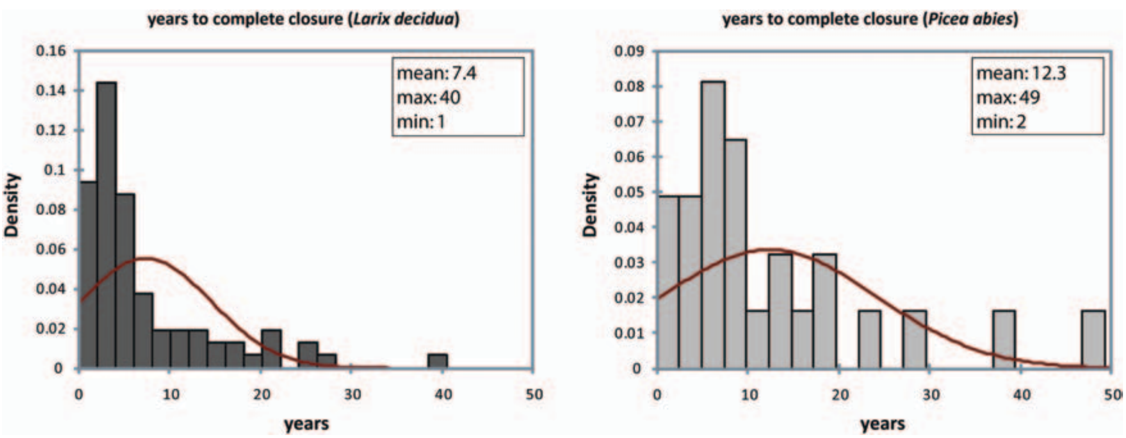

Figure 4. Number of years needed to completely close rockfall-induced injuries in *L. decidua* and *P. abies*. As *L. decidua* normally closes wounds faster than *P. abies*, the total number of years to complete closure is considerably lower.

Wound closure rates were also assessed on a yearly basis for the first 5 years after wounding. Wounding occurred predominantly in the dormant season and thus 'year 1' corresponded to the year after wounding. When the wounding occurred late in the growing season, year 1 corresponded to the subsequent year. In *L. decidua*, closure in years 1 and 2 after the injury was nearly equal (~22°) and decreased considerably in years 3–5 after the impact (Table 2). Interestingly, wound closure in *P. abies* was generally smaller in year 1 (12°) than in year 2 (16°). In the samples of *P. abies*, we regularly observed that no overgrowth occurred in year 1 and wound closure commenced in year 2. The decrease in overgrowth rates in years 3–5 also occurred in *P. abies* but to a lesser extent than in *L. decidua*.

Finally, tree-ring width measurements were used to compare the yearly increment in a specific year with the wound closure rate in the corresponding year. Results showed no correlation between annual increment and wound closure, neither in *L. decidua* nor in *P. abies* ($R^2 = 0.0267$ and 0.0178, respectively; Figure 5).

Factors influencing closure rate

Specific parameters of growth and injury severity were correlated to closure rates to identify factors that potentially influence wound closure (see Table 3). Results suggested that the most important factor controlling the closure of the wound in *P. abies* was the height of the injury on the stem ($r = 0.7$). The higher on the stem an injury was located, the faster the injury was closed. In *L. decidua*, this correlation did not seem to be as pronounced as in *P. abies* ($r = 0.2$). Vitality of a tree before wounding, however, did not seem to influence wound closure, as no correlation could be seen between wound closure and yearly increment before the injury. Similarly, injury size (width and length) was not correlated to wound closure in our sample. Only *L. decidua* showed a weak negative correlation between wound closure and injury size and a weak positive correlation between wound closure and yearly increment after wounding. A negative but not very strong correlation exists for both species for the tree diameter and tree age at the time of wounding. The smaller and the younger a tree was at the time of the injury, the faster the wound was closed.

