


## RESEARCH PAPER

# Summer temperatures reach the thermal tolerance threshold of photosynthetic decline in temperate conifers

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Conifers; heat stress; physiological limitations; tree mortality; water stress.

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**ABSTRACT**

- Climate change-related environmental stress has been recognized as a driving force in accelerating forest mortality over the last decades in Central Europe. Here, we aim to elucidate the thermal sensitivity of three native conifer species, namely Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*) and silver fir (*Abies alba*), and three non-native species, namely Austrian pine (*Pinus nigra*), Douglas fir (*Pseudotsuga menziesii*) and Atlas cedar (*Cedrus atlantica*).
- Thermal sensitivity, defined here as a decline of the maximum quantum yield of photosystem II ( $F_v/F_m$ ) with increasing temperature, was measured under varying levels of heat stress and compared with the turgor loss point ( $\pi_{tlp}$ ) as a drought resistance trait. We calculated three different leaf thermotolerance traits: the temperature at the onset (5%) of the  $F_v/F_m$  decline (T5), the temperature at which  $F_v/F_m$  was half the maximum value (T50) and the temperature at which only 5%  $F_v/F_m$  remained (T95).
- T5 ranged from  $38.5 \pm 0.8$  °C to  $43.1 \pm 0.6$  °C across all species, while T50 values were at least 9 to 11 degrees above the maximum air temperatures on record for all species. Only Austrian pine had a notably higher T5 value than recorded maximum air temperatures. Species with higher T5 values were characterized by a less negative  $\pi_{tlp}$  compared to species with lower T5.
- The six species could be divided into ‘drought-tolerant heat-sensitive’ and ‘drought-sensitive heat-tolerant’ groups. Exposure to short-term high temperatures thus exhibits a considerable threat to conifer species in Central European forest production systems.

**INTRODUCTION**

Forest disturbance is a natural part of forest ecosystem dynamics (Seidl *et al.* 2017), but increasing climate-induced tree mortality has been observed in a wide range of forest ecosystems worldwide (Allen *et al.* 2010; Cobb *et al.* 2017). In European temperate forests, mortality of canopy trees has doubled over the last three decades (Senf *et al.* 2018) and has been primarily linked to climate-induced drought (Senf *et al.* 2020). Tree mortality results in changes to ecological communities, shifts in ecosystem functions with a reduction in ecosystem services, together with unexpected land–climate feedbacks (Anderegg *et al.* 2013). A mechanistic understanding of tree mortality is crucial to lessen economic and cultural harm (Allen *et al.* 2010) and sustain forest production systems. The predicted increases in frequency and intensity of temperature extremes (heatwaves) are unequivocally linked to climate change and occur independently of drought events (IPCC, 2019). However, heatwaves can cause drought stress due to high potential evapotranspiration in combination with little or no rainfall. The duration and intensity of heatwaves can seriously impact the physiological performance of trees (Billon *et al.* 2020), some of which are important timber trees.

Over centuries, Norway spruce and Scots pine have been the most important timber species for the forestry sector in Central

Europe. Large-scale wind disturbance and associated bark beetle outbreaks have been historically major disturbances in forest production systems consisting mainly of Norway spruce (Eriksson *et al.* 2007). However, the increasing frequency and longer duration of heatwaves has favoured bark beetle infestation and replaced windthrow as the main cause of mortality (Hentschel *et al.* 2014). Although Scots pine has been considered relatively drought-tolerant compared to *e.g.*, Norway spruce, an accelerated mortality of Scots pine has been observed in recent years. Besides Norway spruce and Scots pine, other species in Europe are expected to be impacted by the expected rise in drought and heatwaves in future climate change scenarios (irrespective of the actual cause of tree mortality) (Hartmann *et al.* 2018).

Several advantages of conifers over broadleaved tree species, *e.g.*, optimal mechanical wood properties, potentially faster growth rates, larger carbon sink per area and increased economic yield, means forest owners would, in the future, preferably plant a drought-adapted conifer species. Consequently, the native silver fir has in recent years been planted in increasing numbers across Central Europe, aiming to achieve higher drought resistance in forest stands (Muck *et al.* 2008). Likewise, the substitution of former Norway spruce and Scots pine forests by non-native drought-tolerant conifer species or the intermixing of these with native species became common practice

(Bolte *et al.* 2009). The three non-native species, Douglas fir, Austrian pine or Atlas cedar, have been considered as potentially suitable alternatives in forest production systems under a future climate (De Avila & Albrecht 2018). However, criticism arises on admixing non-native species due to their potentially invasive character and potential detrimental impact on forest ecosystems (Pötzelsberger *et al.* 2020). Also, it remains unknown how such species will perform under a changing climate.

