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UNIVERSITÄT FÜR BODENKULTUR WIEN University of Natural Resources and Life Sciences, Vienna

# Trait-based assessment of thermal and drought tolerance of Central European tree species

submitted by

# Ines MÜNCHINGER, B.Sc.

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Supervisor:

Apl. Prof. Dr. Norbert Kunert Institute of Botany Department of Integrative Biology and Biodiversity Research (DIBB)

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#### **1 INTRODUCTION**

#### **1.1** Forests in a changing climate

Forests serve as fundamental habitats for life and play a central role in the cycling of water and carbon within ecosystems. They also provide both physical and economic support for human society and play a crucial role in regulating the Earth's climate by absorbing carbon dioxide from the atmosphere and maintaining ecological stability (Ellison et al. 2017). However, the impacts of climate change, including alterations in temperature, precipitation, and atmospheric conditions, are exposing forest biomes to increased stress, leading to accelerating forest mortality. These changes result in increased temperatures, extremely cold winters, more frequent and severe droughts, potentially exceeding critical forest resilience and resistance thresholds, adversely affecting their physiological state, resources, and species composition (Alizadeh et al. 2020; Liao et al. 2020, Senf et al. 2022). Understanding the limits of plant stress tolerance and acclimation to such stressors is of great significance in predicting the potential and realized limits of plant productivity (Niinemets 2010).

#### **1.2** Heat and drought as limiting factors

Forests play a critical role in regulating the global climate, yet there remains significant uncertainty regarding the response of trees to increasing abiotic stress, especially cooccurring drought during chronic and, or acute hotter climate conditions. Drought exacerbates the negative effects of high temperatures on the productivity and survival of trees (Birami et al. 2020). As climate change leads to alterations in environmental conditions in general, heat and drought events are expected to increase in frequency, duration, and intensity (Alizadeh et al. 2020). In the literature drought is seen as a primary driver of tree mortality, the direct effects of heat, particularly during drought, have received less attention and need to be further studied (Breshears et al. 2021, Hammond et al. 2022, Salomón et al. 2022, Senf et al. 2020).

Temperature is an important factor influencing tree distribution, growth, and development. Rising temperatures pose a triple threat to tree survival by increased atmospheric drought, soil drought, and the direct effects of heat stress (Breshears et al. 2013, Zhang et al. 2022). As temperatures rise, the vapor pressure deficit (VPD) increases, accelerating water loss from soil and trees in hotter periods (Williams et al. 2013). The morphological and physiological processes of trees are dependent on the temperature conditions in which they grow, as each species has an optimal temperature range for maximum growth (Nievola et al. 2017). Elevated temperatures beyond this optimum range can result in stress and a range of negative impacts on plant function and metabolism, including denaturation of cellular structures, protein instability, membrane disintegration, disruptions of metabolic processes, excessive production of reactive oxygen species (ROS) and oxidative stress (Hu et al. 2020). Prolonged exposure to high temperatures can also result in significant alterations in metabolic activities and cellular organization, resulting in reduced growth and development and potential tree mortality (Húdoková et al. 2022).

In plants, one of the most heat-sensitive physiological processes is photosynthesis, with photosystem II (PSII) being the most thermosensitive component (Mathur et al. 2014). Heat stress can have detrimental effects on photosynthesis, ranging from suppression to destruction, manifested in reduced CO<sub>2</sub> assimilation, chlorophyll molecule disintegration, increased fluidity of thylakoid membranes, enzyme disorganization, denaturation of D1 and D2 proteins and separation of reaction centers from PSII. Furthermore, the electron transport chain and the oxygenevolving complex are impaired (Hu et al. 2020, Li et al. 2020).

To guard their photosynthetic apparatus against heat-induced damage, higher plants have evolved various protective mechanisms. Primary acclimation mechanisms encompass the activation and upregulation of heat-shock protein synthesis, and accumulation of secondary metabolites (Mihailova et al. 2023, Sulaiman et al. 2023). These features can vary among different species and populations, reflecting both long-term adaptations and short-term acclimation responses to changing temperatures. This variability can serve as an indicator of the differing abilities of species and populations to respond to temperature changes (Húdoková et al. 2022).

However, it is important to consider that forests are subjected to multiple abiotic stressors. The risk of severe drought has risen in numerous forested areas worldwide, despite increases in precipitation (IPCC 2019). The impact of droughts on forests globally has been exacerbated by climate change and is projected to persist as a key factor in shaping the forest ecosystem, potentially leading to significant reductions in both productivity and carbon storage on a wide-spread scale (Choat et al. 2018, Birami et al. 2020).

Increasing evidence states that hydraulic failure is a primary cause of tree mortality during droughts, which are frequently accompanied by elevated temperatures and heightened atmospheric evapotranspirational demands. Trees have evolved mechanisms to regulate their water status and withstand seasonal and short-term soil and atmospheric drought (Estravis-Barcala et al. 2020). However, exceptional climatic events, such as elevated summer temperatures and low soil water availability, can result in significant damage due to hot droughts. Such

exceptional events have the potential to disrupt the balance between the trees' water needs for survival and evaporative cooling, leading to decreased productivity (Birami et al. 2020).

The regulation of water loss is particularly crucial during hot droughts, when evaporative demand is high and water availability is low. Trees must limit transpiration through the closure of stomata to preserve the integrity of the water-transport system, avoid cavitation and hydraulic failure in the xylem (Martin-StPaul et al. 2017). During intensifying soil water deficit, the water potential in the xylem becomes increasingly negative, leading to the formation of embolisms restricting the water flow. The closure of stomata results in a rapid reduction in photosynthetic carbon dioxide assimilation, which is necessary for supporting osmoregulation and cellular maintenance (Brodribb et al. 2020). Additionally, even after stomata have closed, residual water loss continues. This process is further exacerbated by elevated temperatures (Cochard 2021).

Additionally, the closing of stomata affects various physiological and biochemical processes, such as lowering leaf water content, decreasing chlorophyll quantity, causing chloroplast augmentation, altering ion exchange between root and shoot, and restricting leaf expansion morphologically. Additionally, under high solar radiation and low stomatal conductance, leaf temperatures can significantly exceed air temperature (Brodribb et al. 2020). Drought primarily impairs photosynthesis by increasing the resistance to CO<sub>2</sub> entering chloroplasts. This results in a depletion of non-structural carbohydrates, which impairs the translocation of sugars through the phloem and the production of chemical defense compounds. The imbalance between CO<sub>2</sub> and O<sub>2</sub> available for Rubisco leads to an impaired fixation of CO<sub>2</sub>, which further inhibits the synthesis of ATP and photophosphorylation (Choat et al. 2018).

Trees can also cope with drought by reducing their leaf area, as evidenced by many studies (Schuldt et al. 2020, Hochberg et al. 2017, Wolfe et al. 2016). Water deficit elicits a reduction in leaf size and an increase in leaf number, resulting in elevated boundary layer conductance, reducing the accumulation of heat, and subsequently lowering the leaf surface temperature. This enables the plant to ameliorate the effects of both drought and heat (Leigh et al. 2017). Drought-induced leaf senescence reduces overall tree transpiration; however, this reduction comes at the cost of reduced growth in the mid-term. The rebuilding of canopy structure necessitates the allocation of additional carbon, which can be derived either from non-structural carbohydrate reserves or from the photosynthetic activity of remaining or newly grown leaves once the drought stress has abated (Ruehr et al. 2019, Yan et al. 2017). Other defense mechanisms include biochemical (antioxidant content, hormonal content, secondary metabolite, etc.),

physiological changes (osmotic balance, transpiration, etc.), and morphological changes (increase in root length, early maturation, change in growth stages, etc.) (Oguz et al. 2022).

Plants exhibit some degree of acclimation capacity to cope with increasing temperatures; however, this capability may become overwhelmed during episodes of drought stress. The potential of plants to acclimate may be negatively impacted by both chronic and acute warming and/or severe drought conditions (Salomón et al. 2022) In the context of hotter droughts, trees are presented with a challenging scenario, as the utilization of water for evaporative cooling to mitigate heat stress competes with the need for the same water to survive the drought.

#### **1.3** Aim of the study

This study aims to explore the relationship between functional and morphological traits related to drought of temperate mature conifers and deciduous trees, and their respective leaf heat tolerance and sensitivity traits. The study focuses on heat as a physiological stressor and aims to investigate whether there exists a correlation between leaf thermal properties and the functional and morphological traits of the regional species pool of a cool temperate montane wet forest. The objective of this work, in the face of increasing climatic extreme events, is to improve the understanding of the interplay between thermal properties and leaf traits of the tree species studied to provide further information how these species might respond to changes in temperature and climate. Additionally, an assessment of the viability of wild cherry (*Prunus avium* L.) as a tree species suitable for climate change will be conducted through the comparison of physiological traits and field observations.

