



TREE-RING FEATURES: INDICATORS OF EXTREME EVENT IMPACTS

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ABSTRACT

Wood anatomical features may be visible on the microscopic as well as on the macroscopic scale. While the former can often be quantified by detailed wood anatomical analyses, the latter are often treated as qualitative features or as binary variables (present/absent). Macroscopic tree-ring features can be quantified in terms of frequency, intensity, or classified according to their position within a tree ring, like intra-annual density variations (IADFs) in conifers or frost rings in earlywood or latewood. Although some of these tree-ring features, like *e.g.* missing rings or IADFs are often seen as anomalies, hampering dendrochronologists to perform proper crossdating of tree-ring series, many of these properties are formed under extreme environmental stress or heavy impact, and could mark these extreme events by the manifestation in the wood anatomical structures throughout the lifespan of trees. The described tree-ring features form discrete time-series of extreme events. For example, flood rings may be marked by lunar-shaped earlywood vessels or enlarged latewood vessels in ring-porous oaks. White earlywood rings and light rings indicate reduced cell wall thickness and lignification occurring in very cold years. Frost rings result from cambial cell death during abrupt cooling events in the growing season. Missing rings and IADFs are mainly caused by drought events. Characteristic variations in earlywood vessel size, shape, or number in ring-porous oak species are markers for flood events, defoliation, heat stress, or drought. Traumatic resin ducts may be triggered by a range of biotic or environmental stressors, including wounding, fires or mechanical factors. Reaction wood is indicative of mechanical stress, often related to geomorphic events. In many cases anatomical responses are unspecific and may be caused by different stressors or extreme events. Additionally, the sensitivity of trees to form such features may

vary between species, or between life stages within one species. We critically evaluate the indicative value of different wood anatomical tree-ring features for environmental reconstructions.

Keywords: Missing rings, white rings, light rings, frost rings, flood rings, reaction wood, earlywood vessels, traumatic ducts, extreme events.

INTRODUCTION

Besides their width as expression of growth vigour, the macroscopic appearance of tree rings provides information about environmental conditions during or before the formation of the respective wood. During the past years, improvements of preparatory (*e.g.*, Schneider & Gärtner 2013; Gärtner *et al.* 2014) and image analysis techniques (*e.g.*, von Arx *et al.* 2013) allow the quantitative assessment of many wood anatomical variables at the cellular level (Scholz *et al.* 2013) and at the tree-ring level (*e.g.*, Fonti *et al.* 2010; Olano *et al.* 2013; Hetzer *et al.* 2014). However, some wood anatomical anomalies are markers of certain environmental triggers in a qualitative sense, meaning that either they cannot be meaningfully quantified (*e.g.*, what is the “real” ring width of a wedging ring?), or that their quantitative measurement does not add significant information for their interpretation because the effect-response system of the tree does not respond in a mathematically defined or yet unknown way to the intensity of the triggering agent. Hence, only occurrence in the sense of presence or absence, and the frequency of the respective feature may be recorded. Nevertheless, some of these macroscopic tree-ring features have important ecological indicator value (Schweingruber 1996, 2007; Beeckman 2016; Tarelkin *et al.* 2016). Since they represent manifestation of more or less rarely occurring extreme impacts on trees, they form discontinuous time-series of discrete events.

In the following, we summarize the knowledge on some of the most prominent macroscopic tree-ring features and discuss their possible indicator value for extreme events occurring in a tree’s environment that may have triggered the formation of wood anatomical anomalies. Many of the described phenomena actually only appear in parts of a tree ring, like within the earlywood, the latewood, or occur somewhere within the whole tree ring but leave other parts unaffected, like *e.g.* frost rings or intra-annual density fluctuations (IADFs). Hence, the position within the tree ring is a time marker of their formation within the growing season. Since IADFs are dealt with by De Micco *et al.* (2016a), we will not deal with these features in this paper. For the other macroscopic tree-ring features, their presence within a tree or tree ring, their geographic distribution, and possible causes will be discussed.

Features in response to climatic stress

Missing rings and partly missing rings

A missing ring (MR) is a tree ring that is partially or completely absent. Hence, its absence can only be identified by crossdating with complete tree-ring series (Leuschner & Schweingruber 1996). Wilmking *et al.* (2012) distinguish three types of MRs:

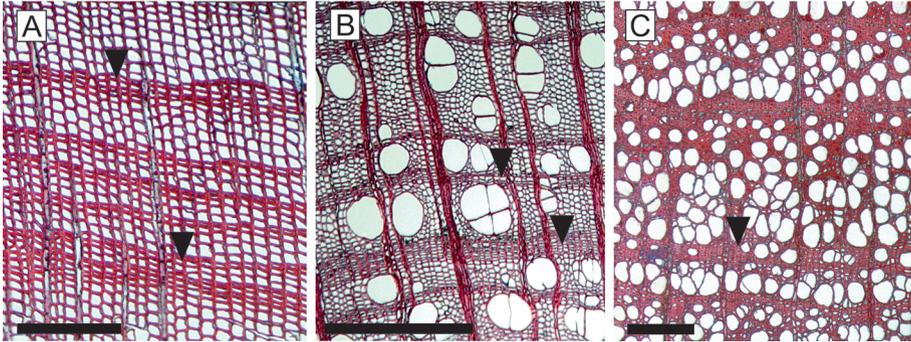


Figure 1. – A: Partially missing rings in *Cupressus torulosa* (Nepal). – B: *Betula utilis* (Nepal), and C: *Fagus orientalis* (Alborz Mountains, Iran). Arrows mark positions where tree-ring boundaries of consecutive rings are merging and the ring is wedging out. – Scale bars in A & C represent 200 μm , in B 500 μm .

1) locally missing rings (LMRs), where one or more growth rings are missing in some part(s) of the plant (also called wedging rings); 2) totally missing rings (TMRs), where a plant does not produce wood anywhere along the circumference of the stem in a specific year, and 3) continuously missing outer rings at the stem base (CMORs). Most common are the LMRs or wedging rings (Fig. 1), a term that is also commonly used in texts on tree-ring anomalies (e.g., Worbes 2002).

All types of MRs can occur in a wide variety of species, growth forms and biomes, suggesting a general strategy of woody plant growth (Wilmking *et al.* 2012). Although MRs, especially LMR, are quite commonly found in all forest types (Table 1), they often only represent <1% of the total measured tree rings. More than half of the tree-ring records reviewed by St. George *et al.* (2013), *i.e.* 1296 of 2359 tree-ring records, did not show a single MR. This indicates that TMRs in stem wood are very rare. However, tree-ring series showing a high number of missing rings are often discarded from tree-ring datasets due to dating problems, and hence there might be a bias towards tree-ring series that are still crossdatable. They can be for instance caused by extremely dry years (Novak *et al.* 2011, 2016).

While quantitative data on the frequency of MRs are more often available in temperate and boreal regions (Table 1), (L)MRs in tropical regions were reported for *Podocarpus falcatus* mountain forests in Ethiopia (Krepkowski *et al.* 2012), for *Juniperus procera*, *Acacia* spp. and *Balanites aegyptiaca* in dry tropical forests in Ethiopia (Wils *et al.* 2011), for *Machaerium scleroxylon* in Bolivia (Paredes-Villanueva *et al.* 2013), for *Tectona grandis* in East Timor (Sousa *et al.* 2012) and for *Terminalia superba* in a Congolese tropical forest (De Ridder *et al.* 2013). Worbes (2002) also provides a list of tropical tree taxa showing a tendency to form LMRs.