The actual drivers and mechanisms causing tree mortality are still under debate and are most probably a result of complex interdependencies of mutually inclusive mechanics (Hajek *et al.* 2020). Most studies on tree mortality focus predominantly on drought stress as the initial trigger of tree mortality (e.g., Pretzsch *et al.* 2020), neglecting heat-induced changes in morphological, physiological and biochemical processes, although these do affect the overall performance, growth and ultimately the survival of plants (Song *et al.* 2014). However, there is growing evidence that heat-induced tree mortality can cause abrupt changes in forest biomass stocks (Chaste *et al.* 2019; Breshears *et al.* 2021), which suggests a limited ability of trees to locally acclimate to higher temperatures (Konôpková *et al.* 2018). Drought-induced effects on forest performance could potentially be mitigated by the application of silvicultural practices, such as stand density reduction (Sohn *et al.* 2013), which in turn reduces the canopy cover, negatively affecting the forest understorey during warm periods (von Arx *et al.* 2012). Thus, short-term management options to increase forest resistance to heat events are even more limited than forest management options to increase forest drought resistance (Burschel & Huss 2003). Therefore, a better understanding of temperature thresholds that trigger forest decline and mortality is necessary for choosing suitable species for future forest production systems.

Photosystem II (PSII) is a pigment–protein complex located in the thylakoid membranes of the chloroplasts and is considered the most heat-sensitive component of photosynthesis (Ashraf & Harris 2013), with temperatures above a critical value leading to irreversible damage to the photochemistry (Tiwari *et al.* 2021; Slot *et al.* 2021). One approach to quantify thermotolerance is to analyse the effect of extreme temperatures on the photochemistry of the leaves. A quantitative measure of the photochemical efficiency of PSII is the ratio between variable and maximum chlorophyll fluorescence ( $F_v/F_m$ ), which is a good indicator of drought and heat stress (Yu & Guy 2004). The temperature at which the quantum efficiency declines by 50% (T50) has been used as a proxy for the critical temperature at which irreversible damage to the photochemistry occurs (Krause *et al.* 2010; Tiwari *et al.* 2021). Data on T50 values are predominantly available from subtropical and tropical regions (Sastry *et al.* 2017; Leon-Garcia & Lasso 2019; Perez & Feeley 2020), where trees have adapted to elevated temperatures. However, tree species from mid-latitudes are expected to have a very narrow thermal tolerance range and thus may be more susceptible to heatwaves (O’Sullivan *et al.* 2017).

In this study, we used the aforementioned temperature-induced changes in  $F_v/F_m$  to assess thermal tolerance for three conifer species native to Central Europe and three that are potentially or increasingly being planted for future forest production systems. We aimed to address the following questions:

(i) will current summer temperatures exceed the thermal thresholds of conifer species, and (ii) how will their thermal tolerance be related to hydraulic leaf properties, namely turgor loss point? The overall goal was to provide a first assessment on thermo-tolerance of the economically most important conifer species and their suitability in forest production systems under a changing climate—in particular under the threat of the increasing frequency of heatwaves in Central Europe.

## MATERIAL AND METHODS

Material from native and non-native conifers was collected in the surroundings of Sickersdorf, in the rural district of Fürth in Middle Franconia, Germany (49°24′04.4″ N 10°56′01.3″ E). The district is characterized by very patchy forest distribution, with approximately 30% of the area stocked with forest. Scots pine (*Pinus sylvestris* L.) has been the main species cultivated in the area, followed by Norway spruce (*Picea abies* Karst.) and European oak (*Quercus robur* L.). A few autochthonous silver fir (*Abies alba* L.) are scattered sparsely throughout those forests. The region has been affected by high tree mortality in recent years. The mortality increased after two very dry summers combined with heatwaves in 2015 and 2016, and accelerated during the following dry and very hot conditions in 2019 and 2020. The non-native conifer species selected for this study, *i.e.*, Atlas cedar (*Cedrus atlantica* ‘Glauc group’ (Endl.) G. Manetti ex Carrière) and Douglas fir (*Pseudotsuga menziesii* (Mirbel) Franco), are commonly grown in urban areas in the district and the botanical material was collected in the adjacent township. Austrian pine (*Pinus nigra sensu lato* J.F. Arnold) was collected from a forest stand on a former military training ground planted by the US military in the 1970s (49°25′16.6″ N, 10°59′47.9″ E). For each species, one sun-exposed branch was sampled from five individuals in early spring 2021. In the forests, we targeted dominant canopy trees, and a minimum diameter at breast height (DBH) of 25 cm. Per individual, needles from 1-year-old shoots were collected. Needles were dark-acclimated for 30 min and tested for initial maximum photosynthetic efficiency ( $F_v/F_m$ ) to ensure leaf health ( $F_v/F_m$  between 0.83 and 0.75) with a chlorophyll fluorometer (MINI-PAM; Walz, Effeltrich, Germany). Thermal dependence of  $F_v/F_m$  was assessed following the protocol of Krause *et al.* (2010). Therefore, needles were placed in Microcloth, separated by cloth layers to prevent anoxic conditions, and transferred into watertight Whirlpack bags. The bags were bathed under water in a precision cooker at varying temperatures for 15 min. The exact temperature was monitored with a digital thermometer (TFA; Dostmann, Wertheim, Germany). The mean temperature during the vegetation period in the region is 15° C (DWD 2021), hence we used 15° C as starting temperature. Temperature treatments covered the range between 15° C and 59° C. We started with 5-degree steps between treatments and lower steps of 2 degrees within the critical temperature range, starting at 30° C. Per individual, about eight needles were selected and each needle was randomly assigned to a temperature treatment. Overall, 40 needles were used to establish one curve. Heat-treated needles were incubated under controlled conditions (15° C, ~20  $\mu\text{mol m}^{-2} \text{s}^{-1}$  light) in Petri dishes containing a thin film of water (Tiwari *et al.* 2021). The next day, the recovery of  $F_v/F_m$  was measured after a 30-min dark adaptation period. We used the data on turgor loss point collected by Kunert