In the following, Chapter 2 starts with a detailed account of the study site and the tree species occurring. Subsequently, the chapter describes the process of sample collection and measurements taken, including thermal tolerance and sensitivity, turgor loss point determination, and functional leaf trait estimation as relevant to drought. The chapter also explains how the data was processed and analyzed statistically before presenting and discussing the results in comparison to previous research. Moving on to Chapter 3, the focus is on evaluating the suitability of wild cherry as a climate change tree. The chapter starts with a brief introduction moving on to introducing the ecology and silviculture of wild cherry before examining and discussing its drought tolerance and heat resistance properties in detail. Finally, a synthesis follows in which the most important results of the two preceding chapters are highlighted.

Chapter two and three were written in a journal style, reflecting their publication in *Journal of Forestry research* and *AFZ-Der Wald*, respectively. It's worth noting that Chapter three was originally written in German and was subsequently translated into English.

# 2 LEAF THERMAL TOLERANCE AND SENSITIVITY OF TEM-PERATE TREE SPECIES ARE CORRELATED WITH LEAF PHYSIOLOGICAL AND FUNCTIONAL DROUGHT RE-SISTANCE TRAITS

Ines K. Münchinger, Peter Hajek, Berivan Akdogan, Astor Toraño Caicoya & Norbert Kunert in Journal of Forestry Research (2023) 34:63-76

#### Abstract

Climate change is causing more frequent and severe climatic events, such as extreme heat and co-occurring drought, potentially accelerating tree mortality. Which tree species will cope better with those extreme events is still being researched. This study focuses on heat as a physiological stress factor and interspecific variation of thermal tolerance and sensitivity traits in 15 temperate coniferous and broad-leaved tree species. We investigate (1) whether thermal tolerance and sensitivity traits correlate with a drought-related physiological trait, particularly the leaf turgor loss point ( $\pi_{tlp}$ , wilting point), and (2) how thermal tolerance and sensitivity traits co-vary within different tree-functional types classified by morphological and physiological traits of the leaf, i.e., leaf mass per area (LMA) and percentage loss of area (PLA). The study was carried out in the Traunstein Forest Dynamics Plot of the ForestGEO network in Germany. The temperature response of the maximum quantum yield of photosystem II (Fv/Fm) on leaf discs was determined, from which various physiological leaf traits were estimated, one of which is the breaking point temperature ( $T_5$ ), the temperature at which *Fv/Fm* declines by 5%. Additionally, the temperature of 50% ( $T_{50}$ ) and 95% ( $T_{95}$ ) decline in Fv/Fm was evaluated. The decline width between  $T_{50}$  and  $T_5$  ( $DW_{T50-T5}$ ) was taken as an indicator of the species' thermal sensitivity. The breaking point temperature ranged from  $35.4 \pm 3.0$  °C to  $47.9 \pm 3.9$  °C among the investigated tree species and  $T_{50}$  ranged between 46.1 ± 0.4 °C and 53.6 ± 0.7 °C. A large interspecific variation of thermal tolerance and sensitivity was found. European ash (Fraxinus excelsior L.) was the most heat-sensitive species, while Wild cherry (Prunus avium L.) was the least heat-sensitive species. Species with a more negative  $\pi_{tlp}$  tended to have a higher breaking point temperature than species with a less negative  $\pi_{tlp}$ . A lower thermal sensitivity characterized species with a higher LMA, and high PLA was found in species with low thermal sensitivity. Accordingly, species with thicker and tougher leaves have lower thermal sensitivity which coincides with a lower wilting point. We conclude that species that develop droughtadapted foliage can cope better with heat stress. Further, they might be able to maintain

transpirational cooling during combined heat and drought stress, which could lessen their mortality risk during climatic extremes.

#### 2.1 Introduction

In 2022, Europe was struck by record-breaking climate extremes, with the hottest heatwave and the longest-lasting drought spell in history (European Union, Copernicus Climate Change Service 2022). 2022 has only been the tip of the iceberg, as the frequency and intensity of hot and dry summers have increased dramatically in recent years (Liao et al. 2020; Rousi et al. 2022). In the face of this rapidly changing climate, it is expected that climatic thresholds of locally adapted forests will be exceeded and are likely to overcome critical forest resilience and resistance thresholds, leading to accelerating forest mortality (Alizadeh et al. 2020; Senf et al. 2022). The effect of surpassed climatic thresholds can already be observed in many forests in Central Europe as large-scale and climate-driven forest mortality events have drastically augmented over the last decades (Senf et al. 2018). In the literature, climate-induced drought is underlined as the main driver for high forest mortality (Senf et al. 2020). However, heat or the combination of heat and drought as possible drivers have received much less attention (Hammond et al. 2022; Salomón et al. 2022). Central European forests may be particularly vulnerable as a few tree species dominate them, i.e., Scots pine (Pinus sylvestris L.), Norway spruce (Picea abies (L.) H. Karst.), European beech (Fagus sylvatica L.) and Pedunculate oak (Quercus robur L.) are particularly susceptible to heat and drought stress (Buras and Menzel 2018; Leuschner 2020; Bose et al. 2021; Húdoková et al. 2022). There is an urgent need to improve our understanding of the thermal tolerance and temperature sensitivity of tree species in the mid-latitude. Species in those areas tend to have the "narrowest thermal safety margins" and are exposed to a high risk of more frequent heatwaves (O'Sullivan et al. 2017). However, little is known about the susceptibility to heat stress of the species forming these forests. Even less is known about which species could substitute those main species, particularly in managed forest systems and in the perspective of heat or combined heat and drought stress.

To understand the extent to which tree species can cope with heat or hotter drought events, species-specific responses can be quantified using leaf functional, morphological, and physiological traits related to heat and drought stress (Reich et al. 2007; Bussotti 2008). For example, Scoffoni et al. (2014) show that the two functional and morphological traits, leaf mass per area (LMA) and percentage loss of area (PLA), are good predictors for the drought tolerance of leaves and correlate with leaf hydraulic traits, such as the turgor loss point ( $\pi_{tlp}$ ). Further, LMA, defined as the ratio between leaf mass and leaf area in g m<sup>-2</sup>, is a key trait in measuring leaf

sclerophylly (Reich et al. 1992; Niinemets 2001; Wright et al. 2004; Ordoñez et al. 2009; Kattge et al. 2011; Kikuzawa et al. 2013), which in turn is linked to xeromorphy via the implication of equivalent leaf anatomical and morphological adaptations to drought (Medina et al. 1990). Xeromorphic leaves typically have, e.g., a smaller leaf area with a multi-layered epidermis, thicker cuticle, compactly arranged mesophyll with low air spaces, and high stomatal density to reduce tissue desiccation during periods of high evaporative demand (Bussotti 2008; Binks et al. 2016; La Riva et al. 2016). Xeromorphic leaves are heavier compared to mesomorphic leaves. According to Schimper et al. (1903), evergreen xeromorphic woody plants which are local to Mediterranean areas with prolonged summer drought, possess sclerophyllous leaves. Moreover, xeromorphism and sclerophylly are combined by implying a higher LMA (Oppenheimer 1960). Although xeromorphism per se is not an adaptation to high summer temperatures, LMA is known to affect leaf heat capacity and rates of change in leaf temperature (Groom et al. 2004). Consequently, LMA is suitable as a key trait to quantify the effects of thermal and co-occurring drought stress on leaf morphology and their ability to withstand them. A higher LMA suggests a higher structural investment in leaf tissues, thus providing longer longevity but lower leaf nitrogen concentrations, growth, and photosynthetic rates (Wright et al. 2002). These observations indicate that species with a higher structural investment in leaf tissue, e.g., with thicker cell walls, might be able to prevent shrinkage of leaf surface area during periods with limited water ability and high evaporative demand. They may also sustain water transport capacity, showing a smaller PLA (Nardini 2022). However, LMA and traits moderating leaf thermal properties are positively correlated (Greenwood et al. 2017).

