Bark insulation: Ten Central Alpine tree species compared

Andreas Bär*, Stefan Mayr

Department of Botany, University of Innsbruck, Sternwartestraße 15, 6020 Innsbruck, Austria

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ABSTRACT

Climate-driven increases in frequencies and intensities of wildfires will affect even relatively humid regions such as the Central Alps. During low- to moderate-intensity fires, the resistance of trees to fire is mainly determined by the insulation capability of their bark, which protects underlying tissues from lethal temperatures. However, the knowledge of fire resistance and bark heat insulation of Central Alpine species is scarce.

In this study, the bark insulation capability of ten tree species was analyzed by bark surface heating experiments. Heat insulation was assessed by the time required to reach a lethal cambium temperature, linked to bark traits and analyzed with multivariate statistics.

Our results revealed a strong overall relationship between bark thickness and cambial temperature responses, but also highlighted the role of bark density in insulating internal tissues. On a species level, additional bark traits, like moisture content, bark surface structure or bark thermal conductivity, contributed to the bark insulation capability.

The bark insulation capability thus varied considerably between species. Identifying fire resistant species and knowledge of the traits determining species-specific bark insulation will help to better estimate impacts of fire disturbances and to face the challenge of an increased forest fire risk within the Alpine region.

1. Introduction

Wildfire is a major disturbance factor in many terrestrial ecosystems worldwide. Depending on the fire regime, tree species have evolved different traits and strategies to survive in fire-prone environments (Keeley et al., 2011; Pausas, 2015a; Pausas & Keeley, 2017; He et al., 2019). In ecosystems with high-intensity crown fires, where live biomass gets fully consumed and killed, plants often rely on resprouting mechanisms or on an enhanced post-fire population recruitment from a seedbank (Pausas et al., 2004; Clarke et al., 2013; Pausas & Keeley, 2017). In contrast, in areas with recurrent surface fires, the survival of tree individuals and/or a slow die back of fire-injured, seed-providing trees is more important to maintain a stable population status (Pausas, 2015a; Maringer et al., 2016). Here, a sufficiently insulating bark is crucial during understory fires (Pausas, 2015b) to protect tissues within the stem from critical temperatures and to guarantee post-fire tree functionality.

During combustion, heat gets transferred to the stem surface via convection and radiation processes. Without sufficient insulation, heat is conducted through the outer bark and affects the underlying phloem, cambium and xylem (Dickinson & Johnson, 2001; Michaletz & Johnson, 2007). Heat transfer can cause the cambium and phloem to exceed lethal temperatures, resulting in tissue mortality which is generally considered to be achieved at 60 °C (Rosenberg et al., 1971; Dickinson & Johnson, 2004). Heat-induced phloem necroses limit the downward translocation of photosynthates and may lead to the depletion of the root’s carbon reserves and, consequently, to carbon starvation (Hare, 1961; Ryan & Frandsen, 1991; Varner et al., 2009; Bär et al., 2019). Additionally, excessive heat is able to impact the xylem’s hydraulic functionality (Balfour & Midgley, 2006; Midgley et al., 2011; Michaletz et al., 2012; Bär et al., 2018; Lodge et al., 2018). Both, phloem/cambium necroses and dysfunctional xylem, can cause post-fire physiological limitations which may ultimately lead to tree mortality (Bär et al., 2019). Therefore, a well insulating bark is a necessary prerequisite to guarantee the survival of trees in fire-prone ecosystems.

The insulation capability of the bark is considered to be primarily determined by its thickness (Pinard & Huffman, 1997; van Mantgem & Schwartz, 2003; Bauer et al., 2010; Lawes et al., 2011; Brando et al., 2012; Pausas, 2015b), and due to its large influence on heat transfer rates into stem tissues, bark thickness is often used as a proxy for heat resistance in post-fire tree mortality models (Woolley et al., 2012; Hood et al., 2018). The bark consists of two distinct regions: the outer bark and the inner bark. It is mainly the outer portion of the bark, which is composed of dead cells, that is associated with the bark’s protective

* Corresponding author.