& Tomsakova (2020) to compare the thermal tolerance traits with hydraulic properties. Thermal and hydraulic traits were sampled on the same tree individuals. We used air temperature data available on the data platform of the Deutscher Wetterdienst (station number 3668; DWD, 2021) to compare the increase in frequency of hot days.

After correcting for a typographical error, we used the same log-logistic curve for the  $F_v/F_m$  response as described by Tiwari *et al.* (2021):

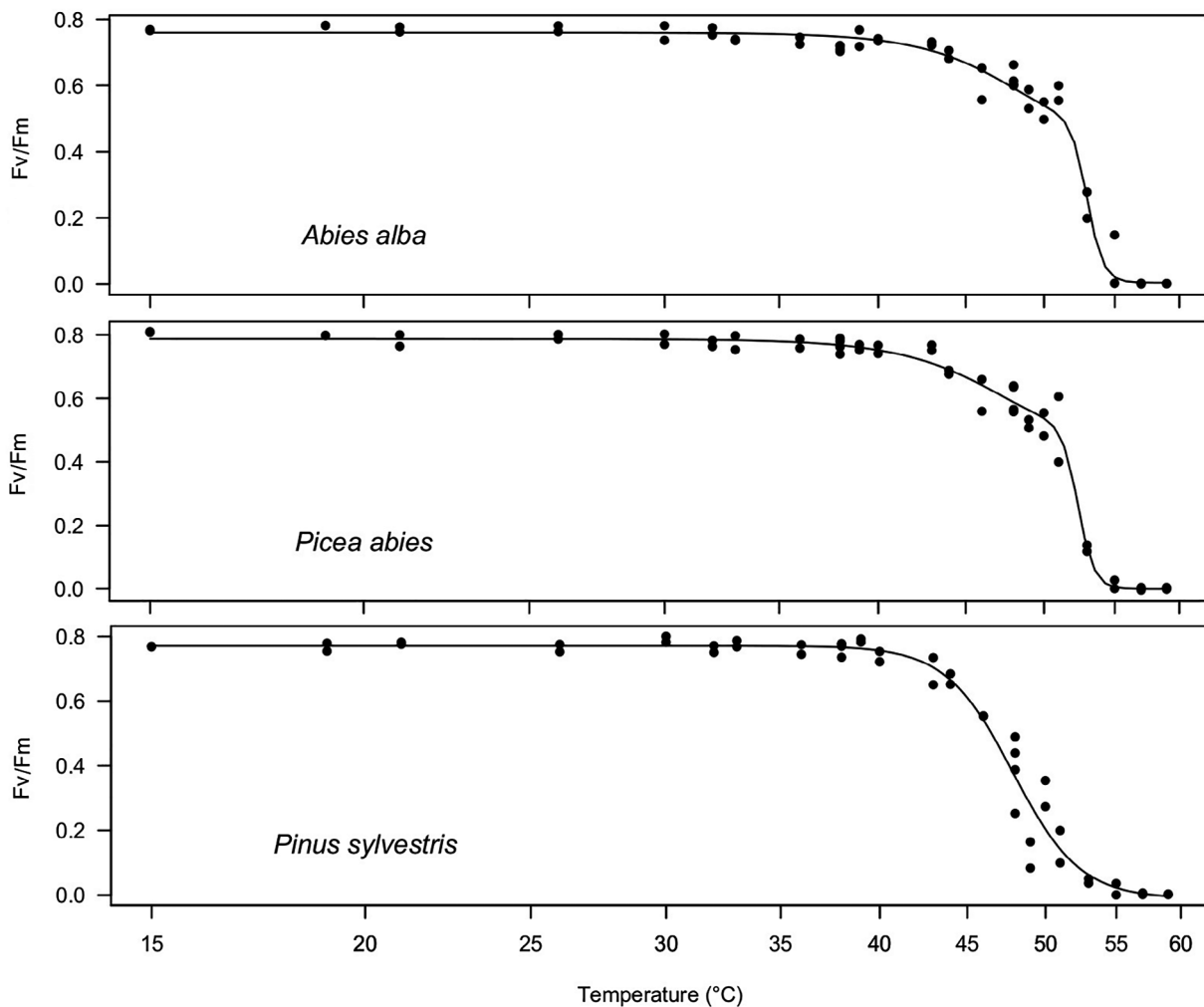
$$F_v/F_m = c + \frac{d - c}{1 + \text{Exp}[b \text{Log}[T/T50]]} \quad (1)$$

where  $T$  represents the temperature,  $c$  is the  $F_v/F_m$  of the lower plateau,  $d$  is the higher plateau,  $T50$  is the temperature at which  $F_v/F_m$  reached 50% of the total decrease,  $b$  is the slope of the curve at  $T = T50$ . Because our initial results showed clearly asymmetric curves for some species, we also used an extension of Equation (1) proposed by Ricketts & Head (1999) allowing for a difference in curvature before and after  $T = T50$ :

