

# When the heat is on: High temperature resistance of buds from European tree species

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## Abstract

The heat resistance of meristematic tissues is crucial for the survival of plants exposed to high temperatures, as experienced during a forest fire. Although the risk and frequency of forest fires are increasing due to climate change, knowledge about the heat susceptibility of buds, which enclose apical meristems and thus enable resprouting and apical growth, is scarce. In this study, the heat resistance of buds in two different phenological stages was experimentally assessed for 10 European tree species. Cellular heat tolerance of buds was analyzed by determining the electrolyte leakage following heat exposure. Further, the heat insulation capability was tested by measuring the time required to reach lethal internal temperatures linked to bud traits. Our results highlighted differences in cellular heat tolerance and insulation capability among the study species. The phenological stage was found to affect both the thermal stability of cells and the buds' insulation. Further, a good relationship between size-related bud traits and insulation capability was established. Species-specific data on the heat resistance of buds give a more accurate picture of the fire susceptibility of European tree species and provide useful information for estimating tree post-fire responses more precisely.

## KEYWORDS

bud traits, cellular tolerance, electrolyte leakage, forest fires, heat injuries, heat resistance, insulation capability, meristem protection

## 1 | INTRODUCTION

The ability of trees to deal with excessive heat becomes increasingly challenged with climate change. Besides raising the number of extreme heat waves (Yao, Luo, Huang, & Zhao, 2013), drier and warmer climatic conditions also enhance the frequency and intensity of fire events in many forest ecosystems worldwide (IPCC, 2014; Seidl, Spies, Peterson, Stephens, & Hicke, 2016). Forest fires constitute a particular heat stress situation, where tree individuals are confronted with high amounts of thermal energy released by

combustion. The heat tolerance of a tree mainly derives from its ability to protect meristematic tissues against lethal heat injuries (Dickinson & Johnson, 2001; Michaletz & Johnson, 2007). Lateral meristems are located underneath and in the bark (the vascular cambium and the cork cambium, respectively) and are responsible for the (re)generation of new xylem, phloem, and bark tissues. If the bark is not able to sufficiently reduce the heat transfer, the vascular cambium can exceed critical temperatures, potentially resulting in limitations to hydraulic and carbohydrate pathways (e.g., Bär, Michaletz, & Mayr, 2019; Gricar et al., 2020; Mundo, González,

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Stoffel, Ballesteros-Cánovas, & Villalba, 2019; Partelli-Feltrin, Smith, Kolden, Johnson, & Adams, 2020), and ultimately in tree mortality. Equally important is the protection of apical meristematic tissues, which are contained in buds, as they are the source for the development of above-ground organs, such as shoots, leaves, and flowers. Depending on the heat transfer processes to the crown (Michaletz & Johnson, 2006a), fires can cause partial or complete necrosis of buds including apical meristems, accompanied by loss of active foliage. Partial bud and foliage necrosis reduce the total leaf area of affected trees, limiting their photosynthetic carbon assimilation. Limitations of the carbon pathway can manifest in decreased growth or even mortality if the tree's carbohydrate demand cannot be fully covered by the remaining foliage (Bär et al., 2019; Hood, Varner, van Mantgem, & Cansler, 2018). A complete fire-induced loss of apical meristems restrains a successful reestablishment of green biomass after a fire, unless the tree is able to form adventitious structures originating from nonmeristematic tissues at wounding sites (Meier, Saunders, & Michler, 2012). In fire-prone ecosystems, trees have evolved important strategies of apical meristem protection to enhance resprouting after fire disturbances (Clarke et al., 2013; Pausas & Keeley, 2017). For example, following fire-induced crown destruction, many fire-adapted eucalypt species resprout epicormically from dormant buds buried in the bark or from basal/belowground bud banks, which benefit from the soil's effective insulation ability (Nicolle, 2006; Pausas, Lamont, Paula, Appezzato-da-Glória, & Fidelis, 2018). Additionally, the structure and arrangement of foliage influence the heat transfer towards buds (Michaletz & Johnson, 2006b), and it is known from fire-resistant coniferous species that long and densely standing needles provide a shielding of aerial buds from heat (Fernandes, Vega, Jiménez, & Rigolot, 2008).

Improving the knowledge of forest fire impacts on tree individuals and predicting post-fire tree mortality are the focus of broad research activities (e.g., Bär et al., 2019; Brando, Nepstad, & Balch, 2012; Catry, Rego, Moreira, Fernandes, & Pausas, 2010; Dickinson & Johnson, 2001; Hood et al., 2018; Michaletz & Johnson, 2007, 2008; Rigolot, 2004; Woolley, Shaw, Ganio, & Fitzgerald, 2012). Naturally, most studies contributing to a better understanding of the fire sensitivity of trees focus on species in fire-prone ecosystems and/or areas where prescribed burning is used as a forest management tool (e.g., Fernandes et al., 2008; Loram-Lourenço et al., 2020; Pausas, 2015; van Mantgem & Schwartz, 2003). However, with ongoing climate change, less fire-prone areas like the European Central Alps will also face an increased risk of forest fires in the future (Arpaci, Malowerschnig, Sass, & Vacik, 2014; Lorz et al., 2010; Müller, Vilà-Vilardell, & Vacik, 2020; Wastl, Schunk, Leuchner, Pezzatti, & Menzel, 2012). In the Central Alps, forests provide a very important ecosystem service: the fundamental protection against natural hazards (Körner, 2012; Tranquillini, 1979). A fire-caused endangerment of this protective function can have enormous consequences, exposing human settlements and infrastructure to avalanches, landslides, and rockfalls. Therefore, obtaining a precise picture of the fire resistance of Central Alpine tree species will become highly important to accurately estimate future forest dynamics and to better assess fire risks.