E-mail addresses: andreas.baer@uibk.ac.at (A. Bär), stefan.mayr@uibk.ac.at (S. Mayr).

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function against fire, while the main task of the living inner bark, including the phloem, is to translocate photosynthates and to store water and other compounds (Rosell, 2016; Rosell et al., 2017; Loram-Lourenço et al., 2020). Besides bark thickness, other traits such as bark density, moisture content or bark surface structure, may contribute to the insulation capability of bark (Pinard & Huffman, 1997; van Mantgem & Schwartz, 2003; Bauer et al., 2010; Lawes et al., 2011) and help explain interspecific differences in heat transfer to underlying tissues.

While fire resistance and bark insulation have been well investigated for tree species in ecosystems, in which fire is an important driver of tree dynamics (e.g. Ryan & Reinhardt, 1988; van Mantgem & Schwartz, 2003; Fernandes et al., 2008; Catry et al., 2010; Lawes et al., 2011; Brando et al., 2012; Hoffmann et al., 2012; Loram-Lourenço et al., 2020), knowledge regarding trees of less-fire prone areas such as the Alpine region of Europe is comparatively scarce (e.g. Bauer et al., 2010; Conedera et al., 2010; Frejaville et al., 2013, 2018). However, an increased risk of forest fires under the impact of future climate changes is predicted also in relatively humid regions like the Central Alps (Lorz et al., 2010; Wastl et al., 2012; Arpaci et al., 2014). Alpine forests provide fundamental protection for human settlements and infrastructure against avalanches, landslides and rock falls (Tranquillini, 1979; Körner, 2012), and a fire-caused loss of the protective function can have enormous consequences. A profound knowledge about the potential fire resistance of dominant tree species thus will be highly important to understand future ecosystem dynamics as well as to improve post-fire management, risk assessment and modelling (Müller et al., 2020).

In the present study, the heat insulation capabilities of ten tree species of the Central Alps were quantified in bark surface heating experiments. Heat insulation of bark samples was assessed by measuring the time required to reach a lethal cambium temperature of 60 °C (τcamb60) was extracted from temperature recordings and bark traits (moisture content, MC; bark density, ρ; bark thickness, BT; bark structure, BS; ratio of outer bark to inner bark, Rout/ibc; thermal conductivity, k) were determined.

2. Materials and methods

2.1. Plant material

The study was performed on ten European forest species. Five coniferous species (Abies alba Mill., Larix decidua Mill., Picea abies (L.) Karst., Pinus cembra L., Pinus sylvestris L.) and five angiosperm species (Acer pseudoplatanus L., Betula pendula Roth, Fagus sylvatica L., Fraxinus excelsior L., Quercus robur L.) were chosen to cover a broad spectrum of silviculturally relevant Central Alpine tree species. Between May and October, bark samples were taken from the main stem of up to five living or freshly cut mature specimens per species, at 50 - 130 cm height. Stem diameter at breast height (dbh) of selected trees varied from 21 to 59 cm. The entire bark including the phloem was carefully removed with a sharp wood carving knife to avoid tissue wounding (the cutting surface corresponded to the cambium tissue), packed in airtight plastic bags and immediately transported to the laboratory. For each species, bark pieces were chosen from different stem regions to cover species-specific ranges of thickness, density, ratio of outer versus inner bark and surface structure variations in the best possible way, and were then cut into individual samples (in total 36 samples) of about 7 × 7 cm size. Therefore, all bark samples from one species were pooled and treated as a statistical unit. Consequently, the moisture content of bark samples was adjusted (see section ‘Moisture Content’ below) before the bark surface heating experiment was conducted and bark traits were measured. Please note, that unless further specified, the term ‘bark’ includes both the outer and the inner bark.