Leaf thermal properties can be evaluated by assessing the temperature dependence of the photochemical efficiency of the photosystem II (PSII). The PSII represents the most heat-sensitive component of the photosynthetic system (Berry and Bjorkman 1980). When critical temperature thresholds are exceeded, permanent impairment of PSII function occurs, and photosynthetic capacity can be severely limited. The effect of heat stress on the photochemical efficiency of PSII can be quantified by the ratio between variable and maximum chlorophyll fluorescence  $(F_v/F_m)$ .  $F_v/F_m$  can be used to calculate thermal tolerance traits such as  $T_5$ ,  $T_{50}$ , and  $T_{95}$ .  $T_5$ represents the breakpoint temperature at which  $F_v/F_m$  drops below 95% of the maximum yield of PSII.  $T_{50}$  defines the temperature at which  $F_v/F_m$  is reduced by 95%. According to Tiwari et al. (2021),  $T_{95}$  also functions as a threshold value above which PS II functions are effectively lost. Additionally, they suggest determining the thermal sensitivity of species by the decline width (DW), defined as the width of the decline of various temperature levels-induced decrease in the photosynthetic conversion rate of PSII. In species considered heat tolerant, maximum PSII quantum yield (QY) is maintained at high temperatures (high  $T_5$ ). However, it is characterized by a rapid decline if the breaking point temperature is surpassed. Conversely, heat-sensitive plants are characterized by low  $T_5$  values, and the decline of PSII in QY occurs gradually over a wide temperature range.

Most studies focusing on the relationship between functional and morphological traits and leaf thermal properties have been conducted in predominantly seasonal dry tropical forests (Sastry and Barua 2017; Sastry et al. 2018) or desert ecosystems (Knight and Ackerly 2003; Curtis et al. 2014). Only a few studies target the interplay between thermal properties and leaf traits in boreal and temperate forests (Ruiz-Pérez et al. 2019; Kitudom et al. 2022). In this study, we wanted to test whether leaf thermal properties are related to functional, morphological, and physiological traits, namely LMA, PLA, and  $\pi_{tlp}$ , in a cool temperate montane wet forest. Therefore, we assessed the sensitivity of the PSII to temperature changes for 15 tree species representing a relatively wide range of the regional species pool in a Central European forest. We investigated (1) whether leaf thermal tolerance and sensitivity vary within different tree-functional types classified by leaf morphological and physiological traits. The study was carried out in the ForestGEO plot in Traunstein, Germany.



Figure 1 Study site used for collecting botanical material from 15 temperate tree species. The site is located at the 25 ha Traunstein ForestGEO plot, part of the Forest Global Earth Observatory network (Davies et al. 2021), in Froschham, Germany. The plot is situated approximately 10 km out of Traunstein in the southeastern part of the country (47.935000°N, 12.666400°E). It is classified as a cool temperate montane wet forest (Holdrige 1947) and is located in the vicinity of the northern Alps at an altitude of 590 m. a.s.l..

#### 2.2 Material and methods

#### 2.2.1 Study site and tree species

The botanical material from 15 temperate tree species was collected at the 25 ha Traunstein ForestGEO plot, which is part of the Forest Global Earth Observatory network (ForestGEO) (Davies et al. 2021), Germany. The study site is located at the former hermitage in Froschham, approximately 10 km outside of Traunstein, in the southeastern part of Germany (47.935000°N, 12.666400°E) (Fig. 1). The forest can be classified as a cool temperate montane wet forest (Holdridge 1947). The plot lies in the vicinity of the northern Alps at an altitude of 590 m. a.s.l. The mean annual temperature is 9.1 °C, and the mean annual precipitation is 1060 mm (Fig. 2). Due to the particular geographical condition, rainfall is not expected to decline with climate change significantly. However, the number of hot days has increased over the last four decades (Fig. 3), and there is a high risk of future heat waves (Senf and Lakes 2011).

In total, 25 different tree species have been identified on the plot, whereby Norway spruce is the dominant, representing 50% of the basal area, followed by Sycamore maple (*Acer pseudoplatanus* L.), European hornbeam (*Carpinus betulus* L.), European beech, and European larch (*Larix decidua*, Mill.) (Giammarchi et al. 2017). At the former hermitage, an arboretum has been established, which offers to investigate a variety of non-native tree species to test their



Figure 2 Climate diagram for the study site based on data obtained at the Trostberg between January 1992 and December 2022.

potential as alternative species to climate change. The Traunstein ForestGEO plot is currently subject to actively managed forest plots and is thus representative of the vast majority of forests in Central Europe. The eastern part of the area is dominated by a homogeneous, mostly mono-specific structure consisting of Norway spruce and a grid of Sycamore maple to increase the wind resistance of the forest. Forest management aims to transform those monospecific stands into uneven-aged mixed-species stands. The western part of the plot is dominated by multi-layered mixed stands where the transformation into complex stand structures has been successfully taking place for decades (ForestGEO 2017).



Figure 3 Climatic trends in the region of the ForestGEO plot in Traunstein over the last 40 years. a Shows the frequency of days warmer than 30 °C per year and b the annual precipitation. Black bars indicate the decadal average.

#### 2.2.2 Sample collection

With our study design, we wanted to screen for the highest possible variation in tree-functional types. Therefore, we chose 15 tree species growing at the Traunstein ForestGEO site. Of those 15 tree species (12 broadleaved and three coniferous tree species), 14 are native to Central Europe, and one is an introduced tree species (a complete list of species is provided in Table 1). The introduced tree species, namely the bald cypress (*Taxodium distichum* (L.) Rich.), was chosen due to its leaf morphology. The bald cypress is a deciduous conifer with needle-like leaves arranged on little branchlets characterized by an LMA in the range of the local broadleaved species (Table 1). In contrast, the two native conifers, Silver fir and Norway spruce have typical needle-like leaves with a 10-fold higher LMA than the broadleaved tree species. We expected a mismatch if the LMA of the two conifers was pooled with the broadleaved species. Therefore, we wanted to test whether tendencies between conifers and broadleaves align if species with a similar range of LMA were chosen.

We chose four mature individuals for each tree species with a minimum diameter of 25 cm at breast height. We collected most of the samples from tree individuals growing at the forest edge where branches could be sampled with a 10 m long pruner. We assumed that intraspecific trait variation was lower than interspecific trait variation in sun-exposed leaves. Therefore, all collected branches were fully sun-exposed and not shaded within the tree crown or the surrounding

Common name	Latin name	Native-intro- duced	T5 °C±SE	T50 °C±SE	T95 °C $\pm$ SE	DW <sub>T50-T5</sub> °C	$\pi_{tlp}$ MPa±SE	LMA g m <sup>-2</sup> $\pm$ SE	PLA %±SE
Silver fir	Abies alba	Native	$42.6 \pm 5.1$	$45.2 \pm 0.6$	$47.9 \pm 6.6$	2.6	$-2.34 \pm 0.04$	$197.8 \pm 0.0$	$6.7 \pm 1.4$
Norway maple	Acer platanoides	Native	$38.1 \pm 1.2$	$53.6 \pm 0.7$	$55.2 \pm 0.2$	15.5	$-1.75\pm0.02$	$11.3 \pm 0.0$	$12.0\pm0.9$
Sycamore maple	Acer pseudopla- tanus	Native	41.4±1.0	$49.8 \pm 0.5$	$55.2 \pm 1.0$	8.4	$-1.74 \pm 0.01$	$23.9 \pm 0.0$	$16.8 \pm 0.8$
European alder	Alnus glutinosa	Native	$43.7\pm0.8$	$48.8\pm0.2$	$51.9 \pm 0.4$	5.1	$-1.87\pm0.02$	$25.1 \pm 0.0$	$36.4 \pm 0.7$
European horn- beam	Carpinus betulus	Native	$41.2 \pm 1.7$	$51.6 \pm 0.6$	$54.6 \pm 1.0$	10.3	$-2.35 \pm 0.09$	$16.7 \pm 0.0$	$14.3 \pm 0.8$
European beech	Fagus sylvatica	Native	$40.7 \pm 1.2$	$51.0\pm0.3$	$55.3 \pm 0.7$	10.3	$-2.58\pm0.04$	$14.9 \pm 0.00$	$14.2 \pm 0.8$
European ash	Fraxinus excel- sior	Native	35.4±1.4	$46.1 \pm 0.4$	$49.6 \pm 0.9$	10.7	$-1.60 \pm 0.03$	$30.4 \pm 0.0$	$35.3 \pm 0.6$
Norway spruce	Picea abies	Native	$41.3\pm0.8$	$46.7\pm0.4$	$50.1 \pm 0.71$	5.4	$-2.41\pm0.06$	$231.0\pm0.0$	$16.9 \pm 2.4$
Wild cherry	Prunus avium	Native	$47.9 \pm 3.9$	$49.5\pm0.9$	$51.2 \pm 2.4$	1.6	$-2.26\pm0.05$	$29.9 \pm 0.0$	$18.0 \pm 0.9$
Common oak	Quercus robur	Native	$44.2\pm0.9$	$47.9\pm0.5$	$51.8 \pm 0.8$	3.7	$-2.23\pm0.04$	$19.7 \pm 0.0$	$12.2 \pm 0.8$
White willow	Salix alba	Native	$42.5\pm0.5$	$48.5 \pm 0.1$	$52.2 \pm 0.2$	6.0	$-2.01\pm0.03$	$30.7 \pm 0.0$	$24.5\pm0.7$
Goat willow	Salix caprea	Native	$42.5\pm0.8$	$47.8\pm0.4$	$51.1 \pm 0.4$	5.4	$-1.35\pm0.03$	$21.7\pm0.0$	$24.7\pm0.2$
Large-leaved lime	Tilia platyphyllos	Native	39.9±1.1	$50.4 \pm 0.2$	$55.2 \pm 0.8$	10.5	$-1.73 \pm 0.05$	$15.5\pm0.0$	19.0±0.8
Bald cypress	Taxodium disti- chum	Introduced	$41.2 \pm 0.7$	$47.2 \pm 0.3$	$54.0 \pm 1.0$	6.0	$-1.94 \pm 0.05$	$29.7\pm0.0$	$35.3 \pm 0.4$
Scots elm	Ulmus glabra	Native	$42.0\pm0.4$	$46.2\pm0.4$	$54.6 \pm 2.1$	4.1	$-1.95\pm0.06$	$20.4\pm0.1$	$24.8\pm0.6$

