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Picea pungens exhibits greatest tolerance to short-time thermal stress compared to *Picea abies*, and *Picea omorika*

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Abstract

Species in the genus *Picea* are well-suited for afforestation on high altitudes and latitudes, but are fairly intolerant to high temperatures. In this study, *Picea pungens, Picea abies*, and *Picea omorika* were subjected to 45 °C, 40 °C, 35 °C, and ambient temperature (CK) for 6 h, and then allowed to recover for 28 d. Changes in phenotype, relative water content (RWC), and maximal photochemical efficiency (Fv/Fm) of photosystem II (PS II) were observed to ascertain their thermal tolerance. Overall, all three species were negatively affected by exposure to 45 °C, but *P. pungens* exhibited full recovery, with the highest RWC, while *P. omorika* exhibited partial recovery, and *P. abies* showed minimal recovery. The PS II of all three species were damaged after 45 °C treatment, but that of *P. pungens* exhibited the most dramatic recovery, with Fv/Fm recovering from 0 to 0.26. In conclusion, *P. pungens* was found to exhibit the greatest thermal tolerance, followed by *P. omorika* and *P. abies*. Thus, thermal tolerance should be considered as a tool for species selection for future reforestation endeavor in the face of climate change that is expected to bring high summer temperature events.

Keywords *Picea pungens* \cdot *Picea abies* \cdot *Picea omorika* \cdot Heat resistance \cdot Needle water content \cdot Fv/Fm \cdot Maximal photochemical efficiency

Introduction

Spruce (*Picea* spp.) trees are widely distributed in boreal and temperate habitats worldwide and are important timber species in much of their range. Additionally, spruce trees have high ornamental value and make excellent landscape trees. They are highly suitable for planting in high altitudes and latitudes, and are generally intolerant to high temperatures and dry heat (Way and Sage 2008; Allen et al. 2010; Zhang et al. 2015; Ivetić and Aleksić 2019; Kunert 2020; Matkala et al. 2021; Kunert et al. 2022). According to the sixth assessment report of the United Nations Intergovernmental Panel on Climate Change (UNIPCC), global surface temperatures are on track to increase by 2.7 °C by the end of the century, potentially leading to substantial negative impacts on the world's ecosystems (https://www.ipcc.

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ch/assessment-report/ar6). Climate change (www.epa.gov/climate-research) is expected to negatively affect the environmental suitability and productivity of spruce trees (Tjoelker et al. 2007). This continued warming, coupled with reduced precipitation, may be unsuitable for growth of spruce trees (Altman et al. 2017; Chen et al. 2017; Kolář et al. 2017; Šijačić-Nikolić et al. 2019).

Long-term heat stress negatively affects the growth of *Picea* seedlings, whose approximated biomass increment decreased under high temperature stress (35 °C), associated with decreased photosynthesis and increased respiration (Zhang et al. 2015). Needle damage of *Picea glauca* increased with increasing temperatures from 40 to 50 °C. Superior families showed significantly higher needle damage (58%) than inferior families (40%) (Bigras 2000). Direct and indirect damage to needles increased exponentially with the duration of exposure to high temperatures for *P. mariana*, and 46°C was the lowest temperature at which direct damage was detected (Colombo and Timmer 1992). The tree-ring records show that radial growth of *P. glauca* has decreased with increasing temperature (Barber et al. 2000). The mortality of *P. abies* in Central Europe might be caused by rising temperatures and that the summer temperatures in the past years (at least three consecutive days with a maximum daily air temperature of >30 °C) were beyond the species thermal tolerance threshold (Kunert 2020).

In plants, one of the most temperature-sensitive physiological processes is photosynthesis (Mathur et al. 2014), which is often inhibited before other cell functions are impaired (Berry and Björkman 1980). This sensitivity is primarily manifested in the photosystem II (PSII), ATP regeneration, and carbon assimilation aspects of the oxygen-evolving complex (OEC). Of these, PSII is the most sensitive to thermal stress (Murata et al. 2007; Húdoková et al. 2022). High temperatures can destroy the structure of the thylakoid membrane, lightcatching antenna system, donor-side oxygen-evolving complex, and reaction center, and negatively affect receptor-side electron transport of PSII (Tang et al. 2012; Húdoková et al. 2022). The maximal PSII photochemical efficiency (Fv/Fm) ratio measures the light energy conversion efficiency of PSII, and can be inactive of photoinhibition (Maxwell and Johnson 2000). Specifically, the Fv/Fm ratio determines the maximum quantum efficiency of PSII, reflecting the linear electron transfer rate and overall photosynthetic capability.