2.2. Bark surface heating

Bark surface heating experiments were conducted in the laboratory to assess the insulation capability of each bark sample. As illustrated in Fig. 1, bark samples were placed above an electrical heat gun (2200 W Hot Air Tool, HL2020E, Steinel Vertrieb GmbH, Herzebrock-Clarholz, Germany), which had been set to produce a heat plume of approx. 200 °C. An exposure temperature of 200 °C was chosen as it is within the flame temperature range of low- to moderate-intensity surface fires (Franklin et al., 1997; Bova & Dickinson, 2008; Battipaglia et al., 2016) and to avoid unintentional sample ignitions. Copper-constantan thermocouples (Type T, operating range: −200 to 350 °C) were used to...
measure the heat plume temperature at the outer bark surface and cambium temperature at the inner bark surface during heating. Thermocouples were connected to a thermometer (PCE-T390, PCE Deutschland GmbH, Meschede, Germany), which logged the temperature data at 2 s intervals. Data were recorded starting approx. 20 sec before the heat treatment in order to record also non-heat-exposed ambient air and bark surface temperatures. Recordings were stopped when the cambium temperature had exceeded a critical threshold of 60 °C or, in case this temperature was not reached, after 90 min of exposure time.

First, temperature recordings were used to determine the time required to reach a cambium temperature of 60 °C ($\tau_{\text{camb}60}$; s), which is considered to be lethal. As the duration that trees can outlast fires without cambial injuries is of high physiological importance, we used $\tau_{\text{camb}60}$ as a parameter to assess and compare the insulation capability of bark samples. Please note that some bark samples of A. alba, L. decidua, P. cembra and P. sylvestris (n = 46) did not reach a cambial temperature of 60 °C within the set experiment duration of 90 min. For those samples, $\tau_{\text{camb}60}$ values were calculated from species-specific linear models after logarithmic transformation (see Fig. S1, Table 2) with respect to bark thickness. With this, all observations could be included in PCA and RDA analyses (see 'Statistical analyses'). Secondly, the thermal conductivity of each bark sample was calculated originating from logged temperature profiles (see 'Bark thermal conductivity').

2.3. Bark traits

2.3.1. Moisture content (MC)

Before conducting the bark heating experiment, the moisture content of bark samples (n = 6) was equilibrated to five different levels of relative humidity (RH; Fig. 1). One sample set per species was stored at 90 °C for 72 h to obtain dry bark samples (0% RH), while four sets were stored in airight boxes, being placed above saturated salt solutions (MgCl2: 33% RH; Mg(NO3)2: 54% RH; NaCl: 75% RH; according to Greenspan, 1977) or distilled water (100% RH). Bark sample weights were controlled on a daily basis until samples were in balance with ambient humidity and weight changes were no longer detectable. Additionally, one sample set remained without manipulation and was measured immediately to retain natural bark moisture content (nat. RH). Fresh weight (FW; g) of each sample was determined before the heating experiment was started. After testing, samples were oven-dried at 90 °C for 72 h and, consequently, dry weight (DW; g) was measured and moisture content (MC; %) calculated:

$$MC = \frac{FW - DW}{DW} \times 100 \tag{1}$$

Effectively achieved MC levels for each species are listed in Table S1.

2.3.2. Bark density ($\rho$)

After DW determination, dry samples were used to measure bark density by the water displacement method. Bark samples were submerged in a water-filled beaker and the displaced water mass was observed gravimetrically. The displaced water volume (V; m$^3$) was corrected for water temperature, and bark density ($\rho$; kg m$^{-3}$) was determined:

$$\rho = \frac{DW}{V} \times 1000 \tag{2}$$

2.3.3. Bark thickness (BT) and bark surface structure (BS)

Thickness and surface structure were determined at the heating position for all bark samples. Following Bauer et al. (2010), bark thickness (BT; mm) was derived from the mean value of minimum bark thickness, maximum bark thickness and thicknesses at two randomly chosen points. A proxy for bark surface structure (BS; dimensionless) was then calculated by dividing the range between maximum (BT$_{\text{max}}$) and minimum thickness (BT$_{\text{min}}$) by the mean bark thickness:

$$BS = \frac{BT_{\text{max}} - BT_{\text{min}}}{BT} \tag{3}$$

2.3.4. Ratio of outer bark to inner bark (Rob/ib)

The outer bark thickness and the corresponding inner bark thickness were measured at two positions of each bark sample. In cases where a clear visual assessment of the boundary between inner and outer bark was not possible, inner and outer bark thickness were measured with the help of a light stereoscope (Olympus SZ61; Olympus Austria GmbH, Vienna, Austria). The ratio of outer versus inner bark was calculated for both positions and, subsequently, the mean ratio (Rob/ib) was determined for further analyses.