Table 1 Summary of the measured thermal tolerance, drought resistance and functional traits of the 15 investigated species

Breaking point temperature at which PSII efficiency declines 5% (T5), temperature at which efficiency is at 50% (T50) of the maximum, temperature at which only 5% of the maximum efficiency remains (T95), decline width between T5 and T5 (DWT50–T5), turgor loss point ( $\pi$ tlp), leaf mass area (LMA) and percentage loss of area (PLA).

forest canopy. One sun-exposed branch was collected per tree. Branches were between 50 and 100 cm long. The freshly cut branches were placed in opaque plastic bags and immediately

transported to the laboratory for further processing as fast as possible (< 30 min). The branches were re-cut under water at least two nodes distal to the initial cutting to avoid embolisms and placed into water-filled buckets covered with an opaque plastic bag to ensure a moisture-saturated atmosphere. The branches were left to rehydrate overnight (> 8 h).

#### 2.2.3 Thermal tolerance and sensitivity measurements

We selected eight healthy and fully functional leaves per tree from the distal end of a given branch to be assigned to one of eight temperature treatments. Leaf disks (diameter 2 cm), excluding the midrib and mayor veins, were cut out of the leaves. To ensure the health of the chosen leaves, photosynthetic efficiency was measured using a chlorophyll fluorometer (MINI-PAM, Walz, Effeltrich, Germany) (Fig. 4) on the leaf disks that had been dark acclimated. We used the recommended setting by Krause et al. (2006) to measure  $F_v/F_m$ . Briefly, the "measuring light burst" mode was used to receive an exact measurement of the initial fluorescence  $(F_0)$ . Therefore, the measuring light frequency was set low (0.6 kHz). A 1.0 s duration saturating light pulse was applied to record  $F_{\rm m}$ . A leaf with an  $F_{\rm v}/F_{\rm m}$  above 0.75 was healthy.

The thermal dependency of  $F_v/F_m$ 



Figure 4 Chlorophyll fluorometer MINI-PAM, Walz, Effeltrich, Germany with measuring light burst mode on to measure the initial fluorescence (F0).



Figure 5 Temperature controlled water bath used to treat samples at 45°C. A sous-vide precision cooker is used to ensure consistent temperature. Leaf disks are fully submerged to ensure exposure of the whole sample.

was assessed following the protocol of Krause et al. (2010). The leaf disks were wrapped in moist tissue and placed into water-tight Whirl-Pack bags. The bags were then immersed in a temperature-controlled water bath and exposed to treatment temperatures for 30 min. We used Sous-Vide precision cookers for precise temperature regulation (25 °C to 60 °C), increasing the temperature in steps of 5 °C (Kunert and Hajek 2022) (Fig.5). Afterward, the leaves were allowed to rest for several hours at a low light level, and dark acclimate for at least 30 min before the final  $F_v/F_m$  measurement.

#### 2.2.4 Determination of turgor loss point

Two leaf samples were collected from three individuals of each species for the determination of water potential at the turgor loss point using vapor pressure osmometry the following day (Fig. 6). We started by cutting two discs per leaf with a 4-mm cork borer and wrapping them into aluminum foil. Then, the samples were submerged in liquid nitrogen (LN<sub>2</sub>) for at least two minutes. After the leaf discs were deep frozen to rupture cell walls, they were pricked about 20 times with a dissecting needle and placed in the



Figure 6 Vapor pressure osmometer used for the determination of πtlp. The device measures the pressure required to maintain an isotonic solution, providing an accurate measurement of the leaf turgor loss point (πtlp).

measuring chamber (10  $\mu$ L) of the vapor pressure osmometer. When the equilibrium was established, the osmolarity values given by the device were used to calculate the osmotic potential at full hydration and the turgor loss point ( $\pi_{tlp}$ ) using the standard conversion factors established by Bartlett et al. (2012).

#### 2.2.5 Estimation of functional leaf traits

For estimating functional leaf traits such as LMA (g m<sup>-2</sup>) and PLA (%), we collected fully expanded leaves of three individuals per species without any symptoms of disease or damage. For the measurement of the LMA, midrib and all veins are considered part of the leaf. We collected and cut the branches with leaves still attached as described above. Before measuring, each leaf was freshly cut from the stem, and the petioles were removed. Next, the freshly cut leaves were scanned with a flatbed scanner (OpticSlim 2610 Plus Scanner, Plustek, Taipei, Taiwan) and stored as image files. The leaf area was calculated from the scanned images using a self-developed R-Script. Subsequently, the leaves were dried in an oven at 60 °C for at least two days. The dried leaves were scanned again, and dry weight was measured. LMA was calculated as the ratio of leaf dry mass to leaf area (g m<sup>-2</sup>), and the PLA was calculated as the ratio of leaf area between dried leaves and freshly cut leaves (%) (Cornelissen et al. 2003).

#### 2.2.6 Data processing

For the calculation of the  $F_v/F_m$  response, a log-logistic curve according to Kunert et al. (2022) was used, Eq. 1:

$$\frac{F_v}{F_m} = c + \frac{d-c}{1+Exp\left[blog(T/T_{50})\right]}$$
Eq. 1

where *T* describes the temperature and  $T_{50}$  describes the temperature above which  $F_v/F_m$  corresponds to 50% of the maximum (Fig. 3). The slope of the curve at  $T = T_{50}$  is described with *b*, while  $F_v/F_m$  of the lower plateau is described with *c* and the  $F_v/F_m$  of the higher plateau with *d*. If an asymmetric curve shape described the thermal response of a species, the following extension of Eq. 1 was used. This allows curvature differences before and after  $T = T_{50}$ , Eq. 2:

$$\frac{F_{\nu}}{F_{m}} = c + \frac{d-c}{1 + fExp\left[b_{1}Log\left(\frac{T}{T_{50}}\right)\right] + (1-f)fExp\left[b_{2}Log\left(\frac{T}{T_{50}}\right)\right]} \text{ with } f = 1 + Exp\left[\frac{b_{1}b_{2}}{|b_{1}b_{2}|}Log\left(\frac{T}{T_{50}}\right)\right] \text{ Eq. 2}$$

where,  $b_1$  and  $b_2$  describe differences in curvature around  $T_{50}$ . To find the best fitting function, the 'modelFit' function from the 'drc' package in R was used (Ritz et al. 2015). Using Akaike's (1974) information criterion based on the selection of the model with the smallest AIC describing the best fit, we decided whether to use Eq. 1 or Eq. 2. Six different values of the fitted curves were calculated to assess if differences in the thermal responses of the species existed. With the ED function, we could calculate  $T_5$ ,  $T_{50}$ , and  $T_{95}$ .  $T_5$  describes the temperature at which the decline is 5%,  $T_{50}$  with a decline of 50%, and  $T_{95}$  with 95% of the maximum change (d-c). Data analysis was performed using the R program, version 4.2.1 (R Core Team 2022).

#### 2.2.7 Statistical analysis

Pearson's product-moment correlation coefficient was utilized to measure the bivariate relationships between  $T_5$  and DW<sub>T95-T5, T50-5, T95-T50</sub> in the tree species sampled in Traunstein (Fig. 4). In addition, correlations were analyzed between  $\pi_{tlp}$ , thermal sensitivity, and thermal tolerance values among the tree species sampled in Traunstein supported by additional data from Vienna (Fig. 5 and 6). LMA and PLA were also evaluated for their correlation with thermal sensitivity and tolerance values of the tree species sampled in Traunstein (Figs. 7, 8, 9 and 10). The assumptions of normality and homogeneity of variance were tested using Shapiro-Wilk and Levene's test, respectively. The data analysis was conducted using the R software package (R Core Team 2022).