In recent years, important steps have been made to quantify the fire resistance of Alpine trees (Bär & Mayr, 2020; Bauer, Speck, Blömer, Bertling, & Speck, 2010; Conedera, Lucini, Valesse, Ascoli, & Pezzati, 2010; Dupire, Curt, Bigot, & Fréjaville, 2019; Frejaville, Curt, & Carcaillet, 2013; Frejaville, Vilà-Cabrera, Curt, & Carcaillet, 2018). However, while most studies focus on bark properties and the related capability to protect stem-internal tissues including lateral meristems, information regarding the heat resistance of crown components is limited for species in the European Alpine region (Bauer, 1972; Fernandes et al., 2008; Wisniewski, Sauter, Fuchigami, & Stepien, 1997).

In the present study, bud heat resistance data of 10 Central Alpine tree species in different phenological stages were collected to gain a more holistic understanding of species-specific fire susceptibilities. The cellular heat tolerance of buds was analyzed by quantifying cell damages at different heat exposure levels and by assessing the heat insulation capability of bud samples with measurements of the times required to reach a critical internal temperature of 60°C, a threshold where cell mortality is typically assumed (Rosenberg, Kemeny, Switzer, & Hamilton, 1971). Further, five different bud traits were measured on each bud sample to explore the respective influence on the insulation capability using multivariate statistics. We aimed to (a) identify differences in cellular heat tolerance among study species, (b) address if there are interspecific variations in the heat insulation capability, and (c) analyze which bud traits are the best predictors for the insulation capability. Further, we studied (d) the influence of the buds' phenological stage on both cellular heat tolerance and insulation capability.

## 2 | MATERIALS AND METHODS

### 2.1 | Plant material

Measurements were conducted on five coniferous and five angiosperm European tree species (Table 1) relevant for silviculture and forest management within the Central Alpine region. In a previous study performed by Bär and Mayr (2020), the bark insulation capability was examined on the same set of species. Between February and May, bud-bearing branches were collected from a minimum of three different mature specimens per species, growing in mixed forest stands situated near Innsbruck or Praxmar, Tyrol, Austria (for locations, see Table 1). First, completely closed, winter resting buds were harvested for all study species. Bud sampling was repeated when buds were clearly swollen, but bud break had not occurred yet. Sampling dates of swollen buds were chosen according to the species-specific phenological progress. For sampling, branches were cut from lower crown portions, packed in plastic bags and immediately transported to the laboratory. Branches were then cut into smaller segments and further processed for the assessment of either the cellular heat tolerance or the heat insulation capability of buds. To best possibly account for intraspecific variations, buds were chosen randomly from branch segments without differentiation between terminal and lateral buds for both analyses.

**TABLE 1** Study species, height of sampled trees, and sampling location coordinates

Species	Tree height (m)	Coordinates of sampling locations
<i>Abies alba</i> Mill.	15–20	47°17'40.8"N, 11°24'37.9"E
<i>Larix decidua</i> Mill.	15–20	47°16'52.6"N, 11°23'06.5"E
<i>Picea abies</i> (L.) Karst.	10–25	47°16'14.0"N, 11°22'17.9"E 47°13'37.5"N, 11°25'05.1"E
<i>Pinus cembra</i> L.	10–15	47°09'20.7"N, 11°08'04.3"E
<i>Pinus sylvestris</i> L.	10–15	47°16'18.2"N, 11°22'26.9"E
<i>Acer pseudoplatanus</i> L.	5–15	47°16'16.5"N, 11°22'25.1"E
<i>Betula pendula</i> Roth	8–15	47°16'16.2"N, 11°22'33.2"E
<i>Fagus sylvatica</i> L.	10–20	47°16'14.6"N, 11°22'24.6"E
<i>Fraxinus excelsior</i> L.	8–20	47°16'17.7"N, 11°22'32.3"E
<i>Quercus robur</i> L.	10–15	47°17'29.6"N, 11°25'36.1"E

## 2.2 | Cellular heat tolerance derived from electrolyte leakage

To determine the buds' cellular heat tolerance, the electrolyte leakage to the apoplast due to heat-induced cell damages was assessed by measuring the electrical conductivity of solutions containing heat-exposed bud samples. Bud-bearing branch segments were exposed to different temperatures (bud-internal target temperatures: 40, 45, 50, 55, 60 and 80°C) in a heat test chamber (MK53, Binder GmbH, Tuttlingen, Germany) for 15 min. As a reference (20°C), one sample set of buds remained without heat treatment. Additionally, heat treatments were also performed at 70°C for *P. sylvestris* (closed stage) and *P. cembra* (closed and swollen stage) due to their comparatively high heat tolerance. Evergreen coniferous branches were heat treated with their foliage attached. Before each treatment, three buds of each species were randomly chosen, and copper-constantan thermocouples (Type T, operating range: –200 to 350°C, diameter of coated wires: 0.3 mm) connected to a thermometer (PCE-T390, PCE Deutschland GmbH, Meschede, Germany) were inserted from the bud base into the centre to monitor internal bud temperatures. These buds were only used for monitoring purposes and were excluded from further measurements. To avoid any heat conduction via the thermocouple wires into the buds, the sheathing was only removed at the wire tips. Thus, only insulated wire parts had contact with the heated air outside buds. For each treatment, the heating chamber was preheated according to the desired bud-internal target temperature, and the integrated fan was set to a speed of 60% to break down the boundary layer around the buds. As preliminary measurements showed that internal bud temperatures mostly remain slightly below ambient temperature levels, the heat chamber temperature was set 1°C above the respective target temperature. Branch segments and buds for temperature monitoring were then placed in the heating chamber. The exposure time of 15 min started as soon as the bud-internal temperature stabilized at the target temperature to