Generalizing the presence of MRs within a species should be regarded with caution. While early dendrochronological studies on *Taxus baccata* were abandoned due to a high frequency of missing rings (Lowe 1897), Galvin *et al.* (2014) succeeded in creating a tree-ring chronology without encountering any MRs.

Table 1. Examples of the occurrence of missing rings in different tree species growing in a variety of environmental conditions.

MR = missing rings; NA = no data available.

Species	% MR	Suggested cause	Authors
<i>Pinus banksiana</i> and <i>Pinus sylvestris</i>	Up to 40% of tree rings during years with severe outbreaks	(Severe) outbreaks of jack pine budworm the current or previous year	Robson <i>et al.</i> (2015)
<i>Larix sibirica</i>	Only 2% of the total tree-ring number	Positive correlation with frequency of hot days in June + drought during the growing season	Khishigiargal <i>et al.</i> (2014)
<i>Tsuga heterophylla</i>	30% of tree rings during the dry year begin 1980s	High number of consecutive dry days and low sum of precipitation	Glawenda <i>et al.</i> (2012)
<i>Juniperus communis</i>	<1% of total tree-ring number	Very irregular shape of stems with strip-bark growth form in older individuals	Pellizzari <i>et al.</i> (2014)
<i>Juniperus tibetica</i>	Up to >5% total tree-ring number	Strip-bark growth form, dry conditions in summer	Bräuning <i>et al.</i> (2001)
<i>Pinus halepensis</i>	19% of total tree-ring number	Dry conditions from January to May, high late winter to spring temperatures	Novak <i>et al.</i> (2011)
<i>Pinus pinea</i>	10% of total tree-ring number	Dry conditions from January to May, high late winter to spring temperatures	Novak <i>et al.</i> (2011)
<i>Pinus</i> sp.	0.8% of total tree-ring number	NA	St. George <i>et al.</i> (2013)
<i>Pseudotsuga</i> sp.	0.6% of total tree-ring number	NA	St. George <i>et al.</i> (2013)
<i>Larix</i> sp.	0.2% of total tree-ring number	NA	St. George <i>et al.</i> (2013)
<i>Larix griffithii</i>	0.2% of total tree-ring number	Deep cooling of the cambium by ice contact	Bräuning (2006)
<i>Picea</i> sp.	0.03% of total tree-ring number	NA	St. George <i>et al.</i> (2013)
<i>Quercus</i> sp.	0.01% of total tree-ring number	NA	St. George <i>et al.</i> (2013)
<i>Terminalia superba</i>	1% of tree-ring number per tree	NA	De Ridder <i>et al.</i> (2013)

Following the definition of Leuschner and Schweingruber (1996), missing rings are caused by lack of cambial activity due to extremely unfavourable growth conditions. Several causes are suggested but drought is most commonly met (Table 1) and caused, *e.g.*, the widespread MRs in southwestern United States during the last millennium (St. George *et al.* 2013). Increasing summer drought in Mongolia is also thought to have caused the repeated occurrence of missing rings in larch since the 1960s, thus MRs could act as an indicator of climate warming (Khishigiargal *et al.* 2014). Also in Europe, the wood formation of beech is strongly influenced by annual climate fluctuations but also by extreme events like heat waves (Ciais *et al.* 2005; Werf *et al.* 2007) and late frosts (Dittmar *et al.* 2006), affecting cambial activity and therefore minimizing tree-ring widths. One example is the year 1953 caused by a late mid-May frost event

followed by a very dry and hot summer in high-elevation beech stands. As a consequence of extreme drought, severe insect outbreaks were registered, also increasing the frequency of MRs (e.g., Pohl *et al.* 2006; Koprowski & Duncker 2012; Robson *et al.* 2015). Interestingly, the cambium as the key tissue for xylogenesis can be locally inactive for several years or even decades and then become active again. The cambium can be inactive in small parts of the stem or in the whole stem or only at the stem base (Wilmking *et al.* 2012).

Under dry tropical conditions, multimodal rainfall regimes are expected to increasingly cause missing rings in sensitive trees, as the wet seasons will often be too short to initiate tree growth (Wils *et al.* 2011). In tropical moist forests, temperature and rainfall are normally not limiting but buttressed roots can cause wedging rings in older trees that grow under poor light conditions and under competition (Worbes 2002).

At high-elevation sites in glacier forefields on the eastern Tibetan plateau, partly missing rings were found in *Larix griffithii*, probably as a result of deep cooling of the cambium by ice contact (Bräuning 2006).

Mann *et al.* (2012) hypothesized that MRs caused by large volcanic eruptions could question the reliability of the global tree-ring chronology network. However, this hypothesis was rejected by Esper *et al.* (2013) who used a compilation of maximum latewood density records, temperature records and documentary data from the European Alps and Northern Scandinavia to prove that there were no MRs after the large volcanic eruption of 1815. St. George *et al.* (2013) reviewed >2300 tree-ring records of the Northern Hemisphere and found that not all tree species form MRs.

Beside environmental causes, tree specific factors like tree age, tree architecture, social position within the forest, as well as local site conditions and sampling height have an impact on MR occurrence (e.g., Swetnam & Lynch 1989; Lorimer *et al.* 1999; St. George *et al.* 2013). No clear conclusion exists on the influence of tree age on MR frequency. In Mongolia, MRs were present in middle-aged and old trees in equal frequencies. However, the frequency of MRs appeared higher in the interior of the forest than at the edges where intraspecific competition for water between individuals is lower (Khishigjargal *et al.* 2014). In 55-year-old plantations of *Terminalia superba*, more MRs were found in the age class 20–30 years than in older age classes (De Ridder *et al.* 2013). Wilmking *et al.* (2012) found a clear correlation between MR frequency and age for a few of their studied species. The age of woody plants is possibly a factor influencing timing and duration of xylogenesis (Wilmking *et al.* 2012). For example, in three conifer species growing at the treeline in the Alps, the onset of cell production in older individuals in comparison with younger individuals was delayed, and total duration of cambial activity was shortened by two to three weeks (Rossi *et al.* 2008). However, it is difficult to distinguish age from tree size effects: at the end of the winter, larger stems with thicker bark remain colder for longer periods (Mayr *et al.* 2006), thereby delaying the start of temperature-dependent xylogenesis and contributing to an increase of MRs.

Another important concern is the sampling height, which is commonly set at breast height. Novak *et al.* (2011) sampled two pine species in Spain along their stems and found that the frequency of MRs gradually decreased from the bottom upward for

Pinus halepensis, whereas no pattern was observed in *P. pinea*. Wilmking et al. (2012) studied 13 species at their distributional limits and generally found the same pattern of MRs as in *P. halepensis*. On the other hand, some studies reported a higher MR frequency in the upper parts of a stem, particularly in trees that have suffered sudden crown damage (e.g., Krause et al. 2003). In general, MRs occur mainly at lower stem portions where supply of auxins produced in the apical meristems and the decreased availability of carbohydrates might play a role in the non-formation of growth rings, especially in drought periods (McDowell et al. 2008).