2.3.5. Bark thermal conductivity ($k$)

Temperature recordings from bark heating experiments were used to calculate the bark thermal conductivity ($k$; W m$^{-1}$ K$^{-1}$). A simplified one-dimensional heat transfer model (Dickinson & Johnson, 2001) was used to first estimate the thermal diffusivity ($\alpha$; m$^2$s$^{-1}$) α:

$$T - T_0 = erf\left(\frac{BT}{2\sqrt{\alpha T}}\right) \tag{4}$$

The left side of Eq. (4) describes the excess temperature ratio and can be calculated from the average flame temperature ($T_F$; °C), the ambient temperature ($T_A$; °C) and the vascular cambium temperature ($T_c$; °C) after the duration of heating ($\tau$; s). The value of the Gauss error function (erf) on the right side of the equation defines the error associated with the excess temperature ratio and can be found in mathematical tables (e.g. Abramowitz & Stegun, 1965). Solving Eqs. (4) allows to derive $\alpha$, which then can be used to calculate $k$ (Dickinson & Johnson, 2001):

$$k = \alpha \cdot \rho \cdot c \tag{5}$$

where $c$ is the heat capacity (J kg$^{-1}$ K$^{-1}$) of the bark sample. Heat capacity of the bark strongly varies with its MC because of the high heat capacity of water. To account for differences in bark MC, heat capacity was calculated as described in Dickinson & Johnson (2001):

$$c = c_{db} + \frac{MC \cdot c_{wp} + \Delta c}{100} \tag{6}$$

where $c_{db}$ accounts for the heat capacity of dry bark, $c_{wp}$ for the heat capacity of water at a temperature (T) of 20 °C and $\Delta c$ for the elevation of heat capacity from the desorption of bound water. $c_{db}$ and $\Delta c$ were computed as suggested by Martin (1963):

$$c_{db} = 1105 + 4.856 \times T \tag{7}$$

$$MC \leq 27, \quad \Delta c = \frac{1277 \times MC}{100} \tag{8}$$

$$MC > 27, \quad \Delta c = 348 \tag{9}$$

2.4. Statistical analyses

All data analyses were conducted using R version 3.6.1 (R Core Team, 2017). A principal component analysis (PCA) was used to explore relationships among the recorded bark traits (MC, $\rho$, BT, BS, Rob/ib, k, $\tau_{\text{camb}60}$) and individual bark samples of different species. PCA was performed with data scaled to unit variance using the R package ‘FactoMineR’ (Le et al., 2008) and PCA results were visualized with ‘factoextra’ (Kassambara & Mundt, 2017). Subsequently, a redundancy analysis (RDA) was performed to assess the influence of bark traits on $\tau_{\text{camb}60}$. RDA is an ordination method, where the canonical axes are formed by linear combinations of response variables, but are also constrained to be linear combinations of explanatory variables, and
represents the percentage of variance of the response variables explained by the constraining variables (Legendre et al., 2011). In this study, the explanatory variables were the bark traits (MC, ρ, BT, BS, k), while $\tau_{\text{camb60}}$ was defined as the response variable. To avoid autocorrelation effects among explanatory variables, the linear correlations between individual bark traits were tested a priori. A strong correlation ($R \geq 0.8$) was found only between $\rho$ and $R_{\text{ob/ib}}$. Therefore, $R_{\text{ob/ib}}$ was excluded from RDA analyses. Since a single response variable was used (which corresponds to a standard multiple regression analysis), only one RDA axis was obtained summarizing the explained variation. RDA scores of bark traits were then extracted, and their absolute values plotted as polar bar charts. RDA analyses were performed for the complete dataset, and on a species level with data scaled to unit variance using the R package ‘vegan’ (Oksanen et al., 2019). ANOVA-like permutation tests (999 permutations of raw data) were performed to assess the statistical significance of the RDA axes. Furthermore, linear models were used to characterize species-specific relations between BT and $\tau_{\text{camb60}}$ (log10-transformed), as well as to explore the influence of $\rho$ on $\tau_{\text{camb60}}$ at a consistent BT (7.5 mm).