exclude potential insulation effects. The actual measured bud-internal temperatures were used for further analyses. Heat experiments were carried out with an exposure time of 15 min to induce pronounced effects (cellular damages) at each temperature level. It should be taken into account that such a long heating treatment reflects an extreme fire situation with a long flame residence time. After heat treatments, 20 buds of every species were cut longitudinally with a sharp razor blade. Five bisected buds were then each transferred into four test tubes filled with 15 ml of distilled water and shaken for 24 hr on a horizontal shaker (ST5 Bidimensional Shaker, CAT, Staufen, Germany) at 5°C. Afterward, sample solutions were re-equilibrated to room temperature, and their electrical conductivity (C1;  $\mu\text{m s}^{-1}$ ) was measured with a conductivity metre (WTW inoLab, Weilheim, Germany). Samples were then autoclaved at 121°C for 20 min (Tutttnauer autoclave steam sterilizer 240 ELV, Syntec GmbH, Wettenberg, Germany) and shaken again for 24 hr at 5°C before the final electrical conductivity measurement was performed for all sample solutions (C2;  $\mu\text{m s}^{-1}$ ). The relative electrolyte leakage (REL; %) was calculated for each sample by relating C1 to C2, including a correction for the electrolyte leakage caused by the cutting of buds:

$$\text{REL} = \left( \frac{C1}{C2} * 100 \right) - \text{REL}_{\text{ref}} \quad (1)$$

where  $\text{REL}_{\text{ref}}$  (%) is the mean species-specific electrolyte leakage of untreated reference buds. Assuming that the bud tissue is completely killed by autoclaving and that no heat-induced cell damages occurred with minimum REL, the percentage of cellular damage (PCD; %) was consequently determined as

$$\text{PCD} = \frac{\text{REL} - \text{REL}_{\text{min}}}{\text{REL}_{\text{max}} - \text{REL}_{\text{min}}} * 100 \quad (2)$$

where  $\text{REL}_{\text{max}}$  is the species-specific mean maximum electrolyte leakage caused by autoclaving, and  $\text{REL}_{\text{min}}$  is the mean REL at the temperature step where the minimum leakage was observed. Heat tolerance curves were then constructed to compare critical thresholds between species and between phenological stages.

## 2.3 | Heat insulation capability

The insulation capability of buds was quantified by measuring the internal temperature dynamics of bud samples to a heat exposure at 80°C. A temperature of 80°C was chosen as it is within the range of heat plume temperatures during low- to moderate-intensity surface fires (Michaletz & Johnson, 2006a; Seto, Strand, Clements, Thistle, & Mickler, 2014). Per species and phenological stage, six buds were chosen, cut from branches and equipped with thermocouples that were inserted through the bud base. Bud samples were then heat exposed in the preheated test chamber, and their internal temperature was logged at 1-s intervals until reaching a critical threshold of 60°C. The temperature in the heating chamber was kept constant at 80°C during the measurement.

Temperature recordings were used to determine the time required to reach a lethal bud-internal temperature of 60°C ( $t_{60}$ ; s), which allowed us to assess and compare the heat insulation capability of bud samples. Further, the thermal conductivity of each bud sample was calculated based on logged temperature profiles (see ‘Bud thermal conductivity’).

## 2.4 | Bud traits

To assess the influence of bud traits on the insulation capability, the following five traits were measured on each bud used in the heat insulation experiment.

### 2.4.1 | Moisture content

Before heat exposure, the fresh weight (FW; g) of each bud was collected. After heat experiments were finished, bud samples were oven-dried at 70°C for 48 hr, and the dry weight (DW; g) was determined. The moisture content (MC; %) was then calculated on DW basis.

### 2.4.2 | Bud diameter ( $D$ )

The diameter of each bud ( $D$ ; mm) was measured at its widest point, which corresponded to the depth of inserted thermocouples.

### 2.4.3 | Bud volume ( $V$ ) and density ( $\rho$ )

Prior to heat experiments, photographs of buds were taken in plan view (Nikon, Coolpix AW130, Nikon Corporation, Tokyo, JP) and processed in ImageJ (ImageJ, 1.52; public domain, National Institutes of Health, Bethesda). Corresponding to the bud contour, black-white negative pictures were created and fed to the software YABBA (Yet Another Bacterial Biovolume Algorithm; Zeder, Kohler, Zeder, & Pernthaler, 2011), which returns accurate biovolume estimations based on the two-dimensional projections irrespective of their shape. From the obtained bud volume ( $V$ ; m<sup>3</sup>) and DW, the bud density ( $\rho$ ; kg m<sup>-3</sup>) was then determined:

$$\rho = \frac{DW}{V * 1000} \quad (3)$$

### 2.4.4 | Bud thermal conductivity ( $k$ )

Temperature recordings from insulation capability experiments were used to calculate the bud thermal conductivity ( $k$ ; W m<sup>-1</sup>°C<sup>-1</sup>). According to Dickinson and Johnson (2001), the thermal diffusivity ( $\alpha$ ; m<sup>2</sup> s<sup>-1</sup>) was first calculated using a simplified one-dimensional heat transfer model:

$$\frac{T - T_e}{T_0 - T_e} = \text{erf}\left(\frac{r}{2\sqrt{\alpha\tau}}\right) \quad (4)$$

The excess temperature ratio (left side of Equation (4)) was calculated from the exposure temperature ( $T_e$ ; °C), the ambient temperature ( $T_0$ ; approx. range: 22–25°C), and the bud-internal temperature ( $T$ ; °C) at depth  $r$  (which corresponds to the bud radius) after the duration of heating ( $\tau$ ; s). The right side of the Equation describes the error function (erf) associated with the excess temperature ratio, whose argument can be found in mathematical tables (e.g., Gautschi, 1965). After rearranging Equation (4) to derive  $\alpha$ ,  $k$  could be determined:

$$k = \alpha * c * \rho \quad (5)$$

where  $c$  is the bud's specific heat capacity (J kg<sup>-1</sup>°C<sup>-1</sup>), which was calculated as follows to account for differences in bud relative MC (Michaletz & Johnson, 2006a):

$$c = \frac{DW * c_{db} + M_w * c_w}{DW + M_w} \quad (6)$$

where  $c_{db}$  is the heat capacity of dry buds (1902.6 J kg<sup>-1</sup>°C<sup>-1</sup>; Phillips, Sastry, & T. M.C., 1983),  $M_w$  reflects the bud's water mass, and  $c_w$  is the heat capacity of water (4,180 J kg<sup>-1</sup>°C<sup>-1</sup>).