In heat-stressed spruce seedlings, the maximal fluorescence (Fm), variable fluorescence (Fv), and Fv/Fm decreased while initial fluorescence (Fo) increased (Bigras 2000). These chlorophyll fluorescence parameters indicated that *P. glauca* seedlings subjected to a heat treatment of 42–43 °C lost the ability to phosphorylate and donate water to PSII (Bigras 2000). Fv/Fm values of *P. abies* exposed to 48 °C were significantly lower than those at the control (25 °C) from May until September (Petrik et al. 2023). However, Fv/Fm did not change significantly under the short-term heat shock of 44 °C, while it was reduced to 63.2% of the control group under 52 °C, and PSII function was inhibited at this moment (Jia et al. 2020). Temperatures between 32 and 36 °C markedly decreased both net photosynthesis and stomatal conductance of *P. rubens* (Day 2000). These impacts of exposure to high temperature on physiological processes reflect on growth and development of plant species. Severe damage can significantly weaken growth of forest trees and lead to accelerated forest tree mortality (Tabbush 1986). Thus, the regeneration of species sensitive to high temperature stress will be poor, thereby affecting the reforestation efforts.

Under high temperature stress, plants are not passive, but can undergo changes in metabolic and physiological processes in order to survive the stress period. It appears that different spruce species had different heat tolerance thresholds for direct damage (Yang 2017; Zhang et al. 2015, 2017). Thus, further understanding of the mechanisms by which the light-capturing system responds and adapts to high temperature stress in less studied spruce species is imperative to choose species suitable for planting under the face of global climate change. In a previous study, we found that European *P. abies* and *P. omorika* and North American *P. pungens* exhibited superior performance in Gansu province of China than the Chinese native *P. crassifolia* (Ouyang et al. 2021). In this study, we formally tested the thermal tolerance and recovery of *P. abies, P. omorika*, and *P. pungens*. Specifically, we examined changes in photosystem II (PSII) chlorophyll fluorescence parameters, needle water content, and phenotype in response to high temperature stress.

Materials and methods

Plant material and experimental design

The seeds of *P. abies* were collected from Tianshui, Gansu, China, which was introduced from Germany in 1983 and has already flowered and borne fruit. The seeds of *P. pungens* were collected from Arizona, Kaibab National Forest, United States and the seeds of *P. omorika* were collected from Rye Nørskov, Denmark, which were both purchased from Beijing Linda Ecological Environment Engineering Co., Ltd. The seeds were used to grow seedlings at the Forestry Science Research Institute of Xiaolongshan Forestry Experimental Bureau in Gansu Province. The seedlings were grown in pots (12 cm x 18 cm), filled with pastoral soil (60%), peat (30%) and slag (10%).

A random sample of four five-year old seedlings of each species were taken and transplanted into planting boxes (diameter: 22 cm, height: 22 cm) filled with humus soil and perlite with 7:3 volume ratio and put in a climate-controlled chamber (HS-408) in Beijing Botanical Garden. The seedlings were grown under the following cultural conditions in the climate chamber: a temperature of 25 °C, relative humidity of 70% and photoperiod of 12 h day and 12 h night. Furthermore, the seedlings were watered every three days and fertilizer was added every two months. After two years of growth under these conditions, the seedlings on the timing of bud set (September) were exposed to high temperatures (35 °C, 40 °C, and 45 °C) and room temperature (25 °C) for 6 h, and physiological parameters were measured both immediately after treatment (0 d) and after a recovery period of 28 d when the seedlings were grown under the above growth conditions. The experimental temperatures were set to 35, 40 and 45°C based on previous work on temperature sensitivity of temperate conifer species (Kunert et al. 2022). The time limit was set based on the natural conditions in the study area, where the high temperature stays for at least six hours per day while a recovery period of one month was chosen to give enough time for seedlings to return to normal status. Each experiment consisted of four biological replicates, one of which was fixed for photography.