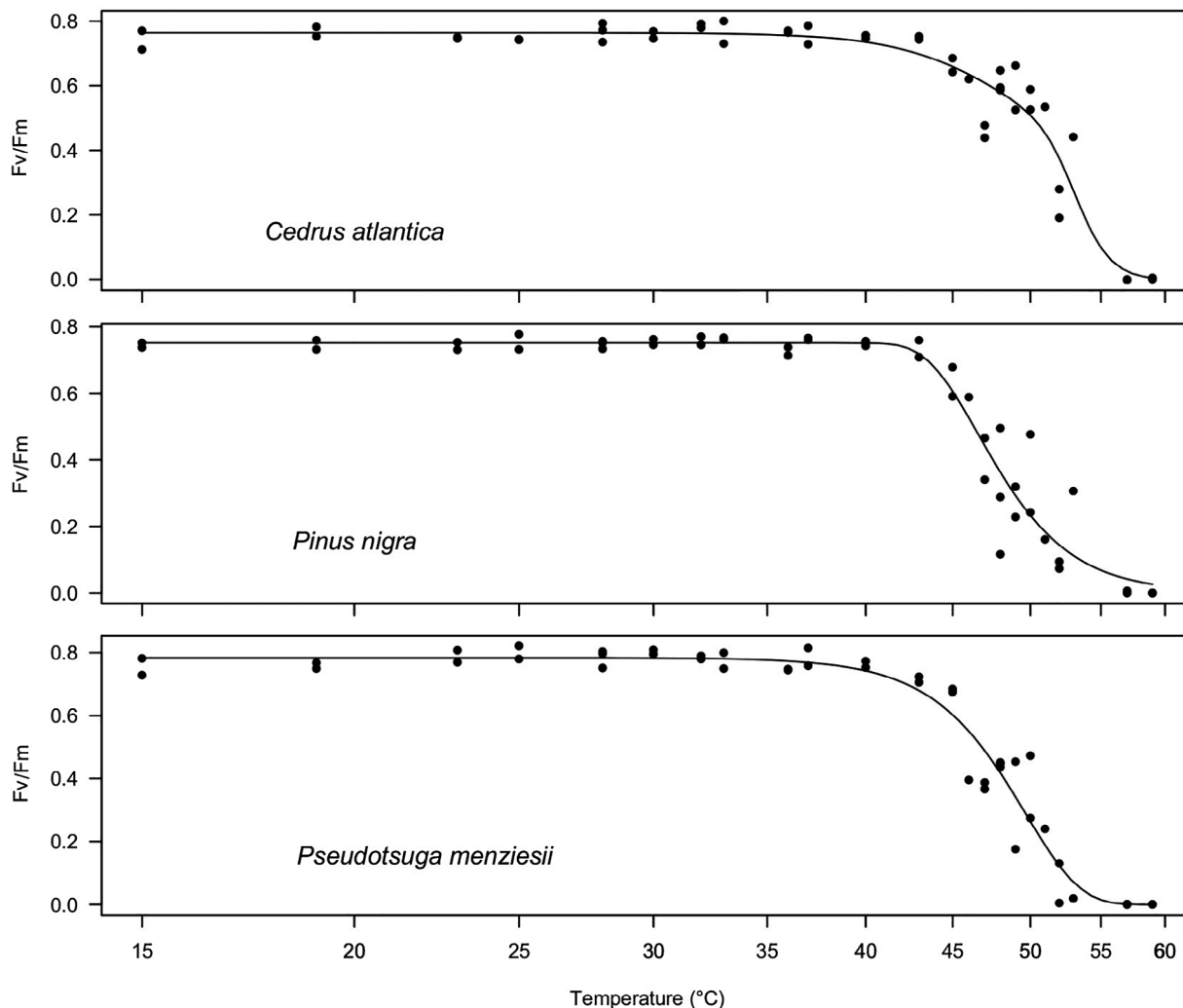
$$F_v/F_m = c + \frac{d - c}{1 + f \text{Exp}[b_1 \text{Log}[T/T50]] + (1 - f) \text{Exp}[b_2 \text{Log}[T/T50]]}$$

$$\text{with } f = (1 + \text{Exp}[\frac{b_1 b_2}{b_1 + b_2} \text{Log}[T/T50]])^{-1} \quad (2)$$

where  $b_1$  and  $b_2$  now represent a possibly different curvature before and after  $T50$ . Both response curves were fitted using the 'modelFit' function of the 'drc' package using the LL.4 (Equation (1)) and baro5 (Equation (2)) methods (Ritz *et al.* 2016) in R. Akaike's information criterion was used to decide between Equation (1) and Equation (2). Half of the species' thermal  $F_v/F_m$  decline could be described by the four-parameter logistic curve (Equation (1); Scots pine, Austrian pine and Douglas fir), whereas the best fitting model for the other half was a five-parameter asymmetric logistic (Equation (2)) function (silver fir, Norway spruce and Atlas cedar) (see Figs 1 and 2). Five different measures were extracted from the fitted curves to compare different species. The first three measures ( $T5$ ,  $T50$ ,  $T95$ ) correspond to temperatures at which the