3. Results

3.1. Associations between bark traits and heat insulation capability

In total, traits and $\tau_{\text{camb60}}$ of 360 bark samples of 10 different tree species were measured. The general relationships among bark traits and $\tau_{\text{camb60}}$ were analyzed with a PCA, whereby the first two components allowed explaining 67.1% of the variance in the dataset (Fig. 2). The PCA showed positive relations between $\tau_{\text{camb60}}$, BT and $R_{\text{ob/ib}}$ while increasing $\rho$ affected $\tau_{\text{camb60}}$ negatively (see also Table S2). Right angles between vectors of $\tau_{\text{camb60}}$ and MC and between $\tau_{\text{camb60}}$ and BS, respectively, indicated weak correlations between these variables within the whole dataset. Additionally, also k had minor effects on $\tau_{\text{camb60}}$. Opposite vector directions of $\rho$ and $R_{\text{ob/ib}}$ indicate a strong negative relationship between these two variables, which highlights the strong role of the outer bark for overall $\rho$. Especially coniferous species, like P. sylvestris or L. decidua, were associated with high $\tau_{\text{camb60}}$, high BT, high $R_{\text{ob/ib}}$, and low $\rho$ values (see also Table S1). Angiosperm study species, like A. pseudoplatanus, B. pendula or F. sylvatica, on the contrary, exhibited a thin bark of comparatively high density and low amounts of outer bark, which limited their bark’s heat insulation capability (low $\tau_{\text{camb60}}$).

Fig. 3 reports the results (absolute scores) of the RDA analysis for the whole dataset with the listed bark trait variables as predictors. Please note that due to the high correlation coefficient between $\rho$ and $R_{\text{ob/ib}}$, and low $\rho$ values (see also Table S1). Angiosperm study species, like A. pseudoplatanus, B. pendula or F. sylvatica, on the contrary, exhibited a thin bark of comparatively high density and low amounts of outer bark, which limited their bark’s heat insulation capability (low $\tau_{\text{camb60}}$).
The present study demonstrated (i) an overall strong relation between BT and \( \tau_{\text{camb60}} \) as well as between both MC and \( \tau_{\text{camb60}} \). In contrast, MC, BS and k had only minor general effects on \( \tau_{\text{camb60}} \). (ii) BT was the best predictor for the heat insulation capability of bark, which holds true for both a non-species-specific comparison and on a species level (except P.
(iii) The heat insulation capability of bark varied among the examined species, with the bark of *L. decidua*, *P. cembra* and *P. sylvestris* providing the highest stem heat protection. Within studied angiosperms, the thickest bark samples and, accordingly, maximum $t_{\text{camb60}}$ values were found in *Q. robur*, although *A. pseudoplatanus* and *B. pendula* provide a higher specific insulation potential (see Fig. 6).

The analyses of the entire dataset revealed several factors of high and medium relevance for bark insulation capability, while other traits played no role. Our findings agree with previous studies, which reported heat insulation capability of bark to be highly related to BT (Pinard & Huffman, 1997; van Mantgem & Schwartz, 2003; Bauer et al., 2010; Lawes et al., 2011; Brando et al., 2012; Pausas, 2015b). Please note that this is based on data obtained from mature trees. As bark traits may vary with tree age, conclusions regarding young trees of small diameters may be limited. BT was the best predictor for the time required to reach a lethal cambium temperature ($t_{\text{camb60}}$) and thus is a useful parameter for estimating species’ resistance to tissue injuries during low- to moderate-intensity fires. The negative relationship found between $t_{\text{camb60}}$ and $\rho$ (Fig. 2, Fig. 6) suggests, that bark tissues of low density provide an additional insulation effect increasing the heat resistance and cambium protection, which can also explain species-specific differences in heat transfer towards underlying tissues despite similar bark thickness (Fig. 5). Low-density bark contains more air-filled spaces reducing the heat transfer through bark due to the low thermal conductivity of air (Dickinson & Johnson, 2001; Bauer et al., 2010). According to the PCA (Fig. 2), $\rho$ is closely linked to $R_{\text{eff}}$ (see Fig. 7).