Measurement of relative water content of needles

The one-year-old needle samples (0.1 g) were collected from the middle section of the annual (one-year-old) branches of each seedling directly after different temperature treat-

ments and after 28 d of recovery and their fresh weights were determined. Thereafter, the samples were oven-dried at 75 °C until constant mass and their dry weight recorded. The relative water content was calculated according to the following equation:

$$RWC\left(\%\right) = \left(\frac{FW - DW}{FW}\right) \times 100$$

where RWC, FW and DW were relative water content, fresh weight and dry weight, respectively. Each experiment consisted of three biological replicates.

Measurement of fluorescence parameters

Fluorescence parameters were measured immediately after different temperature treatments and after 28 d of recovery. A Plant Efficiency Analyser (PEA, Hansatech, UK) was used to measure the chlorophyll fluorescence parameters, and compute the PSII maximum light energy conversion efficiency (Fv/Fm, Strasser et al. 2004) as follows:

 $\frac{F_v}{F_m} = \frac{(F_m - F_0)}{F_m}$, where F_0 is the minimal fluorescence and F_m is the maximal fluorescence. For measuring chlorophyll fluorescence parameters, five or six mature leaves per replicate were selected per seedling and fixed with tape, and the parameters were determined using 15 min dark-adapted needles. Each experiment consisted of three biological replicates.

Data analysis

The data were collated and analyzed with a General Linear Model (GLM) ANOVA, with species, temperature, and interaction as fixed effects and 'e' as a vector of random residual errors. The model used to analyze the relative water content and Fv/Fm was

$$y_{ijk} = \mu + S_i + T_j + ST_{ij} + e_{ijk}$$

where y_{ijk} is the observed value of species *i* in temperature *j*; μ is the mean value of the species; S_i is the fixed effect of species, i=1, 2, 3; T_j is the fixed effect of temperature, j=1, 2, 3, 4; ST_{ij} is the fixed effect of the interaction of species *i* and temperature *j*; and e_{ijk} is the random error. Multiple comparisons of significant means were performed by the Duncan method (alpha=0.05 level). All statistical analyses were performed using SAS 9.4 (SAS Institute, NC, USA).

Results

Phenotypic responses to thermal stress in three spruce species

There was a clear phenotypic variation in needles of three species treated at 45 °C (Fig. 1), although no significant phenotypic changes occurred in response to either the 40 °C or 35 °C treatments. After being subjected to 45 °C for 6 h, *P. pungens* exhibited slightly parched and chlorotic needles on the upper one-year-old branches, *P. abies* significantly dehydrated and displayed chlorotic needles on the upper one-year-old branches, and *P. omorika* became



Fig. 1 Changes in needle phenotype of *P. pungens, P abies* and *P. omorika* one day after exposure to room temperature (CK) and 45 °C for 6 h and after 28 days of exposure to 45 °C

dehydrated and dull in appearance. After a 28-d recovery period, *P. pungens* recovered well and developed new bud and re-flushing, whereas *P. abies* exhibited total chlorosis and shed some of its one-year-old and older needles but developed new buds and re-flushing. *P. omorika* exhibited widespread chlorosis in the upper half of the shoots and shed most of its one-year-old needles with almost no needles in one-year-old shoots, while, the needles of its older shoots were not shed, only become yellow.

Needle water content in three spruce species in response to thermal stress

The relative water content of needles directly after different temperature treatments varied significantly among species (P < 0.001) and interaction between species and temperature (P < 0.01) but not among temperature treatments (Table 1). After the 28-d recovery period, the relative water content of needles varied significantly (P < 0.01) among species, temperature, and species and temperature interaction effects. The relative water content of needles was primarily affected by species (the magnitude of variation was 35.9 - 46.4%) and the interaction effects of species and temperatures (the magnitude of variation was 29.5 -42.1%). Immediately after exposure to different temperatures for 6 h, the relative water content of P. pungens needles was similar while those recovered from 40 to 45 °C exposure were 28–37% higher than that of needles exposed to 35 °C and room temperature (Fig. 2). The relative water content of *P. omorika* needles exposed to 45 °C for 6 h was 4–8% higher than that of needles exposed to 35 °C, 40 °C, and CK, with no significant differences after the 28-d recovery period. However, the relative water content of P. abies needles was 3–31% lower after exposure to 45 °C and after 28-d recovery period than needles exposed to 35 °C, 40 °C, and CK. These results were consistent with the phenotypic observations, which showed that *P. abies* continued to suffer dehydration during the recovery period.