## 2.5 | Statistical analyses

All data analyses were conducted in R version 3.6.1 (R Development Core Team, 2017). Heat tolerance curves were generated using the Weibull function provided by the ‘fitplc’ package (Duursma & Choat, 2017). To assess differences between species and between phenological stages, the temperature at 50% PCD ( $T_{PCD50}$ ; °C), and the associated 95% bootstrapped ( $n = 999$ ) confidence interval were derived from each curve.  $T_{PCD50}$  values with nonoverlapping confidence intervals were considered as statistically different.

Differences in heat insulation between phenological stages were tested with the Student's  $t$  test after testing data for Gaussian distribution (Shapiro–Wilk-Test) and variance homogeneity (Levene test). Non-Gaussian distributed data were compared using the Welch test. All tests were performed at a probability level of 5% (R package ‘jmv’, Selker, Love, & Dropmann, 2019).

Relationships between insulation capability (i.e.,  $t_{60}$ ), bud trait data, phenological stages, and individual bud samples of different species were explored by performing a principal component analysis (PCA). PCA analysis (data scaled to unit variance) and visualization were performed using R packages ‘FactoMineR’ (Le, Josse, & Husson, 2008) and ‘factoextra’ (Kassambara & Mundt, 2017). Additionally, a redundancy analysis (RDA; R Package ‘vegan’, Oksanen et al., 2019) was conducted to estimate the influence of single bud traits on the insulation capability. Linear correlation tests were performed among explanatory variables (bud traits) beforehand, and a strong correlation ( $R = 0.87$ )  $k$  was found between  $V$  and  $D$ . However,

neither  $V$  nor  $D$  was omitted from the RDA as the combination of both variables provides additional explanatory value. As only one response variable ( $t_{60}$ ) was used (this corresponds to a multiple regression analysis), the explained variation is summarized by only one RDA axis. The statistical significance of this axis was tested with an ANOVA-like permutation test (999 permutations of raw data). RDA scores of bud traits were then extracted, and their absolute values were plotted to demonstrate their influence on  $t_{60}$ .

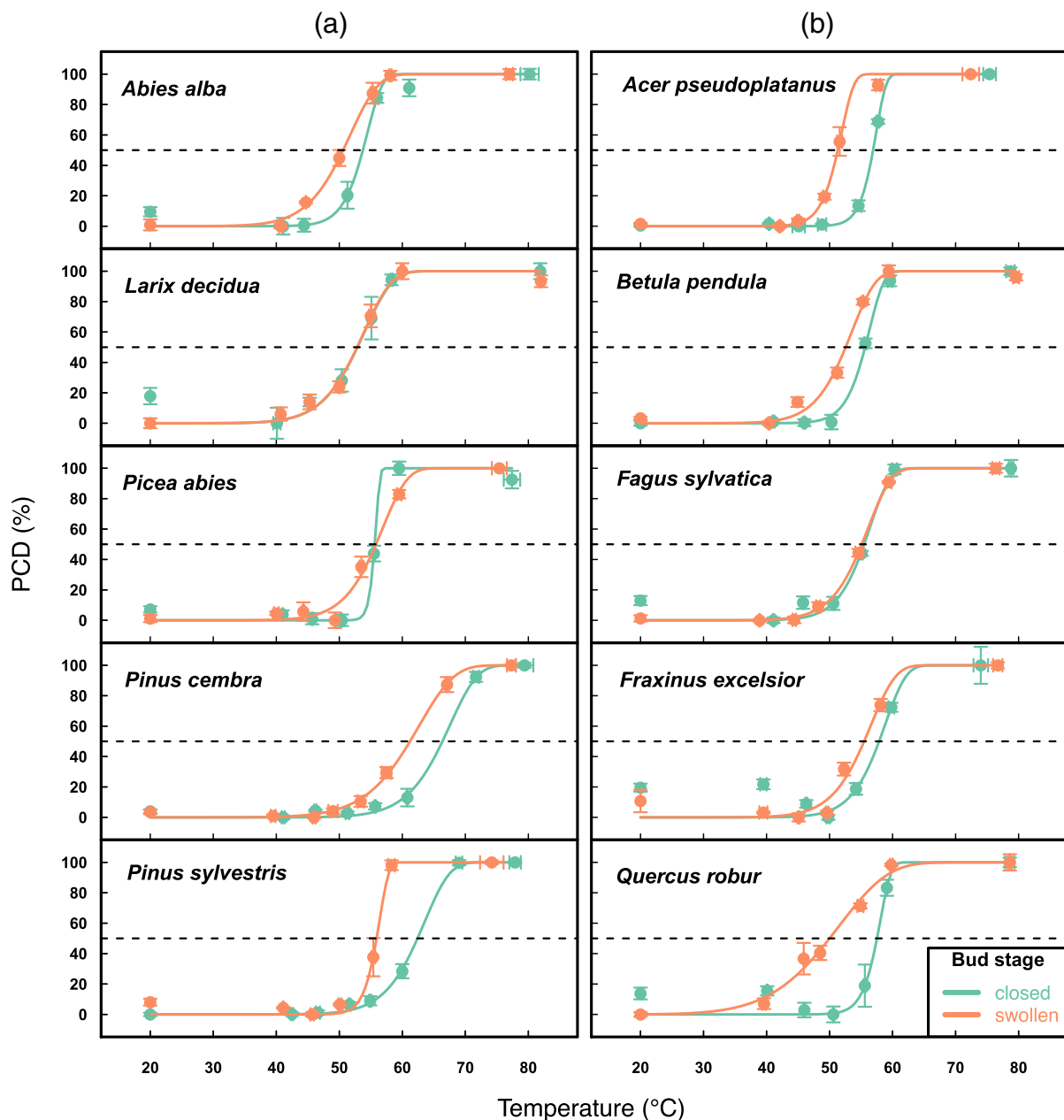
To obtain a better estimation of the overall heat susceptibility of each species, data on cellular heat tolerance and insulation capability were combined. Therefore, species-specific  $T_{PCD50}$  temperature values extracted from heat tolerance curves (Figure 1, Table S1) were

defined as critical thresholds. Then, the average time until reaching these species-related critical temperatures ( $t_{crit}$ ) was calculated.