Closure rates at the different heights along the injury

Closure rates at different heights around the injury are presented in Figure 6. Closure rates were lowest at the height of the maximum extension of the injury (indicated as 100% in Figure 6) and increased the more distant from the wound the sample was taken. Wound closure rate was highest 30 cm below the maximum extension of the injury in *P. abies* and *L. decidua* with up to 220% of the rate at the maximum extension. Above the injury, closure rates were generally higher (105–130%) than at the maximum extension, but remained well below the values observed below the maximum extension. *Abies alba* showed the highest closure rates (220%) at 10 cm below the injury; however, sample depth was rather limited and therefore may have been influenced by a single

Table 2. Wound closure (°) in years 1–5 after wounding.

	L. decidua	*P. abies*
Year 1	21.6	12.2
Year 2	20.7	15.9
Year 3	12.7	10.3
Year 4	6.9	8.8
Year 5	3.3	6.7

Table 3. Pearson's correlations between wound closure and parameters of growth and injury severity. Statistically significant values at the 95% confidence interval are indicated in italic.

	Closure rate (°)	
	L. decidua	*P. abies*
Height of injury	*0.205*	*0.701*
Diameter of stem	*− 0.499*	*− 0.444*
Age at time of injury	*− 0.449*	*− 0.399*
Yearly increment, overall	0.191	−0.082
Yearly increment before wounding	−0.021	0.103
Yearly increment after wounding	*0.321*	−0.039
Injury width	−0.017	−0.079
Injury length	−0.003	0.059
Injury size (area)	*− 0.222*	−0.302

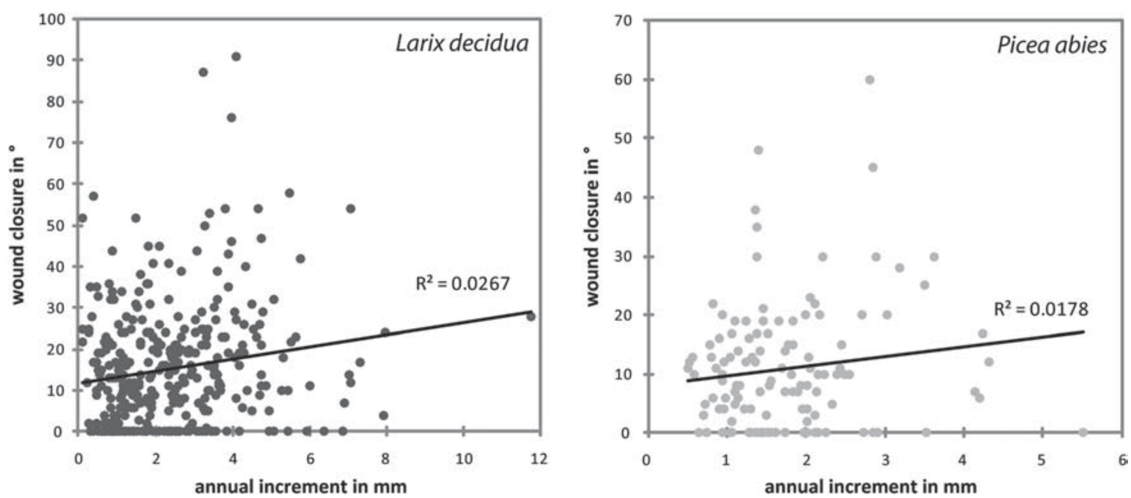

Figure 5. Scatter plots and trend lines for the correlation between wound closure in a specific year and the corresponding annual increment.