Photosystem II fluorescence parameters in response to thermal stress

Species, temperature, and their interaction significantly affected the PSII maximum light energy conversion efficiency, Fv/Fm, (P<0.05, Table 2). The Fv/Fm was primarily affected by temperature, with a magnitude of variation due to temperature effect greater than 97%. After a 28-d recovery period, Fv/Fm was significantly affected by temperature (P<0.05), with a magnitude of variation greater than 96%. The Fv/Fm trend for the three species was consistent after high temperature treatment, with values of around 0.85 for both the CK and 35 °C, which were significantly higher than those of 40 °C (about 0.64) and 45 °C (0) treatments. After a 28-d recovery period, the Fv/Fm values of the 40 °C treatment returned to

Table 1ANOVA results forvariations in relative water con-tent of needles of three sprucespecies as affected by differenttemperature treatments for 6 h(WC0) and after 28 d of recovery(WC28).	Trait	Variance source	Degrees of freedom	Mean square
	The needle rela- tive water content after treatment (WC0)	species	2	66.236***
		temperature	3	4.982
		species*temperature	6	11.137**
		error	24	2.376
Note: ** represent P<0.05; ** represent P<0.01; ***represent P<0.001	The needle rela- tive water content after 28 d recov- ery (WC28)	species	2	1102.936***
		temperature	3	150.616**
		species*temperature	6	282.49***
		error	24	41.83



Fig. 2 Relative water content (RWC) of *P. pungens, P. abies* and *P. omorika* needles exposed to room temperature (CK), 35 °C, 40 °C, and 45 °C for 6 h (WC0) and after 28 d recovery (WC28). Capital letters represent statistically significant differences among different temperature treatments

Parameter	Variance Source	Degrees of freedom	Treated for 6 h		Recovery for 28 d	
			Mean square	Variance component (%)	MS	Variance compo- nent (%)
Fv/Fm	Species	2	0.009**	0.22	0.011	0.21
	Temperature	3	1.135**	97.45	1.097**	96.04
	Species*Temperature	6	0.005*	1.06	0.007	1.09
	Error	35	0.002	1.26	0.003	2.66

 Table 2
 ANOVA results for variations in maximal photochemical efficiency of photosystem II (Fv/Fm) of three spruce species as affected by different temperature treatments for 6 h and after 28 d of recovery



Fig. 3 The maximal photochemical efficiency of photosystem II (Fv/Fm) of *Picea pungens, P. omorika* and *P. abies* seedlings exposed to room temperature (CK), 35 °C, 40 °C, and 45 °C for 6 h (the first three left panels) and after a 28-d recovery period (the last three right panels). Capital letters represent statistically significant differences among different temperature treatments

normal (about 0.85). The Fv/Fm value of *P. pungens* under 45 °C treatment increased from 0 to 0.26, while the Fv/Fm values of *P. abies* and *P. omorika* were almost 0 (Fig. 3).

Discussion

Morphological response to high temperature stress

Thermal adaptation is species-specific, and plants modulate their morphological and physiological characteristics to cope with high temperature stress (Lee et al. 2020). The responses of the three spruce species to 6 h of exposure to 40 °C and 35 °C treatments were similar, with normal physiological responses restored after 28 d. However, the responses of the three species to 6 h of exposure to 45 °C treatment were significantly different. Here, we found that *P. pungens* had the highest thermal limit, exhibiting only minor phenotypic changes in needles in response to 45 °C treatment for 6 h, and full recovery after 28 d. While, P. abies and P. omorika could not recovery normal growth. Previous studies have found that the semi-lethal thermal limits for spruce trees range between 45 and 50 °C, with different species exhibiting slightly different thermal limits (Yang 2017). The damage threshold was as low as 44 °C in P. mariana, when seedlings were exposed for 180 min (Colombo and Timmer 1992). P. abies and P. omorika showed severe chlorosis and needle drop when treated for 6 h at 45 °C and a deteriorating condition during the 28-d recovery period. P. sitchenrsis exposed to 3 h and 18 min of high soil temperature dropped 68% of its needles, which in turn negatively affected growth (Tabbush 1986). Exposure to 46 °C for 60 min resulted in direct damage to 73% of the exposed P. mariana seedlings (Colombo and Timmer 1992). In another spruce species, *P. glauca*, 30 min exposure to 48 °C produced 50% foliar damage (Bigras 2000). Heat stress can limit the amount of carbohydrates available for growth and reduce nutrient uptake resulting in leaf chlorosis and necrosis (Bigras 2000).