The elevation of sample sites seems to be related to the formation of (L)MRs in beech stands. In the Balkan Mountains in Bulgaria, beech covers different altitudes from 600 to 1650 m a.s.l. At the upper elevation limit, we can expect higher sensitivity towards climatic factors. Dimitrov (unpubl. data) reveals that the incidence of LMRs in beech increases from low to high elevations. One possible explanation is the shorter vegetation period at 1650 m. A longer vegetation period at lower elevations enables trees to overcome climatic stress factors and to form on average wider tree rings.

Local site conditions (floodway versus terrace forest) under a similar climate influenced the frequency of MRs for *Pinus strobus* trees (Michigan, USA). The frequency of MRs was generally greater on the terrace compared to the floodway forests, possibly related to the observed higher moisture stress in terrace forests during summer (Chhin et al. 2013). Missing rings were extremely uncommon at high latitudes; from 1 MR on 240 present rings at moderate latitudes to 1 MR on 2500 present tree rings at high latitudes (poleward of 50°N).

Under different environmental conditions different factors can influence the formation of wood negatively and most likely, several factors act interlinked to produce MRs (Wilmking et al. 2012). Figure 1C shows one example from high elevation (1550 m a.s.l.) beech from Bulgaria (Dimitrov, unpubl. data). An overall dry year (1988), and cool spring and dry summer conditions in 1989, in combination with a short vegetation period at higher elevations most likely explain the formation of a LMR in 1989.

If MRs are the consequence of irregular stem shapes like lobate stem forms, stem disks should be sampled rather than increment cores. Multiple measurement paths are necessary but sometimes identification of rings is only possible on one direct or composite path. In the end, crossdating often remains problematic and it can happen that up to half of the disks are rejected to enter a chronology (see, e.g., Pellizzari et al. 2014 for *Juniperus communis* and McDougall et al. 2012 for *Podocarpus lawrencei*).

Apart from their disadvantages, MRs can be used as indicators for several phenomena. Rozas et al. (2011) used missing rings of *Pinus canariensis* to date past severe crown fires in the forests of Tenerife. An increased number of MRs can also help to predict impending tree mortality in conifers and, to this end, dendrochronology can help to record tree decline prior to visible signs of crown damage. This could be especially important in semiarid ecosystems at the distribution limits of many forest species (Novak et al. 2011). This was confirmed by St. George et al. (2013) who observed absent rings only in the southwestern United States but not in other Northern Hemisphere regions. Thus, future increases in the rate of MRs at other locations would indicate that forests are responding to unprecedented environmental stress.

Independent evidence may come from the analysis of stable isotopes that may reveal seasonal variations of environmental conditions not bound to variations in anatomical wood structures (Krepkowski *et al.* 2012).

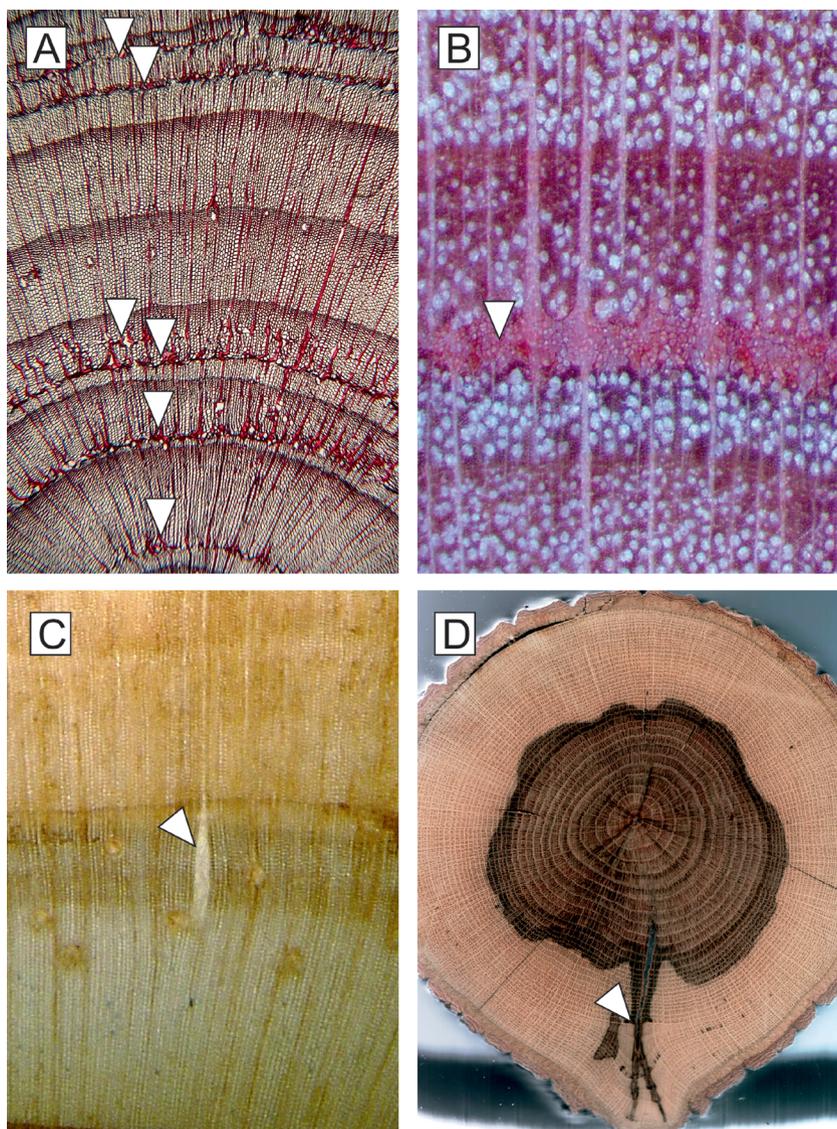


Figure 2. Frost rings (arrows) within *Larix decidua* (European Alps). – A: Some rings show multiple frost rings indicating occurrence of late frost and/or early frost events within one growing season. – B: Frost ring in *Fagus sylvatica* (Balkan Mountain range, Bulgaria). – C: Radial crack in *Pinus sylvestris* (Vitoshka Mountain, Bulgaria). – D: Frost crack in *Quercus* and subsequent discolouration of sapwood and heartwood. The last tree-ring before frost crack formation is highlighted (arrow), it provides dating possibility for the event (Lakatos & Mirtchev 2014).

Frost rings (FRs)

Frost rings consist of a zone of unligified, deformed tracheids, collapsed cells and traumatic parenchyma cells, and subsequently formed tracheids with irregular structure and orientation within a tree ring (Glerum & Farrer 1966; Hantemirov *et al.* 2004) (Fig. 2A, B). FRs may be the most extreme form of wood anatomical imprints of temperature extremes. They are amongst the most studied anatomical markers which offer opportunities for drawing climatic information from tree rings (Wimmer 2002). Frost damage is caused by rapidly dropping temperatures below freezing during the growing season, when cambium is active and secondary wall thickening and lignification of immature xylem cells in the annual ring are not yet complete (LaMarche & Hirschboeck 1984). Hence, FRs serve as a dendrochronological tool to reconstruct past occurrences of late and early frosts in frost-sensitive forest ecosystems (Hantemirov *et al.* 2004; Dy & Payette 2007). From outside to inside of the stem, the phloem freezes first and shrinks, thereby compressing and deforming the delicate cells in the cambial zone (Sorauer 1922). The shrinkage is stronger in tangential than in radial direction and thus causes radial cracks or clefts. Day and Peace (1934), Glerum and Farrar (1966), and LaMarche and Hirschboeck (1984), however, state that freezing promotes extracellular ice formation and dehydration resulting in crushing of the outermost zone of weaker cells, leaving a permanent, anatomically distinctive record in the wood. They consider the dehydrating effect of freezing as more injurious to the cambium than the resulting physical pressure.