### 3 | RESULTS

#### 3.1 | Cellular heat tolerance

Heat tolerance curves obtained from electrolyte leakage experiments (Figure 1) revealed clear differences in heat susceptibility among species as well as between phenological stages. In general, mean  $T_{PCD50}$  values (see also Table S1) ranged from 50.0 to 66.4°C. Within studied



**FIGURE 1** Heat tolerance curves for (a) coniferous and (b) angiosperm species in study. The percentage of cellular damage (PCD; mean values SE) is plotted against exposure temperature for closed and swollen buds. Points represent means  $\pm$  SE. Dashed lines indicate a cellular damage of 50%

coniferous species, closed buds of *P. cembra* ( $T_{PCD50}$ : 66.4°C) and *P. sylvestris* ( $T_{PCD50}$ : 62.4°C) showed the highest heat tolerance, while closed buds of *Q. robur* ( $T_{PCD50}$ : 57.5°C) and *F. excelsior* ( $T_{PCD50}$ : 57.9°C) were found to provide the best cellular thermal stability among angiosperm species in the study. In contrast, a  $T_{PCD50}$  at around 50°C was observed in swollen buds of *A. alba* and *Q. robur*, exhibiting the highest cellular heat susceptibility within this study. Obtained results showed an overall trend towards a reduced heat tolerance with progressing phenology, as mean  $T_{PCD50}$  values of swollen buds were generally lower (except for *P. abies*) than those of closed buds (Figure 1, Table S1). Please note that pre-exposure heating times (until reaching the required bud-internal target temperatures) varied to a certain extent. Pre-exposure heating of buds was generally completed within 1 min, with most buds reaching their target temperatures after approx. 20–30 s. Variations in pre-exposure heating times may potentially influence the level of cellular injuries. However, as the exposure time was 15 min, the effects of variation in heating time can be expected to be minor.

### 3.2 | Heat insulation capability and its relation to bud traits

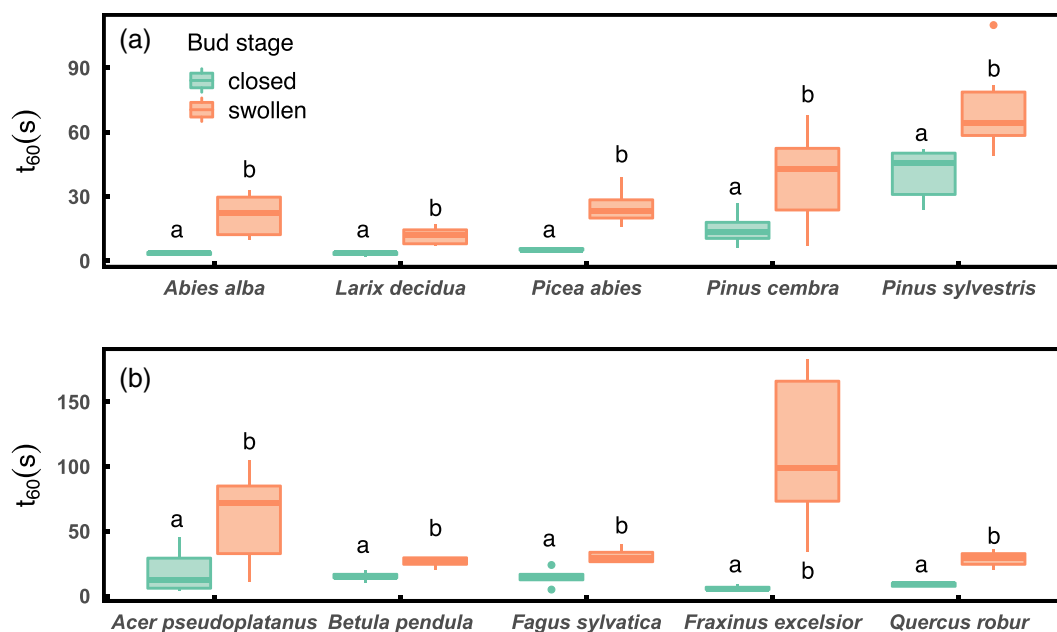
Differences in the heat insulation capability assessed via  $t_{60}$  are illustrated in Figure 2. Compared to the closed bud stage, swollen buds of all species showed a significant increase in the heat protection of internal tissues. Consistent with findings obtained from heat tolerance experiments, buds of *P. cembra* and *P. sylvestris* also provided the best insulation capability within the coniferous subset (Figure 2a).

Within angiosperms, especially swollen buds of *A. pseudoplatanus* and *F. excelsior*, showed an enhanced insulation in comparison to the other species, being able to protect internal tissues from reaching a critical temperature of 60°C for a duration of  $61.5 \pm 15.3$  s and  $111.3 \pm 25.1$  s, respectively (Figure 2b).