**Fig. 1.** Temperature response of PSII efficiency ( $F_v/F_m$ ) to 15-min duration heat treatment of needles of three native conifer species. Top panel: Silver fir (*Abies alba*); middle panel: Norway spruce (*Picea abies*); bottom panel: Scots pine (*Pinus sylvestris*). Five individuals per species were measured to establish the thermal vulnerability curve.



**Fig. 2.** Temperature response of PSII efficiency ( $F_v/F_m$ ) to 15-min duration heat treatment of needles of the three exotic conifer species. Top panel: Atlas cedar (*Cedrus atlantica*); middle panel: Austrian pine (*Pinus nigra*); bottom panel Douglas fir (*Pseudotsuga menziesii*). Five individuals per species were measured to establish the thermal vulnerability curve.

change in  $F_v/F_m$  is 5, 50 or 95% of the maximum change ( $c-d$ ). We fitted a simpler model to species pairs to compare the deviated from the species-specific dose–response curves with an approximate F-test (Ritz *et al.* 2016). In cases where the null hypothesis was rejected, the ‘compParm’ function was used to identify species differences in T5, T50 and T95. Analogous to Tiwari *et al.* (2021), we also defined two decline widths for the temperature difference between different  $F_v/F_m$  levels: before the turning point (T50): T50–T5, and after the turning point: T95–T50. These decline widths are inversely related to the slope parameters  $b$ ,  $b_1$  and  $b_2$ , with smaller values indicating more rapid changes in  $F_v/F_m$ . All presented means are  $\pm$  SE. Data analysis was performed using the R program, version 4.0.4 (R Core Team, 2021).

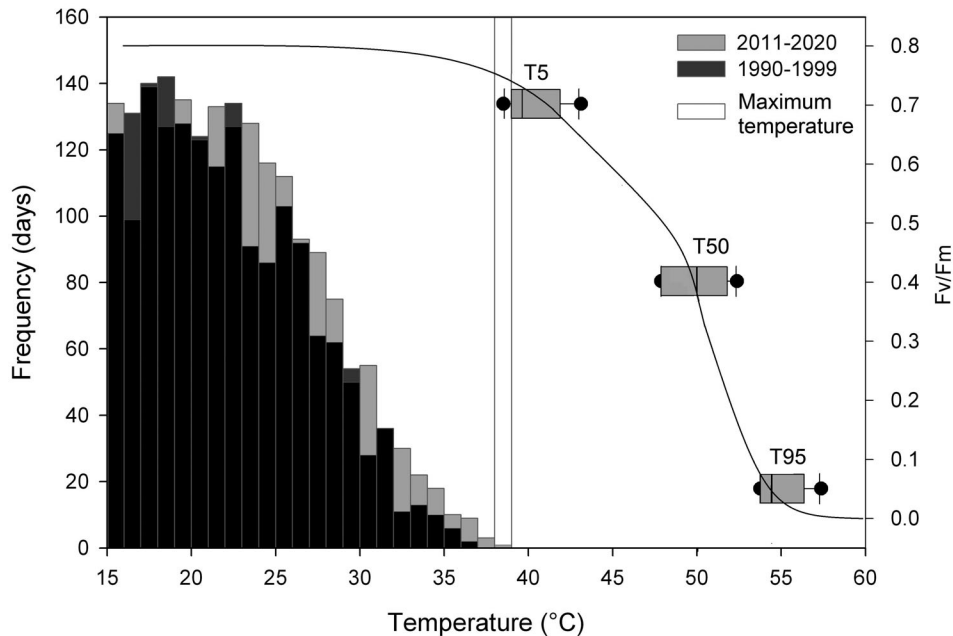
## RESULTS

The T5 was on average at  $40.3 \pm 0.7$  °C across all six conifer species. Austrian pine had the highest T5 ( $43.1 \pm 0.6$  °C) and Norway spruce the lowest T5 ( $38.5 \pm 0.8$  °C). T5 of Norway

spruce was reached by the maximum air temperature recorded in the area (Fig. 3). T50 was on average  $50.0 \pm 0.9$  °C, and silver fir had the highest T50 ( $52.3 \pm 0.2$  °C) of all species, followed by Atlas cedar ( $51.8 \pm 0.4$  °C). The two pine species had both very low T50 values of  $47.8 \pm 0.3$  °C. T95 averaged  $55.2 \pm 0.6$  °C across all species and was highest in Austrian pine ( $57.5 \pm 1.4$  °C) and lowest in Norway spruce and Douglas fir (both  $53.9$  °C; for  $\pm$ SE, see Table 1).