The position of the injury along the inner position of a tree ring is associated with frosts occurring in spring after initiation of cambial activity (Glock 1951; LaMarche 1970; Fritts 1976). Frost injury near the outer boundary of the ring is associated with a freeze late in the growing season before the cambium becomes dormant. Fritts (1976) states that frost rings are less frequently found in the larger stems than in the small branches, probably because of the insulation by the thicker bark of larger trees, a later initiation of cambial activity, and an early growth cessation in portions of trees which are distant from the growing stem apex. Thus, frost rings may be less frequent in outer portions of larger stems, but this does not necessarily imply that frosts were less severe in more recent years. The outermost tree rings formed under the thin bark of young and short trees will be in the inner parts of a stem when these trees get older and higher, whereas the more sensitive zone of the stem with thin bark will move upwards. For example, Waito *et al.* (2013) found FRs in 7–40% of all rings in *Picea mariana* trees studied in central Canada. FR frequency was highest in lower parts of the stems, when the trees were of less than 4 m height. At 16 m height of the stems, FRs were still detected in the innermost 20 rings of the trees (Waito *et al.* 2013).

Frost rings in subalpine Bristlecone pines (*Pinus longaeva* and *P. aristata*) in western USA were reported to occur with high coincidence with major volcanic eruptions over the past several thousand years (LaMarche & Hirschboeck 1984). The damage of these events to the trees is linked to climatic effects of stratospheric aerosol veils on hemispheric and global scales.

Frost rings were also found in tree-ring series from other species (*e.g.* *Picea abies* and *Pinus peuce*) from high altitude locations in Bulgaria in southeast Europe (Panayotov

2007; Panayotov & Yurukov 2007). Along an altitudinal gradient on Vitosha Mountain in Bulgaria (Panayotov *et al.* 2013), FR frequency increased from c. 1% of all tree rings at low elevation sites to c. 3% at higher elevation sites, pointing to an increased influence of the temperature regime at the high-altitude sites. Most of the zones with traumatic cells were found at the beginning of the earlywood, which was explained by frost events recorded in the beginning of May at lower altitude sites or in the middle of May at higher altitudes (Panayotov *et al.* 2013). However, one layer of deformed cells was found within the earlywood and was linked with late frost which occurred on the 9th of June, when the growing season had already started.

Concerning diffuse porous species, FRs in European beech (*Fagus sylvatica*) are marked by traumatic and distorted ray parenchyma (Fig. 2B). Dimitrov (unpubl. data) reported frost rings in *F. sylvatica* from the Balkan Mountains (Bulgaria). The traumatic cells formed within the earlywood of the tree ring of the year 1876 (Fig. 2B) is most likely caused by a very late frost event, but due to the lack of climate records for that year, other traumatic factors negatively affecting cambial activity cannot *a priori* be excluded. However, the occurrence of late frost events do not automatically result in the formation of frost rings. Throughout the 20th century, frost rings in beech stands in Bulgaria were not recorded, despite several years with well documented late frost events.

In ring-porous oaks, frost rings are manifested by collapsed or lunar-shaped vessels, disrupted rays, and abnormal parenchyma in the earlywood zone (Stahle 1990; Land *et al.* 2015). Stahle (1990) mapped the frequency of frost rings in oak trees growing over the Southeastern USA that are caused by sudden cold air intrusions after mild winter temperatures and derived the risk of frost damage for cold-sensitive fruit cultures.

In summary, although frost rings may occur in all climatic or elevation zones with occasional temperatures below freezing, they do not indicate the exact temperature during a frost event. Instead, their formation requires as a predisposition a state of physiological “perceptiveness” of the tree which is the case after or before winter dehardening. Also, trees of different species may show differences in sensitivity to form FRs under identical climate conditions (Gurskaya 2014). As a consequence, frost rings do not allow a quantitative reconstruction of the exact temperature triggering their formation, but from their frequency, geographic occurrence and position within the tree ring they allow conclusions about the temporal and spatial distribution, and a close estimation of the timing of the frost event.

Radial cracks

Radial cracks are caused by internal stress in the wood, mainly by frost, drought, wind, or lightning (Knuchel 1947; Cherubini *et al.* 1997). These cracks are divided into two types: cracks limited within one single tree ring (“internal intra-annual type”) (Fig. 2C), and the open type including a callous margin and overgrowing tissue (Fig. 2D). Although these anatomical features might provide information about past extreme events, they have rarely been investigated in a dendrochronological context, with most studies focusing on intra-annual radial cracks (Cherubini *et al.* 1997; Grabner *et al.* 2001; Grabner *et al.* 2006).

The decisive effect of frost for the formation of cracks in wood has already been recognized by early forest scientists (Nördlinger 1878; Hartig 1896) and has since then been confirmed by more recent studies. Radial cracks or so-called frost cracks can occur at temperatures which induce the freezing of water in wood cell lumens (Cherubini *et al.* 1997). Although freezing water also increases its volume, this type of crack is mainly caused by the cold shrinkage of wood due to internal drying as a consequence of the freezing out of cell wall moisture into the lumens of wood cells. The tangential shrinkage is stronger than the one in a radial direction and leads to tangential tension strain, which triggers cracking (Kübler 1983). Drought may also induce cracks through tangential shrinkage due to water loss (Nordlinger 1878; Barrett 1958; Aigner 1981; Caspari & Sachsse 1990; Booker 1994). Cracking behaviour models of trees influenced by wind stress have been developed by Peters *et al.* (1985) and Ossenbruggen *et al.* (1986).

Cherubini *et al.* (1997) performed a dendroclimatological study on the ecological significance of intra-annual radial cracks in live Norway spruce (*Picea abies*) sampled at two sites in the eastern Alps and isolated trees in the Swiss Jura. The authors suggested that cracking is caused by winter desiccation. These water imbalances occur in early spring when the needles are warmed in sunny weather inducing high transpiration rates, but when soils are still very cold or frozen they do not allow water uptake by the roots.

Grabner *et al.* (2001) investigated intra-annual radial cracks in Norway spruce in southern Sweden. They found evidence that strong weather fluctuations – dry-wet cycles during the growing season, resulted in high internal mechanical tension strains due to tangential shrinkage that exceeded fracture limits of the wood. During such periods the tree rings from the previous year carried the highest load of tangential and vertical tension forces, which triggered the creation of intra-annual radial cracks starting from the middle lamella of two earlywood tracheids or between tracheids and ray parenchyma (Grabner *et al.* 2006 and references therein).