High temperature stress is efficient in breaking endo-dormancy of perennial trees. When hybrid *Populus* trees received a 2 h exposure to temperatures ranging from 20 to 45 °C, there was a significantly greater amount of bud break, particularly in response to exposure to 45 °C (Wisniewski et al. 1997). It was found that the upper temperature limit for breaking of bud dormancy has been found to be as high as 12 °C in P. abies (Hänninen 1990). In the present study, P. pungens and P. abies developed new buds and re-flushing after 28-d recovery from exposure to 45 °C for 6 h, especially for P. abies. Exposing dormant shoots of Prunus persica var. nectariana to high temperature (50 °C for 1 h) transiently inhibited respiration, but hours later activated the pentose phosphate pathway, which may be the cause of early budburst induced by high temperatures (Tan et al. 2013). Rising temperatures may negatively affect the carbon storage of trees (Büntgen et al. 2019). A high degree of sensitivity to elevated temperature indirectly implicates carbon starvation (Adams et al. 2009). At temperatures of 35-40 °C, P. rubens exhibited a zero or negative carbon balance (Vann et al. 1994). Thus, the increasing temperatures may contribute to depletion of carbohydrate reserves relevant to carbon starvation thresholds (Allen et al. 2010) for P. abies which is difficult to recover in response to high temperatures in the present study. The maturity of seedling tissues confers differences in their ability to adapt to thermal stress. For example, Karen et al. (1993) found that the tolerance of different maturities of Pseudotsuga menziesii and P. engelmannii seedlings to temperatures of 52 °C ranged from weak to strong in young seedlings, mature but not lignified seedlings, and lignified and stopped growing seedlings. In our case, the seedlings of the three spruce species have been lignified.

Needle water content in response to high temperature stress

In general, heat stress and drought are linked, and injury resulting from dehydration is the primary factor affecting seedling growth (Adams et al. 2009; Hartmann et al. 2015). In the present study, P. abies was severely dehydrated after high temperature treatment and during recovery, with a needle relative water content significantly lower than that of the room temperature treatment. P. abies is highly sensitive to drought (Trujillo-Moya et al. 2018), which is less drought-tolerant than P. pungens (Qin 2020). Temperature-induced drought stress has disproportionately affected the most rapidly growing *P. glauca*, suggesting that, under recent climate warming, drought may have been an important factor limiting carbon uptake in a large portion of the forest (Barber et al. 2000). When the water potential drops to between -2.0 and -3.0 MPa, the stomata of *P. mariana*, *P. sitchenrsis*, and *P. glauca* close rapidly, the net photosynthetic rate drops to the light compensation point as the water potential decreases (Patterson and Dang 1997; Fan and Grossnickle 1998). Warming has accelerated soil drying, and has been implicated in increased tree mortality (van Mantgem et al. 2009). In many instances, after drought and high temperature stress, the trees are susceptible to insect and disease attacks, which are the primary causes of tree mortality (Breshears et al. 2005; Kurz et al. 2008; Allen et al. 2010).