The relationships among  $t_{60}$  and bud traits (species-specific values of measured bud traits can be found in Table S2) were assessed by performing a PCA. The first two constructed axes (principal components) explained 74.5% of the variance (Figure 3). The PCA showed positive relations among  $t_{60}$ , MC, V, and D, while the opposite vector directions of  $\rho$  and  $t_{60}$  indicated that high  $\rho$ -values negatively affected  $t_{60}$ . PCA results further demonstrated the connection between the phenological bud stage and the insulation capability. Swollen buds, which are highlighted by the light red convex hull in Figure 3, were predominantly associated with higher  $t_{60}$  values, as well as with increases in size (V, D) and MC, and a decrease in  $\rho$ . To clearly identify the traits that mainly influence  $t_{60}$ , an RDA analysis was performed (Figure 4). RDA scores revealed  $t_{60}$  to be mainly determined by V and D, while  $\rho$  and MC proved to be traits with lower predictive power. As also indicated by the PCA analysis, the effect of k on  $t_{60}$  was negligible.

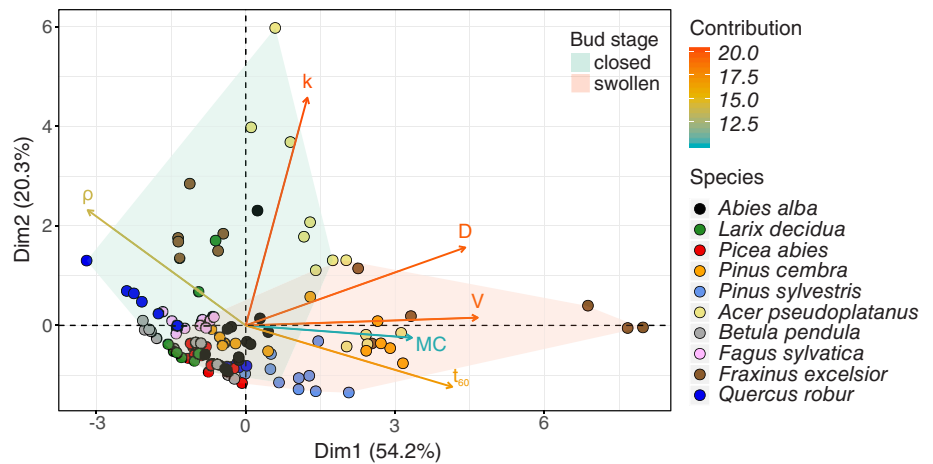
### 3.3 | Integrating cellular heat tolerance into insulation capability

As illustrated in Figure 5, incorporating the cellular heat tolerance widely mitigated the positive effect of bud swelling as the cellular thermal stability declined with progressing phenology in most species.



**FIGURE 2** Boxplots of average times to reach a bud-internal temperature of 60°C ( $t_{60}$ ) at an exposure temperature of 80°C for (a) coniferous and (b) angiosperm species in study. Boxplots indicate the median (thick central line), interquartile range (box), minimum and maximum (whiskers), and outliers (circles). Different letters indicate significant intraspecific differences between closed and swollen buds [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

**FIGURE 3** Principal component analysis (PCA) demonstrating the associations among bud traits (moisture content, MC; bud diameter,  $D$ ; bud volume,  $V$ ; bud density,  $\rho$  and bud thermal conductivity,  $k$ ) and the time to reach a critical bud-internal temperature of  $60^{\circ}\text{C}$  ( $t_{60}$ ). The arrow colour indicates the contribution in percentage (see colour code in legend) of each variable to the principal components. Shaded areas represent convex hulls of the two different phenological bud stages [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]



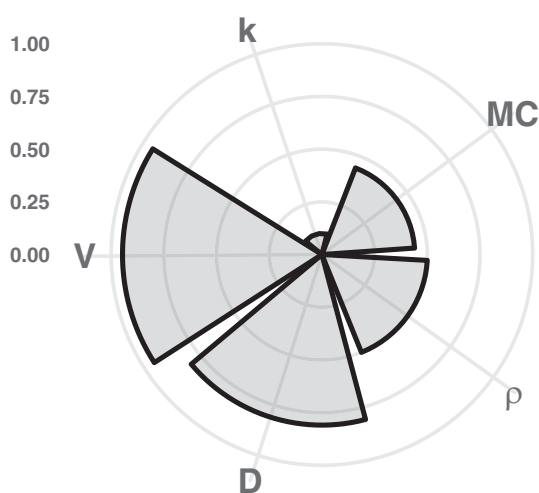
The recalculation of  $t_{crit}$  values further highlights the beneficial heat resistance of *P. cembra* and *P. sylvestris* buds. While  $t_{crit}$  generally decreased in comparison to  $t_{60}$  in all other species, high  $T_{PCD50}$  values above  $60^{\circ}\text{C}$  (see also Table S1) of *P. cembra* (closed and swollen stage) and *P. sylvestris* (closed stage) led to an especially high heat protection of bud tissues.