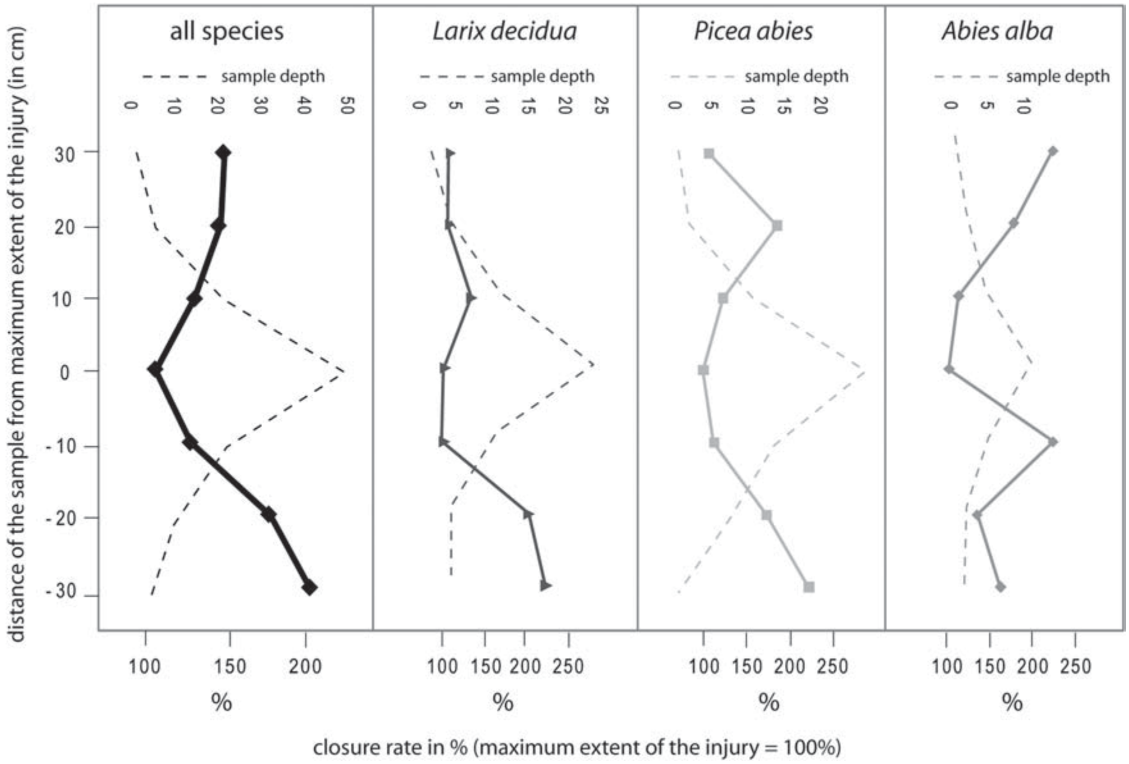

Figure 6. Closure rates at different heights around the injury. Height 0 represents the maximum extension of the injury. Closure rates are expressed in % where 100% corresponds to the value at the maximum extension of the injury. Dashed lines indicate sample depth.

sample with very high values. Nevertheless, we also observed in *A. alba* that closure was faster below the maximum extension of the injury.

Discussion

In this study, we investigated wound closure in mature European conifer trees injured by rockfall. Results show that *L. decidua* overgrew wounds considerably faster than *P. abies*, which is in agreement with findings of other authors. Oven and Torelli (1999) showed that cell reaction to wounding starts earlier in *Larix* than in *Picea*. They report that a new phellogen was observed by day 42 in *Larix* but only by day 49 in *Picea*. Thickening and lignification of the parenchyma cell walls were detected by day 49 in *Larix* and by day 84 in *Picea*. Bangerter (1984) observed similar phenomena and stated that callus formation started earlier and was more pronounced in *Larix* than in *Picea*. Difference in closure rates in our trees may partially be explained by the fact that tree growth was generally faster in *L. decidua* than in *P. abies*. However, as we did not observe a correlation between yearly increment and wound closure it can be assumed that the differences in wound closure observed in our study are most likely species related. The delayed onset of growth reactions after wounding in *P. abies* observed by Bangerter (1984) may also explain the fact that overgrowth was more pronounced in year 2 after wounding than in year 1 in this species. As the majority of wounds were induced before the beginning of the growing season, the trees' ability to overgrow the wound was not temporally limited to year 1. The ability of *Larix* to close wounds rapidly may explain, to some extent, the dominance of this species in exposed areas.

The absence of a correlation between yearly increment before wounding and wound closures and the weak correlation between yearly increment after wounding and wound closure in our sample contradicts the results of Neely (1970) who stated that the closure of wounds on tree stems is associated with stem growth and correlated with the annual increase in stem diameter. Neely (1988) also showed that wound closure is linearly correlated with growth in trunk diameter in both the first and second year after wounding. Our data, however, cannot support these findings, since no significant correlation between yearly increment and wound overgrowth in years 1–5 after wounding was found. We therefore assume that wounding by rockfall does not considerably affect tree growth and that the energy invested by a tree to close the wound is independent from external growth conditions affecting normal tree growth. Similarly, the link between wound healing and injury size as described by several authors (e.g., Neely 1970) could not be confirmed in our study.