Grabner *et al.* (2006) studied the induction of radial cracks in living trees and found that tree rings characterized by very low earlywood density are predisposed for the formation of cracks. Strong summer droughts induced wood desiccation and the resulting tension initiated the formation of cracks reaching into the previously formed low-density ring. Since the cracks are filled with resin but do not show signs of traumatic tissue, they must have been formed in the sapwood but outside the cambial zone (Grabner *et al.* 2006). Radial cracks do not occur in the outermost tree ring, but one to three tree rings away from the cambium, hence they cannot be used to date drought events at an annual resolution.

The open type of radial cracks with callous margin and overgrowing tissue is mainly caused by early spring frosts, or occasionally by late fall frosts. These frosts induce abnormal shrinkage of the sapwood when a stem that was warming during the day is affected by quick cooling and shrinkage of the outer parts of the stem during cold nights (Fig. 2D; Lakatos & Mirtchev 2014). This type of damage is characterized by vertical cracks in the main stem that can extend over more than 10 metres. Frost cracks are usually seen in older trees, especially of oak species. These radial cracks are important

from a phytopathological point of view, because they act as entry points for canker inducing micro-organisms, for example *Nectria* canker (Lakatos & Mirtchev 2014), and wood-decaying fungi or can lead to stem breakage.

Light rings (LRs)

Light rings (LRs) occurring in conifer wood are characterized by one or very few layers of latewood cells of reduced cell wall thickness (Liang *et al.* 1997; Gindl 1999), wood density (Wang *et al.* 2000), and lignin content (Gindl & Grabner 2000), and hence they appear as rings with a usually narrow band of less dark latewood cells (Filion *et al.* 1986; Wang *et al.* 2002), therefore also being termed ‘pale latewood rings’ (Waito *et al.* 2013). Recently, rings with bands of incompletely or non-lignified secondary cell walls were described from high-elevation sites in the Italian Apennines in *Pinus nigra*. Due to their blue appearance in safranin-astrablue died thin sections, they have been introduced as “blue rings” (Piermattei *et al.* 2015) and were assigned to exceptionally low temperatures in the late growing season suppressing lignification. To which degree “blue rings” are another representation of LR identified by using a different detection method remains to be tested.

LRs can be defined visually or by relative densitometric thresholds, and both methods lead to comparable results, at least when the reduction of latewood is pronounced (less than 2 standard deviations from mean latewood; Wang *et al.* 2000). Their occurrence is generally independent of ring width and tree age (Filion *et al.* 1986; Gindl 1999; Wang *et al.* 2002). In comparison with cell wall variables like cell wall to lumen ratio, X-ray density profiles indicate light rings more clearly (Wang *et al.* 2002) which may also be caused by reduced lignin content in light ring latewood cells (Liang & Eckstein 2006).

LRs are reported from various conifer species and increase in frequency towards treeline positions at high latitudes or in subalpine environments, where latewood formation and especially its cell wall differentiation is closely correlated to summer or autumn temperature during a short growing season (Filion *et al.* 1986; Delwaide *et al.* 1991; Gindl *et al.* 2000; Wang *et al.* 2000, 2002; Tardif *et al.* 2011; Piermattei *et al.* 2015). In the polar Urals, LR frequency in *Larix sibirica* and *Juniperus sibirica* amounted 0.2% and 13.5%, respectively (Hantemirov *et al.* 2004). Hence, LR occur in years with reduced spring, summer, or autumn temperature, although not every cold year triggers LR formation (Gindl 1999; Wang *et al.* 2000; Girardin *et al.* 2009), whereas precipitation does not have a great influence on LR formation (Szeicz 1996; Girardin *et al.* 2009). The percentage of trees at a site in a given year affected by LR formation is highly variable, but frequency can reach >50% and increases toward the tree limit (Yamaguchi *et al.* 1993; Szeicz 1996; Gindl 1999; Wang *et al.* 2000). Nevertheless, LR are good markers for cold conditions during the growing season if they exceed a threshold of c. 5% and often occur synchronously over larger areas (Delwaide *et al.* 1991; Yamaguchi *et al.* 1993; Szeicz 1996). In interior North America, LR occur at almost 30% of all years since the early 18th century (Girardin *et al.* 2009). Their occurrence in boreal Canada has been associated with volcanic eruptions, but LR may show a lagged response to a volcanic event of 1–2 years (Filion *et al.* 1986; Yamaguchi *et al.*

1993; Szeicz 1996; Briffa *et al.* 1998). Although LR occurs more frequently than FRs, they can occur synchronously (*e.g.*, Hantemirov *et al.* 2004). From the occurrence of narrow and light rings (although not explicitly called so in their publication) discovered in subfossil pine trees found in northern Switzerland, Friedrich *et al.* (1999) were able to date the prehistoric explosion of the Laacher Lake volcano in central Europe. In contrast to boreal climates, LR formation in Chinese pine growing in semiarid north-west China often co-occurs with narrow rings and was caused by drought in autumn of the prior growth year and dry summers (Liang & Eckstein 2006).

A similar phenomenon as climatically induced LR can be caused by insect defoliation, as has been described for deciduous larch species, like *e.g.* *Larix laricina* in Canada (Liang *et al.* 1997) and *L. decidua* in the European Alps, but in many cases the LR is embedded in a typical pattern of a sequence of abnormal rings (Weber 1997) that can help to distinguish it from climatically induced LR.

LRs were only described from conifer wood, although narrow and light latewood may also occur in hardwood species (*e.g.* *Fagus orientalis*, Pourtahmasi *et al.* 2011), but it is not explicitly called ‘light ring’ and is caused by other factors.

White rings (WRs) and white earlywood rings (WERs)

WERs have been described from various conifer species growing in the boreal zone of Canada. They are characterized by bright appearing earlywood. In *Picea mariana*, cell wall thickness of earlywood tracheids was 11% thinner than in control rings (Waito *et al.* 2013). Lumen diameter of latewood in WERs was also 15% smaller. A possible reason for WER formation is carbon depletion due to defoliation or lack of phytohormones (Hogg *et al.* 2002; Sutton & Tardif 2005). WERs occurred in 5–17% of all rings, in some years co-occurring with FRs. A possible explanation may be reserve depletion after severe frost damage of needles and buds (Waito *et al.* 2013). Along tree stems, WERs are rather evenly distributed but were absent in the upper few metres of a stem, where frost rings were more frequently occurring in the year predating a WER, possibly pointing to a carbohydrate depletion after frost-induced needle damage.

WERs often occurred synchronously in multiple species over wide geographic scales of up to 1000 km. They were rather evenly distributed throughout the stems but were missing in the upper few metres of the stems, where growth hormone concentrations are higher than near the stem base (Waito *et al.* 2013).

In hardwood species like *Populus tremuloides*, WRs consist of fibres with smaller diameter and thinner cell walls and a reduced density of around 20% compared to normal rings (Hogg *et al.* 2002; Sutton & Tardif 2005). They are the probable analogue to conifer WERs (Waito *et al.* 2013) and seem to be caused by similar ecological factors.