## 4 | DISCUSSION

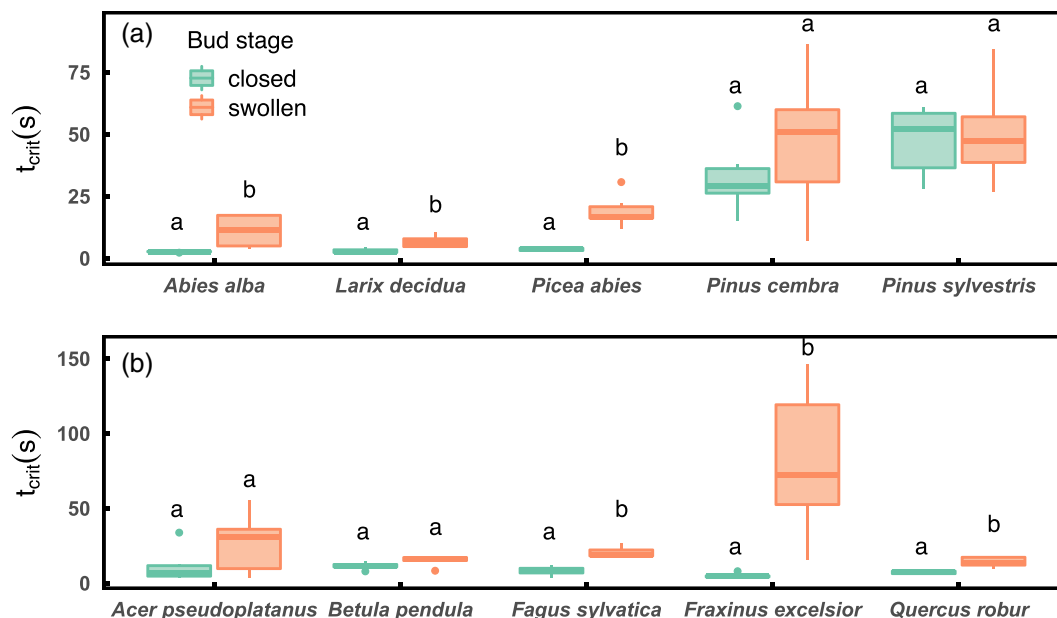
This study demonstrated (a) species-specific temperature thresholds at which critical cell damages in buds occur. Results highlighted the differences in cellular heat tolerance among the studied species, with closed buds of *P. cembra* and *P. sylvestris* being able to withstand the highest exposure temperatures. (b) Also, interspecific variations concerning the insulation capabilities of buds were observed. Here,

swollen buds of *F. excelsior* and *A. pseudoplatanus* as well as buds of *P. cembra* and *P. sylvestris* provided the highest protection for internal tissues. (c) The heat transfer towards the bud centre was mainly influenced by size-related bud traits such as  $V$  and  $D$  but also  $\rho$  and  $MC$  were found to have an impact on the heat insulation of buds. (d) Further, the phenological stage of buds affected their heat resistance. While the heat insulation capability of buds increased with progressing phenology, bud tissues became more susceptible to heat in the swollen stage.

Cellular heat damages are initiated by gross structural changes of cell membranes. Heat-induced protein denaturation and phase changes in membrane lipids lead to permeability alterations or lesions, and, consequently, to a release of cellular contents (Quinn, 1988; Wahid, Gelani, Ashraf, & Foolad, 2007). It has been demonstrated that heat-induced cell injuries start to occur when tissue temperatures rise above approximately  $45\text{--}50^{\circ}\text{C}$  (e.g., Colombo & Timmer, 1992; Daniell, Chappell, & Couch, 1969; Yeh & Lin, 2003). This corresponds well with our findings, as onsets of cellular damages were evident in most species when this temperature threshold was exceeded (Figure 1). However, as heat injuries emerge as a function of temperature and time (Dickinson & Johnson, 2004; Hare, 1961; Peter, Agee, & Sprugel, 2009), cell damages may potentially occur at lower temperatures if exposed for longer time periods. While the direct relationship between cellular injuries and bud break failure was not explored in this study, Wisniewski et al. (1997) demonstrated a 50% electrolyte leakage increase caused by heat damages to result in bud mortality and inhibition of bud break. Therefore, the temperature at which 50% of cellular damages occurred ( $T_{PCD50}$ ) seems to be an adequate physiological parameter to assess the cellular heat tolerance among species and bud stages.  $T_{PCD50}$  values of closed buds ranged from  $52.9^{\circ}\text{C}$  (*L. decidua*) to  $66.4^{\circ}\text{C}$  (*P. cembra*) within the coniferous subset, while the variation within angiosperms was considerably lower (minimum:  $55.5^{\circ}\text{C}$ , *F. sylvatica*; maximum:  $57.9^{\circ}\text{C}$ , *F. excelsior*). It is considered that the thermal tolerances of plant cell membranes are governed by their protein and lipid structures (Wahid et al., 2007), and it has been demonstrated that the total lipid content, as well as composition and saturation degree of fatty acids in membrane lipids, can vary in bud meristems between species (Alaudinova & Mironov, 2009, 2010).



**FIGURE 4** Influence of bud traits (moisture content, MC; bud diameter,  $D$ ; bud volume,  $V$ ; bud density,  $\rho$  and bud thermal conductivity,  $k$ ) on the time required to reach a critical bud-internal temperature of  $60^{\circ}\text{C}$  ( $t_{60}$ ). RDA scores (absolute values) indicate the effect of each trait on  $t_{60}$ . The first (and only) RDA axis accounted for 73.26% of the variance in the response data ( $p < .001$ )



**FIGURE 5** Boxplots of average times to reach species-specific critical bud-internal temperatures ( $t_{crit}$ ) for (a) coniferous and (b) angiosperm species in study.  $t_{crit}$  values were extracted from temperature profiles according to species-specific  $T_{PCD50}$ -thresholds (interpolated temperatures at 50% cellular damage; see Table S1). Boxplots indicate the median (thick central line), interquartile range (box), minimum and maximum (whiskers) and outliers (circles). Different letters indicate significant intraspecific differences between closed and swollen buds [Colour figure can be viewed at [wileyonlinelibrary.com](http://wileyonlinelibrary.com)]

Additionally, the presence of resin may be accountable for the high variation within coniferous buds, as, during sampling preparation, resin depositions were found to be very prominent in *P. cembra* and *P. sylvestris*. It is conceivable that the presence of resin might have a certain stabilizing effect on bud cell physics, as *P. cembra* and *P. sylvestris* showed a remarkably high heat tolerance with closed buds resisting temperatures of above 60°C before a 50% PCD occurred (Figure 1a). Generally, the cellular heat tolerance decreased with bud swelling, and  $T_{PCD50}$  values were found to be lower in the swollen bud stage (except for *P. abies*; Figure 1). These reductions of the cellular thermal stability may be explained by membrane lipid dynamics with progressing phenology. Various studies (e.g., Alaudinova & Mironov, 2010; Chu & Tso, 1968; Hall, Chastain, Horn, Chapman, & Choinski, 2014) demonstrated that during bud/leaf development, desaturation processes take place, increasing the amount of unsaturated fatty acids. While this indicates that a comparatively high degree of lipid saturation is potentially beneficial for cellular thermal stability (Wahid et al., 2007), empirical links between cell membrane lipid characteristics and heat tolerance of bud tissues are currently missing.