#### 2.3 Results

 $T_5$  averaged 41.7 ± 1.5 °C across all 15 measured species. The highest  $T_5$  was observed in Wild cherry (*Prunus avium* L.) at 47.9 ± 3.9 °C and lowest in European ash at 35.4 ± 1.4 °C. Between species, variation of  $T_5$  within the genus was higher for *Acer* with 38.2 ± 1.2 °C to 41.4 ± 1.4 °C than for *Salix* ranging from 42.5 ± 0.5 °C to 42.5 ± 0.8 °C.  $T_{50}$  values were, on average, at 48.7 ± 0.4 °C with Norway maple (*Acer platanoides* L.) having the highest  $T_{50}$  (53.6 ± 0.7 °C). The lowest  $T_{50}$  values have been found in Silver fir (45.2 ± 0.5 °C) and European ash (46.1 ± 0.37 °C). For  $T_{95}$  an average temperature of 52.7 ± 1.3 °C has been found. The highest  $T_{95}$  was measured for European ash (55.3 ± 0.7 °C) and lowest for Silver fir (47.9 ± 6.6 °C).



Figure 7 Temperature response of PSII efficiency (Fv/Fm) to a 30-minutes lasting heat treatment of the leaves of 15 different species.

As for the width of decline between  $T_{50}$  and  $T_5$ , the average was 7.0 °C. The highest DW<sub>T50-T5</sub> was found in Norway maple beeing 15.5 °C and lowest in *Prunus avium* beeing 1.6 °C.

Regarding the  $\pi_{tlp}$ , an average  $\pi_{tlp}$  with  $-2.01 \pm 0.04$  kPa, the most negative  $\pi_{tlp}$  for European beech ( $-2.58 \pm 0.04$  kPa), and least negative for Goat willow (*Salix caprea* L.) ( $-1.35 \pm 0.03$  kPa) were observed. LMA was highest in Norway spruce and the lowest in Norway maple. Leaves of European alder (*Alnus glutinosa* (L.) in Gaertn.) were characterized by the highest reduction in leaf area (PLA) (36.44%) and Silver fir (6.69%) by the lowest reduction (Fig. 7).



Figure 8 Relationships between the breakpoint temperature (T<sub>5</sub>) and the decline width (DW). Three different temperature windows are present. a shows when Fv/Fm declines from 95% to 5% of the maximum F<sub>v</sub>/Fm level (DW<sub>T95-T5</sub>, broadleaved trees (Traunstein): y = -0.90x+51.18, R<sup>2</sup>=0.37, p < 0.05), b the F<sub>v</sub>/Fm decline from 50 to 5% of the maximum F<sub>v</sub>/Fm level (DW<sub>T50-T5</sub>, broad-leaved trees (Traunstein): y = -1.08x + 54.15, R<sup>2</sup> = 0.51, p < 0.05), and c F<sub>v</sub>/Fm declines from 95 to 50% of the maximum F<sub>v</sub>/Fm level (DWT95-T50, broad-leaved trees (Traunstein): y = 0.18x - 2.97, R<sup>2</sup> = 0.04, p > 0.1)



Figure 9 Relationships between thermal tolerance traits and leaf turgor loss point (π<sub>dp</sub>). **a** The breaking point temperature (T<sub>5</sub>, broad-leaved trees (Traunstein, Vienna): y=-1.72x+38.79, R<sup>2</sup>=0.03, p>0.1, **b** the temperature of 50% decline of F<sub>v</sub>/F<sub>m</sub> (T<sub>50</sub>, broad-leaved trees (Traunstein, Vienna): y=-5.09 + 40.22, R<sup>2</sup>= 0.296, p < 0.05, **c** the temperature of 95% decline of F<sub>v</sub>/F<sub>m</sub> (T<sub>95</sub> broad-leaved trees (Traunstein, Vienna): y=-5.11+44.72, R<sup>2</sup>= 0.229, p < 0.05</p>

For the  $T_5$  values, a significant negative correlation with the DW<sub>T50-T5</sub> ( $R^2 = 0.947$ , P < 0.001) were observed. Species with lower  $T_5$  had a wider decline width from  $T_{50}-T_5$  (Fig. 8). The data set was extended by 12 species from Kunert and Hajek (2022) which aligned with these relationships, and species with a higher  $T_5$  showed a steeper and more sudden decline in  $F_v/F_m$  with a narrow DW<sub>T50-T5</sub>. Significant correlations were reported between  $\pi_{tlp}$  and  $T_{50}$  ( $R^2 = 0.296$ , P

< 0.05) and  $T_{95}$  values ( $R^2 = 0.229$ , P < 0.05), but  $T_5$  values did not correlate significantly ( $R^2 = 0.04$ , P > 0.05).

Tree species characterized by a more negative  $\pi_{tlp}$  showed higher  $T_{50}$  and  $T_{95}$  values. The additional data set aligned with the mentioned relationships. A trend could be observed showing that species with a higher  $T_{50}$  ( $R^2 = 0.296$ , P < 0.05) and  $T_{95}$  ( $R^2 = 0.229$ , P < 0.05) were characterized by a more negative  $\pi_{tlp}$  (Fig. 9). No significant statistical relationship was observed between  $\pi_{tlp}$  and thermal sensitivity traits (DW<sub>T95-T5</sub>, T<sub>50-T5</sub>, T<sub>95-T50</sub>) (Fig. 10).

An absence of significant correlation was discovered between LMA and  $T_5$  ( $R^2 = 0.06$ , P > 0.1) in broadleaved trees during the investigation of the relationship between thermotolerance traits and LMA. However, a significant correlation was observed between LMA and  $T_{50}$  ( $R^2 = 0.46$ , P < 0.05), indicating that broad-leaved species with higher LMA have a lower  $T_{50}$  value.  $T_{95}$ was found to significantly correlate with LMA values with  $R^2 = 0.44$ , P < 0.05 (Fig. 11).



Figure 10 Relationships between the osmotic potential at turgor loss ( $\pi_{tlp}$ ) and the decline width (DW). Three different temperature windows are present. **a** shows when  $F_{v}/F_{m}$  declines from 95% to 5% of the maximum  $F_{v}/F_{m}$  level (DW<sub>T95-T5</sub>, broad-leaved trees (Traunstein, Vienna): y = -3.39x + 5.93,  $R^2 = 0.06$ , P > 0.1), **b** the  $F_{v}/F_{m}$  decline from 50% to 5% of the maximum  $F_{v}/F_{m}$  level (DW<sub>T50-T5</sub>, broad-leaved trees (Traunstein, Vienna): y = -3.5x + 1.06,  $R^2 = 0.07$ , P >0.1), and **c**  $F_{v}/F_{m}$  declines from 95% to 50% of the maximum  $F_{v}/F_{m}$  level (DW<sub>T95-T50</sub>, broad-leaved trees (Traunstein, Vienna): y = 0.13x + 4.91,  $R^2 = 2.53e^4$ , P > 0.1).



Figure 11 Relationships between thermal tolerance traits and leaf mass area (LMA). **a** the breaking point temperature ( $T_5$ , broad-leaved trees (Traunstein): y = 0.54x -0.26,  $R^2 = 0.06$ , P > 0.1, **b** the temperature of 50% decline of  $F_v/F_m$  ( $T_{50}$ , broad-leaved trees (Traunstein): y = -2.04 + 122.31,  $R^2 = 0.46$ , P < 0.05, **c** the temperature of 95% decline of  $F_v/F_m$  ( $T_{95}$  broad-leaved trees (Traunstein): y = -2.23 + 140.88,  $R^2 = 0.44$ , P < 0.05).

Furthermore, significant correlations were observed for LMA with DW<sub>T95-T5</sub> ( $R^2 = 0.28$ , P < 0.1) and DW<sub>T50-T5</sub> ( $R^2 = 0.34$ , P < 0.05), showing that species with higher LMA have a smaller DW. Thus, species with smaller LMA have a higher sensitivity to heat (Fig. 12).

In addition, the relationship between PLA and thermal traits was examined. The results showed a correlation between PLA,  $T_{50}$  ( $R^2 = 0.466$ , P < 0.05), and  $T_{95}$  ( $R^2 = 0.238$ , P < 0.1), suggesting that higher PLA is related to lower thermal values for  $T_{50}$  and  $T_{95}$ , and therefore, decreased tolerance to heat stress. There has been no significant correlation between PLA and  $T_5$  ( $R^2 = 0.026$ , P > 0.1). Yet, species with higher PLA tended to show lower thermal values (Fig. 13). No significant correlations were observed between the DW<sub>T95-T5, T50-T5, T95-T50</sub> and PLA (Fig. 14).