Effect of high temperature stress on photochemical efficiency of photosystem II

PSII plays a pivotal role in the photosynthetic reactions to environmental stress (Murata et al. 2007; Liu and Shi 2010), likely due to its thermal sensitivity (Allakhverdiev et al. 2007; Mathur et al. 2014). The Fv/Fm ratio of ecologically-diverse plants tends to be stable under unstressed conditions, remaining near 0.832 ± 0.004 (Björkman and Demmig 1987). Stressful conditions tend to lead to a decrease in the Fv/Fm ratio, indicating that a certain proportion of PSII reaction centers are destroyed or inactivated, a phenomenon called photorepression (Baker and Eva 2004). This is further evidenced in our study where the Fv/Fm ratios of all three spruce species decreased after 6 h of exposure to 40 and 45 °C. Similar to our results, a decrease in Fv/Fm with increasing temperature from 42 to 50 °C was observed in P. glauca foliage (Bigras 2000). The Fv/Fm in P. wilsonii was significantly lower following 35 °C (high temperature) treatment for 4 months than that of 25 °C (moderate temperature) treatment (Zhang et al. 2017). It has been shown that P. abies had the lowest temperature at the onset (5%) of the Fv/Fm decline (38.5 °C) and the temperature at which only 5% Fv/Fm remained (53.9 °C) among six conifer species (Kunert et al. 2022). The chlorotic needles exhibited by the spruce species may be related to the resultant decline in Fv/Fm ratios, as chlorosis suggests the occurrence of photo-oxidation and decreased chlorophyll content (Lamontagne et al. 2000).

The Fv/Fm values vary with the extent of recovery. For instance, if the heat treatment reduced Fv/Fm to values between 0.65 and 0.75, 100% of the *P. glauca* needles recovered; however, if the heat treatment reduced to value of Fv/Fm between 0.25 and 0.35, only 30% of the needles recovered (Bigras 2000). After treatment at 45 °C, *P. pungens* exhibited the greatest recovery, with Fv/Fm increasing from 0 to 0.26. However, the Fv/Fm ratios of *P. abies* and *P. omorika* remained at almost 0, suggesting that the PSII reaction centers of these two species may have been irreversibly inactivated, or the photosynthetic mechanism may have otherwise been damaged (Krause and Weis 1991). A previous study found that *P. abies* was able to recover from PSII damage resulting from short-term exposure to 44–52 °C (Jia et al. 2020). Similarly, a study in *Populus simonii* found that PSII damage resulting from short-term exposure (6 h) resulted in irreversible damage (Song et al. 2013). So whether the value of Fv/Fm could recover or not depends on species and the duration of heat exposure (Colombo and Timmer 1992).

Implication for reforestation

With global climate change, the frequency and severity of extreme climatic events, such as heat waves, increase the risk of leaf damage. Severe damage can significantly weaken forest trees and lead to accelerated forest mortality. High temperature events in the summer has already been witnessed in many areas where spruce species grow. Our results demonstrate that exposure to high temperature reduced photosynthetic activities and caused chlorosis, which may eventually result in stunted growth or total mortality. Thus, thermal sensitivity can be used as a tool to choose species suitable for planting in high altitude and latitude environments. This is further evidenced in the preset study where *P. pungens* appeared to be better tolerant to thermal stress than *P. abies* and *P. omorika*. Compared to *P. omorika* (400–1700 m) and *P. abies* (400–2100 m), *P. pungens* originates from the highest altitude (1750–3000 m). These central continental mountains are also very dry. The species adapted

to them are all drought- and fire-adapted, for the most part. Studies have also shown that at high altitudes, higher temperatures have a positive effect on spruce (Altman et al. 2017). When plants are exposed to high temperatures during germination and maturation, they often develop physiological adaptations to these stressors, such as altering needle thickness, stomatal and chloroplast density, leaf structure and function, and nutrient utilization, thereby improving photosynthetic and physiological performance (Lichtenthaler 1996). Similarly, the high-altitude P. crassifolia has been found to have greater heat tolerance than the low-altitude P. wilsonii (Zhang et al. 2017) and crassifolia also shows greater phenotypic plasticity under adverse conditions (Wang et al. 2019). Compared to other spruces tested, P. pungens had the highest needle fresh weight, dry weight, and water content (An et al. 2018), which showed better adaptation in China (Ouyang et al. 2021). P. pungens also showed greater photosynthetic ability, water use efficiency, and stress resistance under arid, water-scarce, and nitrogen-scarce environmental conditions compared to P. abies, P. crassifolia, and P. smithiana (Zhang 2019). Also, the needles of P. pungens have been found to contain a greater content of total chlorophyll $(2.64 \pm 0.43 \text{ mg/g})$ compared to P. abies $(2.44\pm0.55 \text{ mg/g})$ and P. omorika $(2.33\pm0.68 \text{ mg/g})$ (Song 2015) as well as P. mongolica, P. crassifolia, P. meyeri (Shi et al. 2017). Additionally, some components like isoprene may also confer high temperature tolerance through an antioxidative role (Loreto and Velikova 2001). It was observed that P. pungens yielded a standard emission rate of 12 μ gC g⁻¹ h⁻¹, while *P. abies* emitted very little isoprene (<0.5 μ gC g⁻¹ h⁻¹, Kempf et al. 1996). Isoprene emission may help stabilize photosynthetic complexes in the thylakoid membrane (Sharkey et al., 1996). All of the above mentioned factors may be the reasons for higher temperature tolerance ability for P. pungens.