Analyses of heat insulation capability and associated bud traits revealed that during heat exposure, the size of buds strongly influences the time until critical internal temperatures are reached, while other bud traits had only medium ( $\rho$  and MC) or minor effects ( $k$ ) on heat transfer. Accordingly, size-related traits such as  $V$  and  $D$  (Figures 3 and 4) were found to be the most useful parameters for predicting bud thermal protection. These findings agree with previous studies, which also highlighted the importance of the size of buds for their survival during fires (Byram, 1948; Michaletz & Johnson, 2006a;

Peterson & Ryan, 1986). The influence of bud size also becomes clearly visible when comparing the insulation capability between closed and swollen buds (Figure 2): Swollen buds of all species were able to withstand longer time periods of heat exposure, mainly due to volume increases. Additionally, the swelling process was accompanied by  $\rho$  losses and MC gains (Figure 3), which both affected the heat protection of internal tissues. It is known from bark heating experiments that tissues of low density are advantageous for heat insulation as air-filled spaces in the bark reduce the heat transfer to underlying tissues (Bär & Mayr, 2020; Bauer et al., 2010; Dickinson & Johnson, 2001). In buds, the movement of bud scales with bud expansion may create such spaces where air can accumulate. At the same time, the amount of water in parenchymal and primordial tissues increases with bud swelling, which consequently influences the bud's thermophysical properties. Due to the high heat capacity of water, also the bud's specific heat capacity increases with MC (see Equation 6), and, subsequently, heat transfer rates are slowed down as more energy is required to raise the bud temperature. During longer heat exposure times, buds with higher MC may also benefit from prolonged evaporative cooling until the water is fully vaporized.

Additionally, other factors not addressed in this study may contribute to the variation of  $t_{60}$  among species and between phenological stages. Besides the presence/absence of resin or concentration differences of secondary metabolites in bud tissues, interspecific variations in bud-internal structures might also affect the heat transfer. Pine species, for instance, develop compound buds where each fascicle primordium within the bud is covered by its own set of bud scales (Doak, 1935). Such an internal morphology may create additional heat



barriers enhancing the protection of sensitive tissues. Further, it has to be noted that the presented results may not fully cover intraspecific  $t_{60}$  variation as measured buds were sampled from only one or two sampling sites per species (Table 1). Genotypic variability between separated populations as well as varying environmental growing conditions can affect bud development (Alla, Camarero, Rivera, & Montserrat-Martí, 2011; Kukuk et al., 2015). For example, disturbances such as drought events or biotic attacks may limit shoot and bud growth or make it necessary to set new buds after a second flushing, which both can result in lower bud sizes, and consequently, in reduced insulation capability.

Information on how the timing of fire affects tree responses is necessary to establish appropriate post-fire management of forest stands affected by wildland fires and to determine the best possible burn dates for areas managed with prescribed fires. While it is largely known that post-fire mortality is mainly driven by seasonal differences in fire intensity (Schwilk, Knapp, Ferrenberg, Keeley, & Caprio, 2006; Swezy & Agee, 1991; Thies, Westlind, & Loewen, 2005; Weise et al., 2016), it was also shown by Harrington (1987, 1993) that mortality rates are sensitive to the trees' phenological state at similar fire intensity levels, with a higher probability for trees to survive fires during the dormant season. According to our results, this suggests that once buds are fully opened, the expanded foliage loses the protective function of the bud stage and becomes more vulnerable to heat (see also Wade & Johansen, 1986). In the case of evergreen conifers, the presence of foliage during the dormant season may further improve the heat protection of buds. Foliage alters the heat transfer in the crown and increases the convective resistance of crown components by influencing the boundary layer development (Michaletz & Johnson, 2006b). This also suggests that, due to the lack of foliage, buds of deciduous angiosperm species are confronted with higher amounts of heat in the crown. Please note that, although the cellular heat tolerance was tested on branch segments with attached needles, our study did not assess the protective effects of foliage as boundary layers were broken down intentionally to exclude any insulating effects when analyzing the thermal stability of cells. While the use of experimental heating chambers offers the possibility to study heat effects under controlled and reproducible conditions, mimicking accurate thermal conditions trees experience during an actual wildfire is hardly possible. Therefore, further research is needed, combining experimental findings and field observations and relating organ level processes to whole-plant and ecosystem functioning.

## 5 | CONCLUSION

The heat resistance of buds depends on their insulation capability, mainly driven by their volume, as well as on the species-specific heat tolerance of bud tissues. Our results outline differences in bud heat susceptibility among species and highlight the importance of the bud's phenological stage as it influences its ability to protect the apical meristem from critical temperatures. With respect to forest fires, the timing of a fire can therefore be crucial for bud survival. This becomes especially important as spring is one of the main fire seasons in the European Alpine region

(Conedera et al., 2018; Müller et al., 2020). Bud-related data further complements our knowledge on the heat resistance of European tree species and provides useful information for managing areas of high fire risk and for modelling post-fire tree mortality.

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## CONFLICT OF INTEREST

The authors declare no potential conflict of interest.

## AUTHOR CONTRIBUTIONS

**Andreas Bär and Stefan Mayr:** Designed the research. **Andreas Bär and Dennis Marko Schröter:** Performed data collection and analyses. **Andreas Bär, Dennis Marko Schröter and Stefan Mayr:** Interpreted the data and prepared the manuscript.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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## SUPPORTING INFORMATION

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