**Table 2**

Parameters of species-specific linear relationships fitted between bark thickness and time required to reach a lethal cambium temperature ($t_{\text{camb60}}$, log10-transformed).

| Species                  | $R^2$  | $P$    |
|--------------------------|--------|--------|
| *Abies alba*             | 0.738  | < 0.001|
| *Larix decidua*          | 0.904  | < 0.001|
| *Picea abies*            | 0.851  | < 0.001|
| *Pinus cembra*           | 0.833  | < 0.001|
| *Pinus sylvestris*       | 0.668  | < 0.001|
| *Acer pseudoplatanus*    | 0.890  | < 0.001|
| *Betula pendula*         | 0.658  | < 0.001|
| *Fagus sylvatica*        | 0.314  | < 0.001|
| *Fraxinus excelsior*     | 0.708  | < 0.001|
| *Quercus robur*          | 0.961  | < 0.001|

$P$-values indicate statistical significance of all linear models.
also Table S2), which indicates that \( p \) is highly influenced by the relative amount of less dense outer bark tissue. In fact, \( p \) was highly correlated with outer bark thickness (\( R = 0.82 \); data not shown) in these studies, which highlights its importance in reducing the heat transfer and supports the assumption that the fire protection function is mainly carried out by the outer portion of the bark (Rosell, 2016; Rosell et al., 2017; Loram-Lourenço et al., 2020). Across species, differing MC levels had no relevant effect on \( \tau_{\text{camb60}} \) which also is in line with previous findings (van Mantgem & Schwartz, 2003; Lawes et al., 2011; Brando et al., 2012). However, in some species, increasing MC supported cambial heat protection (see e.g. P. abies, P. cembra and F. excelsior in Fig. 4). Water in the bark can enhance its protective function as heat gets absorbed with phase change. During evaporation, the local temperature in the bark is limited to the saturation temperature of water (100 °C) until vaporization is completed, which extends the timespan before cambium injuries occur (Jones et al., 2004; Brando et al., 2012). Furthermore, MC influences the bark’s thermophysical properties. Because of the high heat capacity of water, MC affects the heat capacity of bark and, consequently, \( k \) of the bark (Dickinson & Johnson, 2001; see also Table S1). Accordingly, effects of \( k \) on \( \tau_{\text{camb60}} \) are recognizable in the above-mentioned species, but the overall variation of \( k \) was too low to have a considerable effect across all species. BS had only a minor general effect on cambial protection. On a species level, however, BS was found to be the second-best predictor for \( \tau_{\text{camb60}} \) in L. decidua and P. sylvestris. The negative relation between BS and \( \tau_{\text{camb60}} \) in both species indicates that fissures can act as weak points within the bark where the heat transfer towards the cambium is facilitated. However, it has been shown that the heating in fissures can be less intense during fires, which may offset the negative effect of a locally thinner bark (Fahnestock & Hare, 1964).