Figure 12 Relationships between the leaf mass per area (LMA) and the decline width (DW). Three different temperature windows are present. **a** shows when  $F_v/F_m$  declines from 95% to 5% of the maximum  $F_v/F_m$  level (DW<sub>T95-T5</sub>, broad-leaved trees (Traunstein): y = -0.91x + 32.82,  $R^2 = 0.280$ , P > 0.1), **b** the  $F_v/F_m$  decline from 50% to 5% of the maximum  $F_v/F_m$  level (DW<sub>T50-T5</sub>, broad-leaved trees (Traunstein): y = -0.91x + 32.82,  $R^2 = 0.280$ , P > 0.1), **b** the  $F_v/F_m$  decline from 50% to 5% of the maximum  $F_v/F_m$  level (DW<sub>T50-T5</sub>, broad-leaved trees (Traunstein): y = -0.99x + 29.79,  $R^2 = 0.34$ , P > 0.1), and **c**  $F_v/F_m$  declines from 95% to 50% of the maximum  $F_v/F_m$  m level (DW<sub>T95-T50</sub>, broad-leaved trees (Traunstein): y = 0.32x + 20.97,  $R^2 = 0.01$ , P > 0.1).



Figure 13 Relationships between thermal tolerance traits and percentage loss of area (PLA). **a** the breaking point temperature (*T*<sub>5</sub>, broad-leaved trees (Traunstein): y = -0.11x + 55.61,  $R^2 = 0.026$ , P > 0.1, **b** the temperature of 50% decline of  $F_v/F_m$  (*T*<sub>50</sub>, broad-leaved trees (Traunstein): y = -0.17 + 52.91,  $R^2 = 0.43$ , P < 0.05, **c** the temperature of 95% decline of  $F_v/F_m$  (*T*<sub>95</sub> broad-leaved trees (Traunstein): y = -0.11 + 55.61,  $R^2 = 0.24$ , P < 0.1).



Figure 14 Relationships between percentage loss of area (PLA) and the decline width (DW). Three different temperature windows are present. **a** shows when  $F_{v}/F_{m}$  declines from 95% to 5% of the maximum  $F_{v}/F_{m}$  level (DW<sub>T95-T5</sub>, broad-leaved trees (Traunstein): y = -0.29x + 25.45,  $R^2 = 0.02$ , P > 0.1), **b** the  $F_{v}/F_{m}$  decline from 50% to 5% of the maximum  $F_{v}/F_{m}$  level (DW<sub>T50-T5</sub>, broad-leaved trees (Traunstein): y = -0.62x + 26.75,  $R^2 = 0.07$ , P > 0.1), and **c**  $F_{v}/F_{m}$  declines from 95% to 50% of the maximum  $F_{v}/F_{m}$  nevel (DW<sub>T95-T50</sub>, broad-leaved trees (Traunstein): y = 1.32x + 16.69,  $R^2 = 0.08$ , P > 0.1).

#### 2.4 Discussion

The present study is the first comparative analysis of thermal and drought resistance traits in a wide range of mature temperate coniferous and broadleaved trees. The results demonstrate that thermal sensitivity is related to morphological and physiological traits that describe drought resistance. Species characterized by higher drought resistance tended to have higher breaking point temperatures than species characterized by lower drought resistance. This was further reflected in the thickness and toughness of the leaves, as species with higher xeromorphy were less sensitive to heat stress.

#### 2.4.1 Dependence of thermotolerance on drought resistance traits

Our study suggests that the adaptation strategy of trees from temperate forests to extreme heat cannot be separated from their adaptation to resist drought stress. We found that species with higher thermal tolerance were characterized by physiological traits representing higher drought resistance, particularly  $\pi_{tlp}$  (Kunert et al. 2021a; McGregor et al. 2021; Vargas et al. 2022). From an evolutionary perspective, a co-adaptation of temperate trees to both stressors, heat, and drought, is very likely for two reasons. First, periods of extreme heat and water limitation potentially co-occur during the summer (Kurjak et al. 2019), and second, extreme heat can induce water shortage due to increased atmospheric evaporative demand (Chaves et al. 2003; De Boeck and Verbeeck 2011). In this sense, Konôpková et al. (2018) suggested that a tree species' thermal sensitivity strongly depends on its drought avoidance strategy. Trees exposed to heat face the trade-off between cooling through transpiration, the risk to suffer from water limitation, or avoiding water stress by stomatal closure, but the risk of overheating foliage. Tree species

characterized by a higher drought tolerance can be assumed to have evolved adaptations to resist higher temperatures. From a trait-based perspective, species with more negative  $\pi_{tlp}$  can cool leaves during heat waves for a longer period than tree species with a less negative  $\pi_{tlp}$ (Kunert et al. 2021a; Kunert and Hajek 2022) due to their ability of soil water uptake under more negative soil water potential. However, various studies suggest that a combination of drought and heat might affect the thermotolerance of trees. For example, pre-exposure to drought stress has been found to influence the thermostability of the PSII in trees (Epron 1997; Ladjal et al. 2000). An early summer drought might act as a trigger to enhance the thermostability of coniferous tree seedlings, and accordingly increase their thermotolerance (Ladjal et al. 2000). In turn, we suspect that with no pre-exposure to drought or in regions with high precipitation rates, forest trees might be especially susceptible to sudden heatwaves. Our field site in Traunstein is historically well supplied with sufficient rainfall due to the orographic lift in the vicinity of the alps. Evidence was found that the trees at the study site are characterized by a higher sensitivity to heat stress compared to trees at already drier sites. For example, Kunert and Hajek (2022) describe  $T_5$  and  $T_{50}$  values collected in the Vienna woods for the same species that are several degrees higher than at the Traunstein site (e.g., Sycamore maple:  $T_5 = 41.7$  °C in Vienna and 38.2 °C in this study). Indeed, both sites are characterized by climatic differences, as other factors than climate might also play a role, e.g., soil quality. Further, the combination of plant stress caused by heat and drought with other stressors, e.g., air pollution can have synergistic negative effects on plants and can produce somewhat similar responses in plants (Bormann 1985). The Traunstein plot received, on average, 1060 mm of rainfall per year, whereas the Vienna woods received less than 1000 mm and in the southern parts only 600 mm of rainfall. However, regional temperature differences might also be crucial in the intraspecific variation of thermal tolerance traits. Kurjak et al. (2019) found that European beech growing at warmer sites was characterized by a higher thermotolerance than at colder sites. This would also apply to the abovementioned example, as the mean annual temperature at Traunstein (7.3 °C) is much lower than at Vienna woods (10.9 °C).

#### 2.4.2 Leaf functional traits and thermotolerance

This study presents the first evidence of a relationship between leaf functional traits and the leaf thermal sensitivity of tree species growing in a temperate forest with high precipitation rates. At our study site, thicker leaves (higher LMA) and leaves shrinking less upon desiccation (lower PLA) were characterized by a lower thermal sensitivity. Both higher LMA and PLA

reflect a greater investment in leaf structural components resulting in more rigid leaves and leaf xeromorphy. Those attributes improve a species' ability to withstand abiotic and biotic stress (Onoda et al. 2011). The observed relationship between functional leaf traits, particularly LMA, and thermal sensitivity has been described predominantly in hot and dry environments (Sastry et al. 2018). Despite the distinct different climatic conditions at our study site compared to the earlier study (Kunert and Hajek 2022), we found a significant relationship between LMA and thermal sensitivity, which is congruent with studies from a large variety of ecosystems worldwide (e.g., desert ecosystem, Curtis et al. 2014; tropical dry forest, Sastry and Barua 2017; desert and coastal ecosystem, Knight and Ackerly 2003). Most of the mentioned studies were conducted in, at least seasonally, arid and hot environments. Plants growing in arid and hot environments represent the highest end of xeromorphy, and xeromorphic leaves can be expected to have low thermal sensitivity.

In the literature, the variation of LMA is described to be linked to the "slow-fast" resource acquisition spectrum (Wright et al. 2004; Reich 2014). Further, we propose that LMA is a good indicator of the xeromorphic spectrum of an ecosystem, particularly with PLA as a co-explaining trait. In contrast to mesomorphic leaves, xeromorphic leaves show a reduced external area in relation to their thickness and are characterized by certain modifications in internal leaf structure (Shields 1950). For example, more xeromorphic leaves have a decreased cell size, thicker cell walls, and a denser network of veins. Furthermore, the palisade mesophyll has a great expansion relative to the spongy mesophyll (Schimper et al. 1903; Maximov and Krasnosselsky-Maximov 1924). These internal anatomical characteristics have important effects on the shrinking behavior of leaves upon desiccation, and xeromorphic leaves will shrink less upon desiccation than mesomorphic leaves. The shrinking behavior of leaves has been shown to affect the cell's structural integrity and leaf hydraulic vulnerability (Scuffoni et al. 2014). PLA as a functional leaf trait represents a proxy of xeromorphy as it has been shown to predict growth reduction during drought in combination with  $\pi_{tlp}$  (McGregor et al. 2021). Accordingly, a combination of LMA and PLA might be an easy and measurable approach to extend the current work on a larger species pool to choose species for the climate change adaption strategy in Central European Forests.