In contrast, the correlation found in this sample between the height of the injury on the stem and wound closure rates is in agreement with the finding of Neely (1970). Injuries located higher on the stem are closed more rapidly than wounds at the base of the stem. This finding can be explained by the fact that tree growth in spring in these species originates high in the stem and is delayed towards the base (Neely 1979) and that late-season tree growth in temperate regions in autumn ceases at the stem base first. Higher parts of the stem therefore have a longer growing season, which allows for more wound overgrowth. In our data, this effect was much more pronounced in *P. abies* where the correlation between overgrowth and injury height was 0.7 compared with 0.2 in *L. decidua*. Our results also suggest that young and small trees overgrow wounds more efficiently than older trees with larger stem diameters even though the correlation is only moderate. The high vitality of young trees may have been a positive factor for efficient wound closure. Similarly, it is possible that an injury of a certain size is more threatening for a small tree since a larger percentage of the stem surface is affected compared with the same injury on a larger tree.

The seasonality of the wounding did not influence wound healing. Most injuries (77%) occurred outside the growing period and the number of samples with injuries occurring in other parts of the year was less frequent (23%). However, we did not find any statistically important difference in wound overgrowth between injuries formed during or outside the growing season. This is in disagreement with other authors who state that wounds induced during the growing season are closed faster than those induced during dormancy (Neely 1970, Dujesiefken et al. 1991, Schmitt and Liese 1992, Haavik and Stephen 2011). This discrepancy may stem from the fact that most of the above studies (i) focused on broadleaved trees and because the internal structure is different compared with conifers, the process of wound closing may also be different and (ii) are based on artificial and very superficial wounding of trees, whereas the rockfall wounds investigated here were generally deeper and formed through higher impact forces than under laboratory conditions. The high energy may have a considerable effect on wound closure because it influences internal tissues and probably masks other differences.

Analysis of the entire extent of the injuries and the closure rates at different heights showed that closure was more important at the upper and lower extent of the injury than at the maximum extension. This is in agreement with findings that the formation of tangential rows of resin ducts related to mechanical wounding is also more pronounced above and below the injury than at its maximum extension (Fahn et al. 1979, Bollschweiler et al. 2008, Schneuwly et al. 2009*b*). Lev-Yadun (2002) also observed a similar phenomenon in *Pinus pinea* (L.) and stated that the effect of the wound spreads further in the axial direction than in the transverse direction. Studies on *Prunus africana* (Hook. f.) Kalkman also support these findings (Delvaux et al. 2010). *Abies alba* does not normally have resin ducts in the xylem but produces traumatic resin ducts only after mechanical impacts (Schneuwly et al. 2009*b*), which represents a genetic difference compared with *P. abies* and *L. decidua* and may also influence the process of wound closure.

Conclusion

Our study on *L. decidua* and *P. abies* trees wounded by rockfall showed that *L. decidua* overgrows wounds more efficiently than *P. abies*. The fast overgrowth of wounds and the earlier complete closure of the wound make *L. decidua* a tree species that is well adapted to environments with frequent disturbances such as rockfall slopes, as can be observed in their dominance in many exposed areas in mountain environments. Injury size and yearly increment did not influence wound overgrowth in our sample. In contrast, we observed a moderate and statistically significant negative correlation between age and size of trees and wound overgrowth. It therefore seems that young and small trees close wounds more efficiently than older and thicker trees. The higher on the stem an injury was located, the faster the wound was closed in *P. abies* as growth in spring starts in the tree crown and propagates towards the stem base. In *L. decidua*, this fact could not be confirmed. Anatomical reactions to wounding seem to propagate more in the axial than in the tangential direction, inferred from the higher wound closure rates at the upper- and the lowermost borders of injuries. In many tree-ring studies, recent activity of rockfall or other geomorphic processes is generally overestimated because visible wounds are recorded and, non-visible wounds are not taken into account, which leads to sampling bias. An understanding of wound closure duration in different species may help estimate the time interval in which such an overestimation may occur, and thus act as a way to reduce bias by aiding field data collection and interpretation.

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Conflict of interest

None declared.

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