The T5 and decline width (T95–T5) were not significantly related ( $r^2 = 0.385$ ,  $P = 0.188$ ; Fig. 4a). However, T5 correlated significantly with the decline width before the turning point (T50–T5) and after the turning point (T95–T50) (see Fig. 4b and c). Species with lower T5 were characterized by a wider decline width from T50–T5. Species—namely the two pine species—characterized by a high breakpoint temperature show sudden and steeper  $F_v/F_m$  decline over a narrow decline width.

The T5 values of the six species correlated significantly with the turgor loss point ( $\pi_{tp}$ ; Fig. 5a). Species with a higher T5 were characterized by a less negative  $\pi_{tp}$ , and species with a



**Fig. 3.** Thermal tolerance of conifer needles for six species represented by a boxplot diagram (note: boxplot y-ordinate positioning indicative and not absolute, the logistic curve indicates combined fit for all six species). Thermal tolerance was measured as  $F_v/F_m$  temperature response to 15-min duration heat treatment. The histogram highlights the warming trend in daily maximum air temperature relative to the two 10-year periods between 1990–1999 and 2011–2020. Black bars are difference in frequency between the two periods. Maximum temperature represents the temperature record observed in the region as recorded in 2020.

lower T5 by a more negative  $\pi_{tlp}$ . There was no significant relationship between T50 and  $\pi_{tlp}$ , nor T95 and  $\pi_{tlp}$  (Fig. 5b and c).

## DISCUSSION

We report the first temperature-dependent  $F_v/F_m$  measurements made on foliage of mature conifers from a temperate region. The most important finding is that the breakpoint temperature T5, the temperature when  $F_v/F_m$  starts to decline, lies on average at  $40.3 \pm 0.7$  °C. For all six species, T5 is similar or marginally above the maximum summer air temperature recorded in the study area, and T50 values that were at least 9 to 11 degrees above the maximum summer air temperatures on record. Further, T5 correlates with leaf turgor loss point, indicating two diverging mechanistic strategies of species to deal with heat and drought stress. Species are classified as either ‘drought-tolerant heat-sensitive’ or ‘drought-sensitive heat-tolerant’.

### Summer temperatures reach thermal threshold of photosynthetic decline

We found clear evidence that summer temperatures measured during heatwaves exceed the thermal threshold, when the functioning of PSII of the investigated conifer species is significantly affected. The most sensitive species was Norway spruce, in which the maximum temperature measured during a heatwave in 2021 in the region (38.5 °C; see Fig. 2) will already result in initial PSII damage (T5 =  $38.5 \pm 0.8$  °C). Ideally, the thermal tolerance thresholds should be related to leaf rather than air temperature; however, during heatwaves, limited access to soil

water commonly results in stomatal closure. Stomatal closure, in turn, results in a rise of leaf temperatures to a level that even exceeds the ambient air temperature (Krause *et al.* 2010). In the course of a heatwave, trees in full sunlight are exposed to critical temperatures and high light intensities that can significantly change physiological and biochemical processes (Tiwari *et al.* 2021). The latter changes would likely affect the overall performance, growth and, ultimately, the survival of Norway spruce. Hence, thermal stress may contribute to the accelerated mortality of Norway spruce. We expect two possible consequences when the thermal threshold is surpassed, which might have a direct lethal outcome or induce long-term physiological disorders in Norway spruce. First, thermal stress often triggers leaf senescence (Way, 2013). In the case of severe damage to the foliage, the canopy will be defoliated, leading to irreversible loss of carbon reserves as this species is unable to resprout new leaves within the same season (Galiano *et al.* 2011). Second, less severe damage to PSII can reduce electron transport rates that may decrease photosynthesis. A reduction in photosynthesis rate may weaken the defence mechanisms of Norway spruce and increase its susceptibility to bark beetle attacks (Huang *et al.* 2020) in the subsequent vegetation period.