#### 2.4.3 Diverging trends in trait relation in coniferous and broadleaved trees

Our study highlights the urgent need to implement large-scale climate-change adaptation to the managed forest in Central Europe. This study was conducted in an area that is currently not experiencing a significant reduction in precipitation. In the area, Norway spruce is currently the dominating tree species, and due to expected low shifts in precipitation, this species is not expected to be as heavily affected by drought-induced mortality as in other regions. However, Kunert (2020) proposed that the trigger for Norway spruce mortality is less related to droughtinduced stress but more to low thermal tolerance. This hypothesis is supported by the finding that Norway spruce has a more negative  $\pi_{tlp}$  of -2.41 MPa than most species. A more negative  $\pi_{tlp}$  indicates a higher drought tolerance (e.g., Bartlett et al. 2012; Kunert et al. 2021b; Vargas et al. 2022), and Norway spruce were accordingly even more leaf-level drought resistant than common oak (-2.23 MPa) and almost as resistant as European beech (-2.58 MPa). In contrast, the thermal tolerance of Norway spruce, expressed as  $T_{50}$  (46.7 ± 0.4 °C), was at the lower end of the found values compared to the average  $T_{50}$  of the entire species pool (48.7 ± 0.4 °C). Kunert et al. (2021a) show the same relationship, a more negative  $\pi_{tlp}$  combined with a comparably low thermal tolerance, identifying Norway spruce as a very heat-sensitive species. It should be noted that Kunert et al. (2021) found a negative relationship between leaf thermal tolerance and  $\pi_{tlp}$  in conifers. Conifer species that are more drought tolerant were found to be less thermal tolerant, while drought-sensitive species were found to be more thermal tolerant.

In this study, only three conifer species were available, so it was not possible to verify the previous findings of Kunert et al. (2021a). In the Traunstein study, a positive relationship between thermal tolerance and drought resistance traits was found in broadleaved species. It is thought that the difference in the direction of the relationship may be due to the different anatomy of conifer and broadleaved tree species. For example, evergreen coniferous leaves have extended leaf longevity (Norway spruce four to seven years and Silver fir up to 11 years in the lowlands) compared to broadleaved winter-deciduous leaves. This longer leaf longevity means a much higher investment into leaf structure from the beginning and is notable in our study's LMA of the conifers. The LMA of the evergreen conifer leaves was distinctively different from the broadleaved trees (10 times higher than the highest LMA of the broadleaved species). Therefore, it is suggested that evergreen conifers and broadleaved tree species should be treated separately in studies focusing on thermal traits due to their differing leaf anatomy. Interestingly the thermal traits and LMA of broadleaved-like deciduous conifer leaves, like the leaves of the bald cypress, align well with the relationship commonly found among broadleaved species.

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#### 2.5 Conclusions

This study demonstrates that the species pool of a wet temperate forest contains a range of species with notable differences in thermal tolerance and thermal sensitivity. The leaf thermal properties of the species are largely explained by leaf functional and morphological traits and significantly increase with higher drought tolerance. The observed breaking point temperatures at the lower end towards drought-sensitive species indicate that various species are already negatively affected by peak temperatures during the summer. As those peak temperatures will be higher and more frequent in the future, heat waves will be a significant challenge in Central European forests. It is shown that broadleaved species with a less negative turgor loss point and low leaf mass per area are less resistant to heat and more sensitive to drought. Therefore, broad-leaved species with more negative turgor loss points and high leaf mass per area should be in the focus of climate change adaptation strategies. We conclude that species with drought-adapted foliage can potentially deal better with heat stress by maintaining transpirational cooling during climatic stress.

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#### **3 WILD CHERRY – A TREE FOR CLIMATE CHANGE**

Norbert Kunert, Ines K. Münchinger

#### in AFZ-Der Wald

#### Abstract

The recent intensification of drought and heat has emphasized the urgent necessity to adapt cultivated forests to the rapidly changing climate. The selection of tree species capable of withstanding these conditions in a sustainable manner is currently a topic of extensive discussion, Recommendations for practival cultivation trials of alternative tree species are primarily based on either correlative species distribution models or empirical observations. In this study, we evaluate the potential of wild cherry as a candidate for climate change mitigation by assessing its suitability based on plant physiological parameters.

#### 3.1 Introduction

Due to the rise in weather extremes brought on by climate change, the cultivation of several key tree species important for forestry in Central Europe, such as spruce, pine, and beech, is now at higher risk of being negatively affected. The summer drought, as well as the extreme heat that occurred last year, will further increase this risk. Silvicultural measures, such as reducing stocking rates or rotation times, can counteract drought stress, but their impact on mitigating the threat posed by heat is limited. For example, reducing stand height to shorten the water transport path in the trunk and lower the risk of cavitation, or reducing competition for soil water, can help alleviate drought stress. However, these measures do not significantly enhance the resilience of existing stands during extreme heat waves. One option to increase heat resistance is to genetically adapt stands with heat-tolerant provenances or, as a last resort, to replant with heat-resistant tree species. However, the genetic diversity of the above-mentioned relevant tree species has become limited, necessitating a shift in species. Recommendations on the suitability of tree species as climate change trees are very diverse but are frequently based on conventional correlative species distribution models that do not account for factors such as species interactions or local pathogen pressures. Hence, field observations by practitioners are of great importance. In Central Franconia, which is strongly affected by climate change, wild cherry has emerged as a very competitive climate change tree species in recent years and is increasingly used in the reforestation of heavily stressed stands (Fig. 1). Here, observations from the field will be compared with plant physiological parameters and the suitability of the tree species as a climate change woody plant will be evaluated.



Figure 15 Successfully reforested area in the district of Fürth with wild cherry trees after a damage event and 100% failure of pine trees.

#### **3.2** Ecology and silvicultural use of the bird cherry

The wild cherry tree, due to its great importance for fruit cultivation and ecology, is one of the most important European deciduous trees of the rose family (Rosaceae). It is a natural component of various mixed forest types. Generally, the bird cherry tree is seen as a pioneer species that quickly colonizes clearings and grows very quickly. In its early youth, it tolerates strong shading, but its light needs to increase as it ages (Paciak 2013). Accordingly, it is used for forestry as a group intermixture with sycamore maple and ash, as well as for filling gaps in beech stands. The rotation period varies between 60 and 90 years depending on the location. In terms of its site requirements, the wild cherry tree prefers deep, fresh, nutrient-rich, lime-rich soils with good water supply and high base saturation. South-facing slopes are particularly preferred, indicating a preference for a sunny, warm location. With sufficient base saturation, it shows a pronounced resistance to drought. Severe winter frosts with temperatures below -20 °C endanger young stems. Late frosts can disrupt bud development and flower formation. Due to its flowers and fruit, the wild cherry tree is an important food source for many insects and bird species. In addition, through extrafloral nectaries at the top of the petiole, on the leaf edges,

or in the leaf axils, it provides numerous insect species, particularly ants, hoverflies, and beetles, with sugar sap even beyond the flowering period (Schmid 2006, Welk et al. 2016). Furthermore, the wild cherry tree is interesting for its wood. It belongs to the deciduous hardwoods and is characterized as medium heavy with a wood density of 0.57 g/cm<sup>3</sup>. As a result, the wood has a high calorific value and is assigned to the same firewood category as maple, willow (Salix spp.), or elm (Ulmus spp.) (Paciak 2013, Ducci et al. 2013, Wauer 2010). The drawback of the wild cherry tree is its vulnerability to diseases. Especially when afforesting with wild cherry, bacterial blight caused by *Pseudomonas syringae* is one of the main dangers. A fungal infestation by Monilia spp. leads to tip dieback and shoot death. In addition, crown vitality is impaired by Monilia. In this case, young plants show strong constriction on the stem, and the lower stem section loses value. Fungal leaf damage can be caused by the leaf spot pathogen Apiognomonia erythrostroma, the leaf spot disease (Phloeosporella padi), and the shot hole disease (Stigmina carpophila). Further damage to young plants is caused by browsing and trampling by deer and mouse feeding. Aphids such as the cherry aphid (Myzus cerasi) pose a significant threat, as excessive infestations can lead to significant growth losses, especially in young plants (Welk et al. 2016, Schröder et al. 2010). A major danger in the age of cutting maturity is root rot, which begins at the age of 50 and spreads strongly until the age of 80, followed by stem rot. The infestation with root rot leads to a reduction in valuable wood and increases the risk of windthrow, especially due to the shallow root system. The infestation with stem rot regularly starts at the age of 80. If the tree is infested, it quickly succumbs to stem rot.