Earlywood anomalies in ring-porous species

Several characteristics of the earlywood vessels of ring-porous oak trees (size, number, and/or distribution) vary across sequences of tree rings (Fig. 3A), and have been recently used to obtain time series, as they appear to contain valuable environmental information (Fonti *et al.* 2010; García-González *et al.* 2016). However, year-to-year variation in earlywood appearance is small and extreme values in time series of ear-

lywood features rare. Hence, it is not straightforward to identify earlywood markers (*e.g.*, remarkably anomalous vessel size or number of vessels). This is probably the reason why these features have received little attention. Schweingruber *et al.* (1990) suggested the size of earlywood vessels as one of the characteristics that should be observed to identify pointer years in dendrochronology, whereas Leuschner *et al.* (1996) proposed a method to classify some of them. The number of studies that illustrate these features in ring-porous trees is scarce (Priya & Bhat 1998; Schweingruber 2007), which contrasts with the attention other tree-ring features received, for example IADFs (*e.g.*, De Micco *et al.* 2014, 2016a).

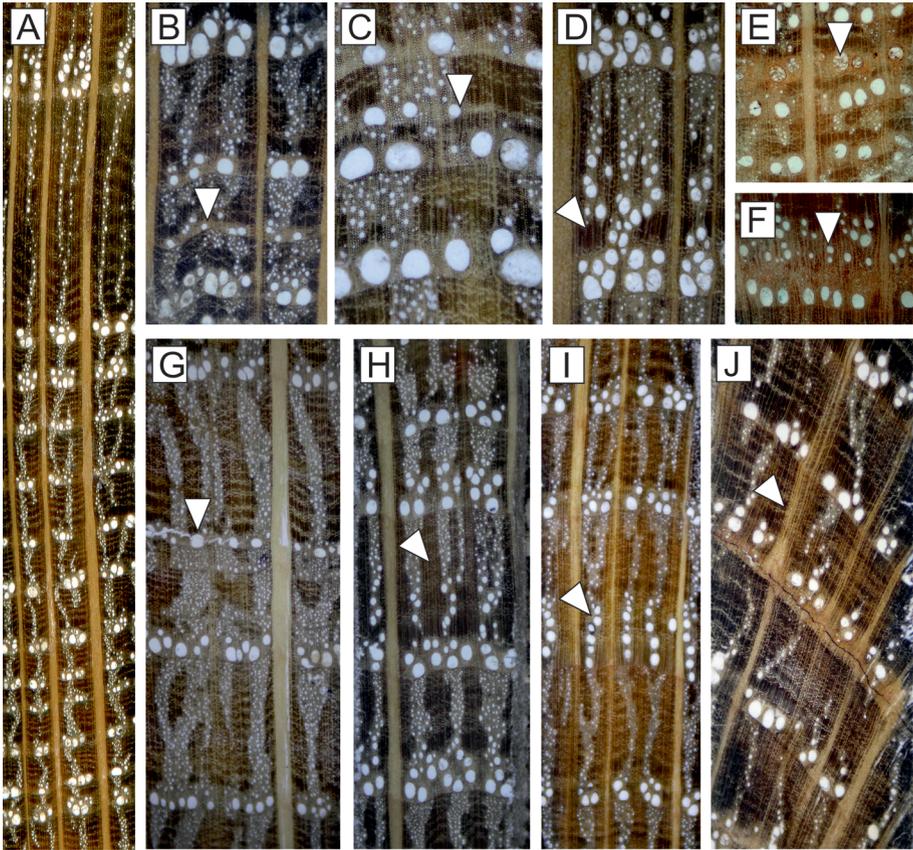


Figure 3. Special features in ring-porous oaks (*Quercus* sp.). – A: Variation of size, number, and/or distribution of earlywood vessels of ring-porous oak trees in different tree rings. – B: Ring with reduced earlywood vessel diameter (arrow). – C: Ring with narrow latewood followed by rings with small and few earlywood vessels (arrow). – D: Ring with complex of fibres without vessels in transitional zone from earlywood to latewood (arrow). – E: Set of few rings with tyloses within sapwood (arrow) indicating a traumatic event. – F: Double ring (arrow). – G: Latewood ring with smaller earlywood vessels (arrow). – H: Very wide rings after a growth release with large complexes of fibres (arrow). – I: Rings with earlywood vessels aligned in radial rows (arrow). – J: Modified rays after cambial wounding (arrow).

The frequency of rings with exceptional earlywood is rather low, but any deviation from the usual wood anatomical appearance, *i.e.* rings that are clearly different from the surrounding ones should always be considered (*i.e.*, ring with only one row of vessels in a sequence of rings with two or more rows of vessels, abnormally large or small vessels, peculiar vessel distribution, etc.) as a potential source of environmental information. Very often, only a minority of trees at a site presents peculiar earlywood, but the characteristic may be widespread over many sites. These features usually assist in cross-dating difficult ring-width sequences when developing dendrochronological series. Some of the most common or significant groups of features are detailed in the following; for the sake of simplicity, they were classified into three heterogeneous groups, explaining the most common earlywood vessel variations: 1) features associated with small vessels; 2) features associated with exceptionally wide rings; 3) presence of traumatic tissue.

Rings with clearly smaller vessels are often observed across sequences of tree rings (Fig. 3B). Sometimes only vessel size differs from the surrounding rings, whereas vessel number or distribution can be involved in other cases. Thus, very thin latewood is often followed by a ring with scarce and small earlywood vessels in the following year, as was the case for 1994 in northwestern Iberia (Fig. 3C); in such cases, crossdating is required to identify the presence of both rings.

Abundant small earlywood vessels in oak have been suggested as a marker for flooding events (Astrade & Bégin 1997; St. George *et al.* 2002; Copini 2015). Recent experimental approaches have gained further insight in the formation process of “flood rings”. Artificial flooding of at least two weeks provoked a reduction of earlywood vessel size of around 50% in flooded parts of *Quercus robur* stems (Copini 2015). While the duration of flooding had no effect on flood ring formation, the timing of flooding had a strong impact on wood anatomy: if flooding occurred during earlywood formation, collapsed, lunar-shaped earlywood vessels in addition to many anomalously small vessels were formed. In contrast, floods that start and end during latewood formation result in a flood ring with anomalous large latewood vessels (Copini 2015). After three weeks of flooding, oaks formed enlarged traumatic latewood vessels (Land 2014). In softwoods like *Taxodium distichum*, tracheids in flooded stem parts are shorter, slightly wider, and had thinner walls than tracheids (Yamamoto 1992), whereas – in contrast – in *Pinus pinaster*, Ballesteros *et al.* (2010) found earlywood tracheids formed after flash floods to be reduced in lumen area about 38%.

Regarding the spatial arrangement, ring-porous trees by definition form the largest vessels at the beginning of the season, and vessel size abruptly decreases in successive rows. Any distinguishable deviation from this pattern, *i.e.*, the presence of a first row of smaller vessels, is a feature to be considered as a potential indicator of environmental information. In fact, García-González *et al.* (2003) associated the appearance of such a ring in oak (Fig. 3G) with very dry conditions at the moment of cambial resumption in 1990 in coastal areas of the northern Iberian Peninsula. Conspicuously small earlywood vessels in European oaks (*Quercus robur*) were associated with abnormally severe winters and cold springs (Fletcher 1975).