The thermosensitivity is important with respect to global climate change and species migration patterns (Vann et al. 1994). *P. abies*, economically very important conifer species, has been massively affected by accelerated tree mortality in recent years across Europe (Allen et al. 2010). Kunert et al. (2022) conclude that the main underlying mechanism of accelerating *P. abies* mortality does not lie in water stress but rather in heat stress caused by heatwaves, which was also confirmed in our research. *P. omorika* is a extremely narrow ranged tertiary relict tree species whose natural range and the number of mature individuals declines constantly (Ivetić and Aleksić 2019). The response of forest tree populations to rapidly changing environment is extirpation or persistence achieved by migration or adaptation (Aitken et al. 2008). However, the migration ability of *P. omorika* is exceptionally low and it is much more threatened by suffering from the dieback caused by the global warming (Ivetić and Aleksić 2019). These adverse conditions lead to the physiological debilitation of trees, making them more vulnerable to pests and diseases, which ultimately lead to tree death. It is very likely that *P. omorika* will disappear from its natural habitats in the near future due to the rapid climate change (Ivetić and Aleksić 2019).

The search for suitable species for a climate change adapted forest should go imminently for increasing both drought and heat stress tolerant species (Kunert et al. 2022). It is clear that *P. pungens* may be better adapted to hotter and drier conditions than the other studied species. This is important for forest managers to know because few nurseries offer *P. pungens* as reforestation stock, and many are offering spruce cultivars which are poorly adapted to drought and high heat conditions (Ivetić and Aleksić 2019; Rosvall 2019). This, in turn, leads to poor performance of restoration endeavors. The same could be said for urban forestry, which is under considerable pressure to find and utilize drought and heat tolerant

species because cities are increasingly becoming "urban heat islands", with catastrophic implications for their urban forests (Percival 2023). *P. pungens* is tolerant of warm microclimates which is a better choice for many urban sites than *P. abies* (Hirons and Sjöman, 2019), which was recommended heat-tolerant tree species for urban landscapes (Appleton et al. 2015; Percival 2023). Heat tolerance of trees is also affected by genetic factors (Bigras 2000). Some species of trees are naturally heat-resistant, and many cultivars are available that have been developed for their ability to withstand high temperatures (Hirons and Sjöman, 2019). Therefore, the search for excellent families or elite single trees with high heat and drought resistant should be conducted in the future to cope with climate change (kunert 2020).

Conclusions

The results from the present study demonstrate that short-term exposure to high temperature (45 °C) of *P. pungens*, *P. abies* and *P. omorika* resulted in chlorosis, reduced relative water content of needles and damage to photosystem II. Only *P. pungens* exhibited full PSII recovery and maintained a healthy shoots with flushing of new buds. The findings also suggest that the photosynthetic activity of PSII provide an important reference for the thermal stress response of spruce, and Fv/Fm is an important indicator of thermal tolerance in spruce. Thus, thermal sensitivity could be used as tool to choose species suitable for reforestation on high altitude and latitude environments in the face of global climate change; particularly *P. pungens* is more suitable than *P. abies* and *P. omorika*.

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Authors' contributions Ouyang F wrote the main manuscript text and Sun M, Cui X, Deng J prepared the data. Wang J, Wei Y, He R prepared the experimental design.Mulualem Tigabu and Hui Zhang revised the manuscript text. All authors reviewed the manuscript.

Declarations

Competing interests The authors declare no competing interests.

Conflict of interest The authors declare that they have no conflict of interest.

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