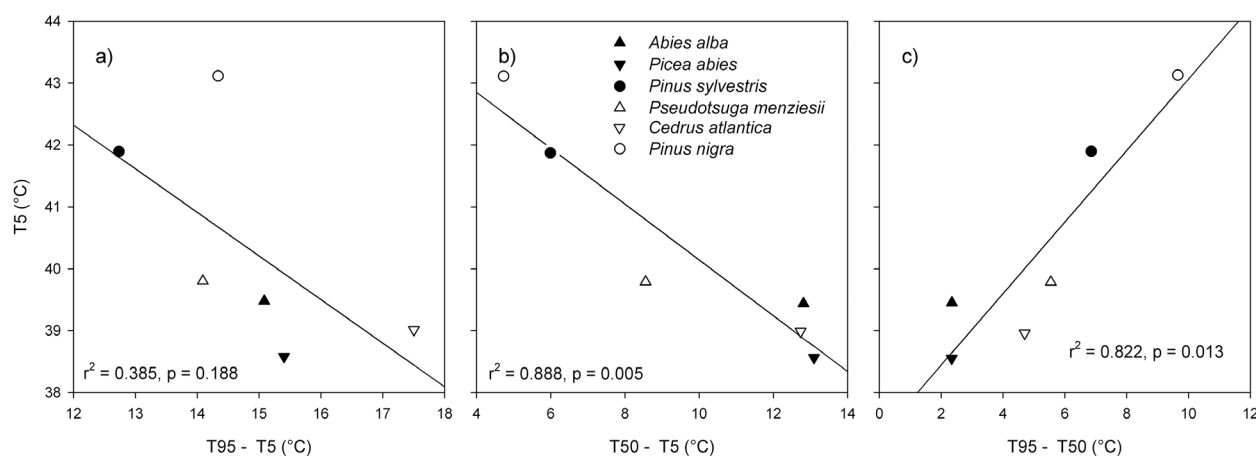
Air temperatures above 40 °C have been observed on a regular basis at different climate stations throughout Central Europe in the last few years (*e.g.*, Herold & Schappert, 2019). Only Scots pine and Austrian pine had a substantially higher T5 ( $41.9 \pm 0.7$  °C and  $43.2 \pm 0.6$  °C, respectively), whereas T5 values of silver fir, Douglas fir and Atlas cedar were only marginally above the recorded temperatures. Temperature extremes, in particular more frequent and hotter heatwaves, have significantly increased on a regional and global scale over the last few decades (Perkins-Kirkpatrick & Lewis 2020).

**Table 1.** Summary of the measured thermal tolerance for the six European conifer species.

Common name	Latin name	Native/introduced	T5 °C ± SE	T50 °C ± SE	T95 °C ± SE
Silver fir	<i>Abies alba</i>	Native	39.5 ± 1.0 <sup>a</sup>	52.3 ± 0.2 <sup>a</sup>	54.6 ± 0.7 <sup>a</sup>
Norway spruce	<i>Picea abies</i>	Native	38.5 ± 0.8 <sup>a</sup>	51.6 ± 0.2 <sup>a</sup>	53.9 ± 0.2 <sup>a</sup>
Scots pine	<i>Pinus sylvestris</i>	Native	41.9 ± 0.7 <sup>b</sup>	47.8 ± 0.3 <sup>b</sup>	54.6 ± 1.0 <sup>b</sup>
Douglas fir	<i>Pseudotsuga menziesii</i>	Non-native	39.8 ± 1.0 <sup>a</sup>	48.3 ± 0.3 <sup>a</sup>	53.9 ± 0.6 <sup>a</sup>
Austrian pine	<i>Pinus nigra</i>	Non-native*	43.1 ± 0.6 <sup>b</sup>	47.8 ± 0.3 <sup>b</sup>	57.5 ± 1.4 <sup>b</sup>
Atlas cedar	<i>Cedrus atlantica</i>	Non-native	39.0 ± 1.6 <sup>a</sup>	51.8 ± 0.4 <sup>a</sup>	56.5 ± 1.2 <sup>a</sup>
Mean			40.3 ± 0.7	50.0 ± 0.9	55.2 ± 0.6

Breaking point temperature at which PSII efficiency declines 5% (T5), temperature at which efficiency is at 50% (T50) of the maximum, and temperature at which only 5% of the maximum efficiency remains (T95). Superscript letters indicate significant differences between species (z-test).

\*Austrian pine is native to Central Europe, but does not naturally occur in the study area.



**Fig. 4.** Relationships between PSII maximum quantum yield ( $F_v/F_m$ ) breakpoint temperature, T5, and decline width. The temperature windows are shown when  $F_v/F_m$  declines from (a) 95% to 5% of the maximum  $F_v/F_m$  level (T95–T5), (b) the  $F_v/F_m$  decline from 5% to 50% of the maximum  $F_v/F_m$  level, and (c)  $F_v/F_m$  declines from 50% to 95% of the maximum  $F_v/F_m$  level.

Increasing temperature extremes have also been observed in our study area (Fig. 3). The latter trend is predicted to intensify in the near future, with forests likely to experience increasing levels of thermal stress resulting in tree mortality events, potentially amplifying positive climate–carbon cycle feedbacks.