On a species level, barks of P. cembra, P. sylvestris and L. decidua showed the best insulation capability. Cambium protection of all three species was more advantageous already at lower BT, which can be attributed to their comparatively low \( \tau_{\text{camb60}} \) (Fig. 6). Pinus is a genus that shares a long and close history with fire (Keeley, 2012; Pausas, 2015a), and the relatively thick and well insulating bark of P. sylvestris reflects an evolutionary adaption of the species to environments, where low- to moderate-intensity fires reoccur. Especially mature trees are considered to survive surface fires due to their increased bark thickness (Fernandes et al., 2008). It has been demonstrated that individuals with a 16 mm thick bark are able to reduce cambial damages to 5% during slash-rich fires (Sirén, 1974). As P. sylvestris is also able to increase its crown base height with increasing age to avoid canopy fuel ignition, it can be considered as the most fire-tolerant species within this study. Similarly to P. sylvestris, also the bark of P. cembra showed a considerably high insulation capability. Interestingly, bark samples thicker than 8 mm showed a noticeable increase of their insulation potential (Fig. 5), which may be caused by species-specific morphological changes to a more scaly bark with increasing age (Schweingruber et al., 2019). However, unlike P. sylvestris, P. cembra has strategically avoided fire-prone ecosystems in history and radiated into more humid alpine environments (Keeley, 2012). With the lack of fire disturbance, P. cembra didn’t have to necessarily evolve a very thick bark and is today one of the species with the thinnest bark within the genus (see also Table S1). In comparison to P. sylvestris, the limited bark thickness of P. cembra restricts its fire protection, especially during more intense forest fires. Additionally, the low crown base height (Frejaville et al., 2018) of P. cembra and its high bark flammability (Frejaville et al., 2013) constitute unfavorable traits during fires, making the species comparatively fire-sensitive. As in previous studies (Moris et al., 2017; Dupire et al., 2019), also the bark of L. decidua was found to provide a good heat protection to inner stem tissues. Although the fire-ecological background of L. decidua is poorly understood, it is known that L. decidua shows fire-related traits like a thick and well insulating bark, a strong post-fire recruitment (Moris et al., 2017) and low bark flammability (Frejaville et al., 2013). Therefore, also L. decidua can be considered as a species with a relatively low susceptibility to low- to moderate-intensity fires. A. alba has previously been described as a relatively fire-intolerant species with high post-fire mortality rates especially in young stands (Tinner et al., 2000; Dupire et al., 2019). The bark insulation capability of the species was found to be moderate in comparison to other species in our study (Fig. 5). However, as A. alba typically doesn’t develop thick bark (see also Frejaville et al., 2013, 2018), the overall cambial heat protection has to be considered as limited during forest fires. Across coniferous species, P. abies was found to provide the lowest heat insulation to stem internal tissues. Its thin bark allows only short times of
heat exposure before cambial necroses and/or xylem impairments may occur. Accordingly, *P. abies* has to be classified as highly susceptible to fire disturbances (Bär et al., 2019). Within the studied angiosperm species, the low bark thickness of *A. pseudoplatanus, B. pendula* and *F. sylvatica* strongly limited their insulation capability, while thicker barked *Q. robur* stems were best protected from heat. These findings agree well with previous studies, which described *Q. robur* as highly resistant to fires of low intensity (Conedera et al., 2010; Dupire et al., 2019), while *F. sylvatica* and *B. pendula* are known to be susceptible to endure stem damages due to their poor insulating barks (Bauer et al., 2010; Conedera et al., 2010; Frejaville et al., 2013). Additionally, within angiosperms, bark samples of *Q. robur* showed the lowest ρ values (Fig. 6) with comparatively high amounts of outer bark (Table S1), increasing thermal cambium protection due to the presence of more air spaces in the bark.

As the forest fire risk is predicted to increase in the Central Alps with ongoing climate change (Lorz et al., 2010; Wastl et al., 2012; Arpaci et al., 2014), adapting tree composition and creating more “fire-smart” forests at fire prone locations will become important to reduce the vulnerability of forests to future disturbances. Especially forest stands, which protect human settlements and infrastructure against natural hazards, and which are dominated by *P. abies*, should be carefully reviewed with respect to fire sensitivity in order to maintain their protective function in the long term.

5. Conclusion

Our results confirm that the bark insulation capability of the investigated Central Alpine tree species is mainly driven by its thickness, but they also demonstrate a strong correlation between bark density and cambial protection. Information on the species-specific bark insulation characteristics helps to better understand and quantify fire sensitivity of Central Alpine trees. Linking bark insulation data with information on other fire-resistance traits (e.g. heat susceptibility of crown components, crown base height, flammability), post-fire physiology and recruitment ability will be the base to better estimate future impacts on forest ecosystems and to develop strategies to cope with increased forest fire risks.

CRediT authorship contribution statement

Andreas Bär: Conceptualization, Methodology, Investigation, Formal analysis, Data curation, Writing - original draft. Stefan Mayr: Conceptualization, Methodology, Formal analysis, Writing - original draft.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary material

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