Very wide rings often show peculiar variations within the earlywood. For example, a conspicuous band with few or no vessels but with more intensively lignified fibres

(Fig. 3D) could probably be associated with a warm and dry period during spring, while favourable conditions for the formation of earlywood in a specific year could result in a considerably higher number of vessel rows (Fig. 3I). It is also common that wide rings resemble juvenile wood (Helinska-Raczkowska 1994), even if occurring many years after the juvenile period. In the case of oaks, it is common to find radially-elongated vessels followed by a transitional area of large vessels arranged in radial rows (Fig. 3H), and when affecting only very few rings within a sequence, they are often a marker of growth releases, for instance due to thinning.

Some features within the earlywood can also be of traumatic origin and affect both the axial and radial systems. These mainly involve the presence of tyloses, callus tissue, and/or abnormal vessels. The presence of tyloses in only a single or few rings within the sapwood (Fig. 3E) should be considered of great indicator value, especially if repeated in other parts of the tree, or across several individuals, because it is commonly a consequence of vascular dysfunction (Cochard & Tyree 1990), and could consequently be related to damages as, *e.g.*, an intense defoliation. De Micco *et al.* (2016b) review how vessel occlusions like tyloses or gum deposits are often induced by cavitation in the sapwood vessels. Callus tissue and distorted (lunar-shaped) vessels are often associated, and are produced by a strong disturbance during the early season (Fig. 3F); the tissue formed after the event is usually normal. One of the most common causes considered has always been late frost affecting cambial derivatives (Stahle 1990; see paragraph above on frost rings), which is mainly restricted to the youngest parts of the trees as the bark is thinner. But other events (*e.g.* intense defoliation by late frost or insect outbreaks immediately after bud burst), are also a feasible explanation, especially if found after the first vessel row; a ‘double ring’, *i.e.*, the existence of a second ring of large vessels as a consequence of a second flushing, may also be present. Other anomalies may include the presence of undifferentiated cells in any part of the ring, the presence of compartmentalization, collapsed cells, or modified rays, and are often the result of cambial wounding (Fig. 3J).

Features in response to mechanical stress or impact

Reaction wood

The upright orientation of tree stems is basically controlled by a negative gravitropism of the apical meristem, forcing the stem to always grow against gravity. This results in an upright stem, no matter if the tree is growing on a flat plane or a steep slope (Tasaka *et al.* 1999; Morita & Tasaka 2004). The centre of gravity in an upright stem is always balanced above the root collar to guarantee stability, since a tilted stem and continuous height growth will sooner or later shift the stem’s centre of gravity upwards and finally reduce its stability, in extreme cases resulting in stem breakage or uprooting. As soon as trees are tilted by external forces or by mechanical stresses on the stems or crowns (*e.g.*, by unstable ground, snow load, heavy wind stress or geomorphic processes), they counteract these forces by developing reaction wood (Sinnott 1952; Wardrop & Dadswell 1955; Wardrop 1965; Côté & Day 1965; Scurfield 1973; Wilson & Archer 1977; Donaldson *et al.* 2004; Gardiner *et al.* 2014). The formation of reaction wood is related to gravitropic signals rather than being caused by compression or tension forces

(Jaccard 1938; Raven *et al.* 1999; Gardiner *et al.* 2014). As soon as a tree is moved out of its vertical position, reaction wood is formed on one side of the stem resulting in an eccentric shape of the rings (Bamber 2001; Wistuba *et al.* 2013). This eccentricity occurs on the lower side of the inclined plant part in coniferous trees (compression wood) and on the upper side (tension wood) in dicotyledonous trees. Reaction wood also plays a role in supporting a species specific tree architecture by maintaining the basic orientation of branches after mechanical strain due to external (*e.g.* snow load) or internal (*e.g.* size dependent weight) forces (Fisher & Stevenson 1981; Brüchert & Gardiner 2006).

Compression wood is recognizable macroscopically by its dark colour (Fig. 4A), and characterized by rounded tracheids (and therefore showing intercellular spaces) and

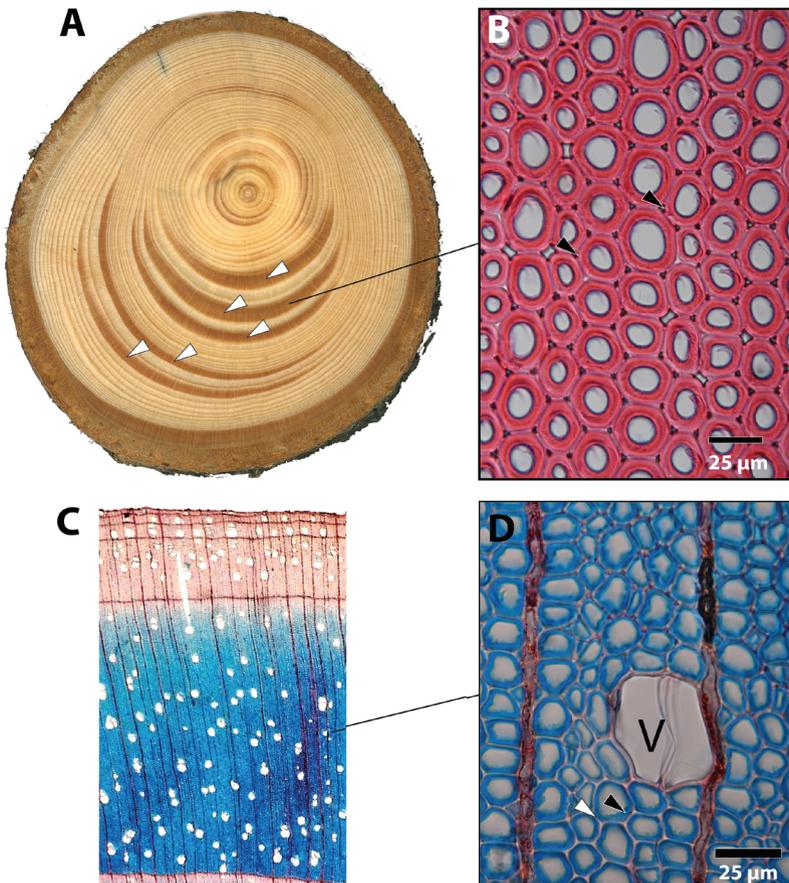


Figure 4. – A: Compression wood in a disc of *Picea abies* (white arrows). – B: Section showing the anatomical structure of compression wood, tracheids are rounded showing intercellular spaces (black arrows), the secondary walls are thick. – C: Very wide ring of *Betula pendula* showing tension wood (blue zone). – D: Detailed view of tension wood showing unligified G-layers (gelatinous fibres in blue [stain: astrablue]; black arrow). The S₁ + S₂ layers of fibre cell walls are thin and lignified (red [stain: safranin]; white arrow). – V = vessel.

thick, highly lignified secondary cell walls with helical cavities and high microfibrillar angles (Timell 1986).

Tension wood is hardly visible macroscopically, which is an obstacle related to environmental analyses, especially in geomorphology (Gärtner & Heinrich 2013), although it is usually credited with a silvery sheen (Côté & Day 1965). Proper detection of tension wood requires microscopic inspection. Tension wood fibres are characterized by a gelatinous layer (G-layer) (Côté & Day 1965; Coutand *et al.* 2004; Gärtner & Heinrich 2013), which is unlignified and has highly crystalline microfibrils running nearly parallel to the fibre axis (Clair & Thibaut 2001; Clair *et al.* 2005; Abedini *et al.* 2015).