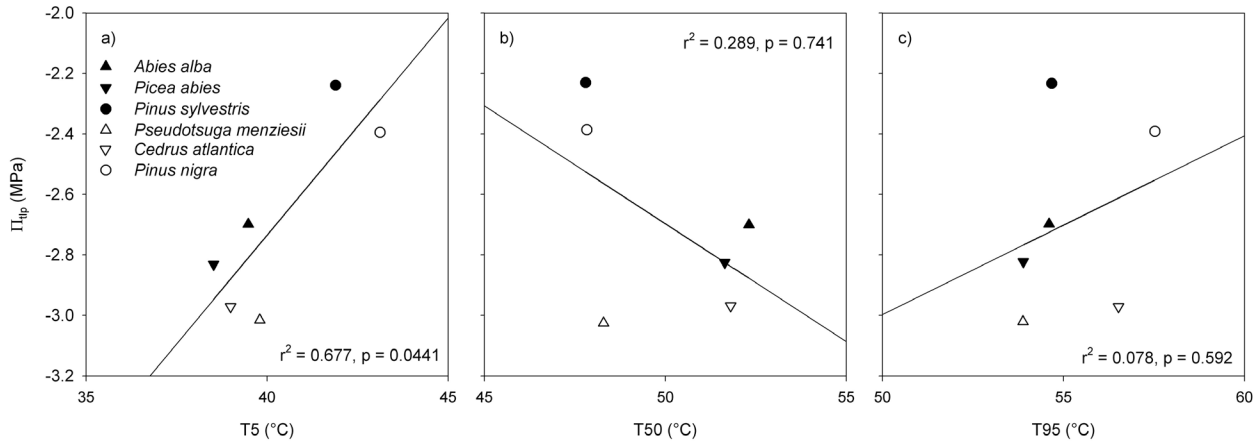
#### Heat tolerant or sensitive

Tiwari *et al.* (2021) describe a continuous spectrum of strategies found in six tropical broadleaved tree species. Our results suggest that the investigated six temperate conifer species can be classified as either ‘heat-sensitive’ or ‘heat-tolerant’: Douglas fir, silver fir, Norway spruce and Atlas cedar represent the heat-sensitive species, characterized by an early decline in  $F_v/F_m$  and wide decline width in particular between T5 and T50.  $F_v/F_m$  in these mentioned four species declined rapidly after T50 (narrow decline width from T50 to T95). Both pine species, namely Scots pine and Austrian pine, can be classified as heat-tolerant species, with a higher T5 and a narrow decline width between T5 and T50. The decline width of the pines between T50 and T95 was wider than in the other conifers, indicating a broader tolerance to high temperatures. Differences among species in their tolerance to high temperatures supports the Tiwari *et al.*

(2021) hypothesis of classifying species into ‘heat-sensitive’ and ‘heat-tolerant’; however, the total decline width between T5 and T95 was found to be a rather weak indicator of thermal sensitivity ( $r^2 = 0.385$ ,  $P = 0.188$ ), whereas the decline widths T50–T5 ( $r^2 = 0.888$ ,  $P = 0.005$ ) and T95–T50 ( $r^2 = 0.822$ ,  $P = 0.013$ ) were good predictors of heat tolerance strategies in the investigated conifers.

#### Trade-off between hydraulic and thermal vulnerability in leaves?

Heat sensitivity is intrinsically linked to drought avoidance; plants can either cool through transpiration, thus risking drought stress, or speedily close the stomata to avoid drought stress while risking heat damage (Konôpková *et al.* 2018). In our case, the first group comprising the two pine species has a less negative turgor loss point (–2.24 MPa and –2.39 MPa; Scots pine and Austrian pine, respectively) than the other four species (all between –2.70 MPa and –3.02 MPa; see Kunert & Tomsakova 2020). The second group might keep stomata open for longer durations under more water-limiting conditions while pines trigger early stomatal closure in response to a water deficit. Turgor loss point is a ‘robust proxy of a species’ degree



**Fig. 5.** Relationship between thermal tolerance (T5, T50 and T95) and leaf turgor loss point ( $\pi_{tip}$ ).  $\pi_{tip}$  data from Kunert & Tomaskova (2020), except *Cedrus atlantica* (Kunert, unpublished data).

of anisohydry (Meinzer *et al.* 2017) and, accordingly, the two pine species could be classified as being more drought-sensitive than the other four conifer species, which are classified as drought-tolerant. The drought-tolerant species may follow another strategy by using transpirational cooling of the leaf to avoid or reduce heat stress instead of adopting a more heat-tolerant photochemistry, as found in drought-sensitive species. In our study, the conifer species with high drought tolerance tend to be more heat sensitive (*i.e.*, have a lower breaking point temperature), but might compensate for this through maintaining transpirational cooling under drought and/or heat stress. The latter strategy could be described as ‘drought-tolerant heat-sensitive’ while, conversely, ‘drought-sensitive heat-tolerant’ species (*e.g.*, Scots pine, Austrian pine, etc.) are more sensitive to a water deficit but can tolerate high temperatures. The latter confirms the findings of Kunert (2020) that pine mortality is triggered predominantly by a complex of interdependencies related to drought stress. Further, spruce mortality is more likely the result of heat stress. However, the

results also show that tree species can follow different strategies to occupy the same ecological niche.

## CONCLUSIONS

We found considerable variation in the thermal tolerance of the investigated temperate conifer species. During heatwaves, all six species were already operating very close to their thermal tolerance threshold. Species follow different strategies and either adapt their photochemistry to function under higher temperatures or adapt their osmotic potential to enable more transpirational cooling. Further research is required to understand how the interaction between heat stress and water limitation is affecting forest ecosystems. In the meantime, we suggest that the temperature of incipient PSII damage (T5) could be used to parameterize forest ecosystem models, enabling us to predict the effects of a future climate with increasing heatwave frequency and intensity.

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