#### 3.3 Drought tolerance and heat resistance of the wild cherry tree

Based on its ecology, it appears that the wild cherry tree can be an interesting climate change tree. Through physiological measurements, this potential as a climate change tree should now be confirmed. Two plant physiological parameters were used to evaluate the climate tolerance of the wild cherry tree. One is the leaf water potential, at which turgor loss occurs, or also equal to the soil water potential, at which the turgor pressure generated in the cell vacuole is lost and the plant begins to wilt irreversibly, called the permanent wilting point. The more negative the species-specific value of the permanent wilting point, the more tolerant the species are to soil drying. The other physiological parameter was the efficiency loss of photosystem II (Fv/Fm) in relation to temperature, which is considered a good measure of the species-specific tolerance to heat stress. Efficiency loss can be determined by a chlorophyll fluorometer and the temperature-dependent change in efficiency reflects irreversible damage to the photosystem. In terms of heat

tolerance, various meaningful parameters can be derived from these temperature dependent measurements. Here, the critical threshold temperature (T5) and the limit temperature (T50) are of particular importance. T5 reflects at which temperature Fv/Fm already shows a loss of 5% and T50 the temperature at which the photosystem only shows half of its maximum efficiency.



Figure 16 Physiological leaf characteristics of wild cherry in comparison to other native species. Leaf water potential at the point of turgor loss of wild cherry in comparison to the main tree Norway spruce (*Picea abies* L..), Scots pine (*Pinus sylvestris* L.) and Common beech (*Fagus sylvatica* L.). The higher the absolute values, the higher the tolerance of the respective species against drought stress. The green band falls within the 25 % and 75 % percentiles of the wilting points of the most common Central European woody plants.

The wild cherry has a wilting point of -2.37 MPa (Kunert and Tomaskova 2020), which is also confirmed by its preference for locations with good water supply. Therefore, it is relatively drought tolerant compared to other native woody plants (shown in the figure as the 75% percentile of wilting points of the 40 most common Central European woody plants). Wild cherry is seen to be less drought tolerant than beech and spruce, which show wilting points of -2.62 MPa and -2.83 MPa, respectively. However, the wild cherry is considerably more drought tolerant than the Scots pine, which has a wilting point of only -2.24 MPa. This highlights the importance of considering various stressors when assessing the factors that contribute to

increased mortality of a species, as drought stress is not always the sole stressor that predicts increased mortality. Based on the wilting point, the spruce is highly drought tolerant. However, the observed tolerance of spruce to drought contradicts the general assumption in the literature (Kunert 2020a). Based on the critical threshold temperature (T5) and the limit temperature (T50), spruce is particularly vulnerable to heat rather than drought. Here, spruce shows a significant loss of efficiency of photosystem II at temperatures as low as 38.5 °C in some places (Kunert and Hajek 2021). On the other hand, the wild cherry shows an extremely high resistance to heat and only shows a 5% efficiency loss at an ambient temperature of 47.9 °C. In comparison to the average curve, its critical threshold temperature is well above the average of 41.7  $\pm$  2.8 °C (Figure 3). From an ecological perspective, this high threshold temperature also explains its competitiveness in natural forest communities on sunny, warm sites, such as southern slopes. The limit temperature is 49.5 °C, which is around the mean value of 48.7  $\pm$  2.3 °C. Therefore, the wild cherry can be considered one of the most heat-tolerant tree species in our native woody flora.



Figure 17 Heat tolerance of the leaves of wild cherry compared to the average temperature sensitivity of a representative Central European woody flora, determined by a temperature-dependent chlorophyll fluorescence. The red curve shows the reaction of wild cherry leaves to extreme temperature treatment, the black curve represents the reaction of a representative selection of species of the native woody flora.

#### 3.4 Conclusion

The Wild cherry can be classified as a relatively drought-tolerant and extremely heat-resistant tree species based on its physiological characteristics. Therefore, it has a high potential to be successfully cultivated as a climate change tree. However, there are also an above-average number of pathogens known, which is probably due to the fact that it's better studied as a more important ornamental tree than the average forest tree. Therefore, clear, especially large-scale cultivation recommendations in pure stands should be used with caution. However, the wild cherry will gain in importance in mixed plantings, as its introduction not only brings high tolerance to climatic changes but also ecological advantages. It can clearly be seen as an ecological enhancement of stands, as it is a relatively rare woody plant and its rich flowering and extrafloral nectaries are beneficial for insects.

#### 4 SYNTHESIS

As a conclusion to this thesis, the most important findings of the individual publications will be integrated and placed into a comprehensive context. The present study represents the first comparative analysis of thermal and drought resistance traits of a wide range of mature temperate coniferous and deciduous trees. Moreover, it provides the first evidence for a relationship between leaf functional traits and leaf thermal sensitivity of tree species growing in a temperate forest with high precipitation rates.

Chapter two revealed a high diversity of species with remarkable differences in thermal tolerance and thermal sensitivity within the pool of species occurring in a moist temperate forest. This was demonstrated, e.g., by the highest T5 value, as a thermal tolerance trait, of wild cherry with 47.9 +- 3.9 °C, whereas European ash exhibited the lowest T5 value of 35.4 +- 1.4 °C, indicating that the wild cherry is the most thermal tolerant of the species studied. It is also associated with the lowest thermal sensitivity by having the narrowest DW<sub>T50-T5</sub> with 1.6 °C. In addition, it is shown that the thermal properties of the species' leaves can largely be explained by functional and morphological leaf traits which increase significantly with increasing drought tolerance. This confirms our suggestion, that the adaptation strategy of trees from temperate forests to extreme heat might not be separated from adaptation to resist drought stress. This was evident, e.g., by the fact that species with a higher LMA, lower PLA, reflected in the thickness and toughness of leaves, exhibiting a higher xeromorphism and more negative  $\pi_{tlp}$ , showed higher thermal tolerance and sensitivity values. It has been demonstrated, that LMA, with PLA as a co-explaining trait, is a good indicator for the xeromorphic spectrum of an ecosystem.

According to the findings presented in chapter two, the wild cherry tree exhibits characteristics that make it a promising candidate for climate change adaptation. This is due to its relatively high drought tolerance and remarkable heat resistance. In chapter three, a user recommendation is proposed based on a comparison of the wild cherry's plant physiological parameters, including  $\pi_{tlp}$ , T5, and T50, with those of three prominent tree species: the European beech, Scots pine, and Norway spruce. The wild cherry demonstrates relatively high drought tolerance with a  $\pi_{tlp}$  of -2.37 MPa and exceptional heat resistance with T<sub>5</sub> values of 47.9 °C and T<sub>50</sub> with 49.5 °C. However, despite its drought tolerance, several factors must be considered to predict mortality factors, as multiple factors contribute to a species' survival. The Norway spruce, with its more negative  $\pi_{tlp}$ , has a higher resistance to drought, but with a lower T<sub>5</sub> of 38.5 °C, it is more susceptible to heat than drought. The wild cherry, on the other hand, is considered to be one of the most heat-tolerant tree species among Central European woody flora. The research also

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provides guidance on the practical applications of wild cherry in forestry, including its use as a group admixture with other tree species, its orcharding and ecological significance, and its susceptibility to pathogens, such as bacterial blight.

To summarize, the results of this study show that high summer temperatures negatively impact several forest species, particularly drought-sensitive species. Heatwaves pose a significant challenge to Central European forests, and prioritizing broadleaved species with drought-adapted foliage in climate adaptation strategies may be beneficial. A simple and measurable method of selecting suitable species for adaptation strategies could be combining leaf mass per area (LMA) and percentage loss of area upon desiccation (PLA). It is recommended to study evergreen conifers and broadleaved species separately when examining thermal traits due to their differing leaf anatomy. Notably, the thermal traits and LMA of deciduous conifer leaves align with those of broadleaved species. Further research is needed to better understand the interactions between heat stress and water limitation and their impact on forest ecosystems. These findings have implications for forest management and further research in the face of climate change in Central Europe.

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## **Oath declaration**

I hereby certify that I have written this thesis independently. I have not used any sources or aids other than those indicated and have marked as such all content taken verbatim or in spirit from other works. The submitted master thesis was or is neither completely nor in essential parts subject of another examination procedure. The electronic version of the submitted master's thesis corresponds in content and formatting to the copies printed on paper.

Ines K. Münchinger Wien, 01.09.2023