Field experiments revealed that the intensity of tension wood formation clearly has a negative impact on vessel size and number (Heinrich *et al.* 2007), which is also indicating a shift from hydraulic towards mechanical functionality.

While several major monographic reviews of compression wood in gymnosperms exist (*e.g.*, Westing 1965; Timell 1986; Gardiner *et al.* 2014), tension wood in angiosperms in general has been studied less (Gardiner *et al.* 2014). Therefore, there is a need to define and further analyse existing variability in the expression of tension wood, before it can be used as an ecological indicator (Clair *et al.* 2006; Fang *et al.* 2008).

Regarding ecological indicators, the occurrence of reaction wood as well as its multiple variations is frequently used to reconstruct geomorphic processes such as landslides, debris flows, avalanches, or even glacier fluctuations (*e.g.*, Bräuning 2006; Butler & Sawyer, 2008; Gärtner & Heinrich 2013).

Resin ducts

Resin ducts (RDs) are an important part of the defence system of conifers to protect them against potential attacks of herbivores and pathogens (Nagy *et al.* 2000). RDs are an aggregation of secretory and subsidiary cells and consist of epithelial cells producing the resin accompanied by parenchyma cells, building up a channel to which the resin is transferred. Wiedenhoft and Miller (2002) named this system the “resin canal complex”. They frequently occur in the xylem of most Pinaceae species (Richter *et al.* 2004) and can be regarded as passive protection as long as single ducts are randomly distributed within the xylem. The axial resin ducts, easily detectable in cross sections are connected to radially oriented resin ducts localized within the rays. Through these connections they form a three-dimensional network within the xylem (Gärtner & Heinrich 2013). However, these ducts are not restricted to the xylem, they also occur in the phloem or the needles of a conifer (Evert 2006; Sheue *et al.* 2014).

All non-Pinaceae conifers (*e.g.*, Taxaceae, Cupressaceae, Podocarpaceae, Araucariaceae) do not show this “passive” network in the regular xylem (Schweingruber 1996; Richter *et al.* 2004), but only form resin ducts in case of a damage to the cambium by insect attacks or mechanical wounding. Surviving cambial cells adjacent to the disturbance start producing dense, tangentially oriented row(s) of resin ducts surrounding the wounded area (Nagy *et al.* 2000), which can be seen as an “active” defence system. The occurrence of traumatic tangential rows of resin ducts is always an indicator for any kind of disturbance exerted to the cambium, as *e.g.* by insect attacks or mechani-

cal wounding of the tree (Schweingruber 2007). The timing of their formation after a disturbance can be seen as crucial when aiming to reconstruct, *e.g.*, recurrence intervals of avalanches or debris flows (Gärtner & Heinrich 2009; 2013). This time lag was analysed using various techniques, *e.g.* by directly spraying methyl jasmonate on needles to trigger the formation of resin ducts (Martin *et al.* 2002), or by experimental wounding during the vegetation season (Christiansen *et al.* 1999). Nevertheless, the response time of the formation of traumatic rows of resin ducts after mechanical wounding is species specific and also depends on the timing of the impact (Gärtner & Heinrich 2009). Therefore, a precise dating of mechanical disturbances using traumatic rows of resin ducts is not possible without the presence of additional indications as, *e.g.*, compression wood or growth reductions, nor can the trigger be quantified in terms of physical units of force or its nature without further evidence (*e.g.*, wind speed after wind damage or the magnitude of debris flow events or avalanches).

CONCLUSION AND PERSPECTIVES

If macroscopic or microscopically detectable tree-ring features occur synchronously, they can support dendrochronological crossdating between tree individuals of a stand or even region (*e.g.*, Fillion *et al.* 1986). However, although the described macroscopic tree-ring features represent clearly distinguishable and recordable anomalies of the wood anatomical structure of trees, several open questions remain and practical issues are to be resolved before full use can be made of their indicator value.

Problems for analysing macroscopic wood anatomical features arise from the fact that they are often only formed or visible in parts of a tree stem (*e.g.*, reaction wood, flood rings), or their distinctness and intensity may vary within one individual. Mostly, they are only present in a portion of tree individuals at a site. In addition, some wood anatomical features are often not independent, but may be intercorrelated (Wimmer 2002). Hence, sampling strategies for analyzing wood anatomical features need to be adapted to the specific research question. Since many anatomical features are not formed in all trees of a site, the sample number often needs to be higher than for dendrochronological studies to achieve a statistically robust sample number. Wilmking *et al.* (2012) and Novak *et al.* (2011) recommend the application of serial sectioning for wood species growing in hostile environments. Pinning experiments covering the whole length of the stem may provide better insights into the phenomenon of MR formation concerning hormone transport and cambial activity.

The identification of certain macroscopic tree-ring features like, *e.g.*, LRs or WERs, is based on experience and expert knowledge; hence there may be a risk that the frequency of some features are underestimated by individual researchers just using visual detection approaches. Quantitative wood anatomical analysis, which becomes more and more a semi-automatic routine process with more powerful image analysis tools (*e.g.*, von Arx *et al.* 2013; von Arx & Carrer 2014) may be useful in defining objective thresholds for the detection of some of the respective features.

Some wood anatomical anomalies like *e.g.* frost rings or light rings are very specific in terms of the triggering agent, whereas other features like *e.g.* missing rings or

traumatic resin ducts are unspecific and may be caused by different environmental factors. Hence, to interpret them correctly, additional anatomical, chemical, morphological, ecological, geographical, or historical information is needed. Refined wood anatomical characteristics may help in the future to distinguish sub-types of macroscopic wood anatomical features and assign their formation to more specific environmental factors. New statistical tools like, *e.g.*, coincidence analysis (Donges *et al.* 2015) may further help to disentangle different climatic triggers leading to uniform tree-ring responses, and non-linear statistics like multivariate adaptive regression splines (MARS) may prove helpful to deal with the non-linear threshold behaviour of some macroscopic tree-ring features like, *e.g.*, light rings (Girardin *et al.* 2009).

Due to the more coincidental observation of wood anatomical features within wood anatomical or dendrochronological studies, little is still known about the occurrence of such features in economically less important and less studied tree species or about the susceptibility of regional ecotypes of widespread species for the formation of wood anatomical anomalies in response to extreme climatic events. Parallel investigations of trees planted in provenance trials may be useful in studying the genetic predisposition of different populations towards climatic extreme events and hence may help to select better-adapted species or provenances to make future forests more resilient towards climatic impact.

One big advantage of wood is that specific events can be reconstructed back in time, so specific tree-ring indicators help in reconstructing changes in the occurrence of pest infestations or fungal attack and provide useful information on ecosystem stability, climate change, and forest ecology. Since cracks and other wounds provide pathways for pathogens and since resource depletion is also weakening the defence of trees towards infestations, specific macroscopic tree-ring features may also be used as early warning signs for changing infection risks of forest trees. New categories of macroscopic anatomical features like, *e.g.*, the distinctness of tree-ring boundaries (Tarelkin *et al.* 2016) may provide additional indicators useful for monitoring tree health under climatic regime shifts.

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