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SHORT COMMUNICATION

Leaf temperatures of an Austrian oak are below photosynthetic temperature thresholds during a heatwave in Central Europe

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Abstract

The summer of 2022 has been the so far hottest summer on record in Central Europe. High temperatures negatively affect the physiology of plants and cause considerable thermal stress in particular on the leaf level. The assessment of the temperature-dependent decline of the quantum use efficiency of the photosystem II (Fv/Fm) has gained much popularity to quantify the leaf-level sensitivity to thermal stress. An open question is whether leaves heat to those in vitro estimated threshold temperatures on hot days or if plants can avoid heat stress through transpirational cooling. Therefore, leaf temperatures were monitored on a non-native Austrian oak (*Quercus cerris*) during a heatwave in July 2022 and compared to observed air temperature and leaf thermal traits assessed with a chlorophyll fluorometer. The highest air temperature recorded during the heatwave was 42.5 °C and surpassed the breaking point temperature (temperature at 5% decline of Fv/Fm; T5) by 0.3 °C, but was 6.1 °C lower than T50 (temperature at 50% decline of Fv/Fm). However, during the hottest day, the maximum leaf temperature was significantly below the air temperature. Even the directly illuminated leaf facing south reached a maximum temperature of only 38.7 °C but reached 39.8 °C on the second hottest day when the air temperature went up to 39.6 °C. All leaves showed a certain degree of homeothermy as the slope between leaf temperature and air temperature was 0.83 ($P < 0.05$). In conclusion, Austrian oak can buffer thermal stress during heatwaves to a certain degree, however, leaf temperatures are only marginally below critical threshold temperatures.

Keywords Austrian oak · Climate change · Chlorophyll fluorescence · Photosynthetic decline · Thermal stress

In the last decade observations of extreme climatic events, such as heatwaves and droughts, accumulate due to global climate change worldwide (Sippel et al. 2020). The summer of 2022 has been the hottest and driest summer on record, in particular in Central Europe (Münchinger et al. 2023). In July, maximum temperatures exceeded 41 °C in many areas and some regions received no drop in rainfall for several weeks (European Union, Copernicus Climate Change Service 2022). Such extreme climatic events like in summer 2022 have catastrophic implications on forest ecosystems. In many cases, climatic thresholds of locally adapted forests are surpassed leading to accelerated climate-driven forest mortality (Alizadeh et al. 2020; Senf et al. 2022). In the face of the increasing climatic threat to forest trees, leaf trait-based approaches to assess the climate resistance of the vast number of tree species are gaining much importance (e.g. Vargas et al. 2022; Tordoni et al. 2022). Regarding leaf-level heat resistance, the in vitro method by Krause et al. (2010) and Curtis et al. (2014) to assess the temperature-dependency of the photochemical efficiency of the photosystem II (PSII) via chlorophyll fluorescence is receiving increasing attention. The method takes advantage of the most heat-sensitive component of photosynthesis, which is a pigment-protein complex located in the thylakoid membranes of the chloroplasts (Ashraf and Harris 2013). When

Key message During a heatwave Austrian oak maintained transpirational cooling and kept leaf temperatures several degrees below the recorded maximum ambient air temperature.

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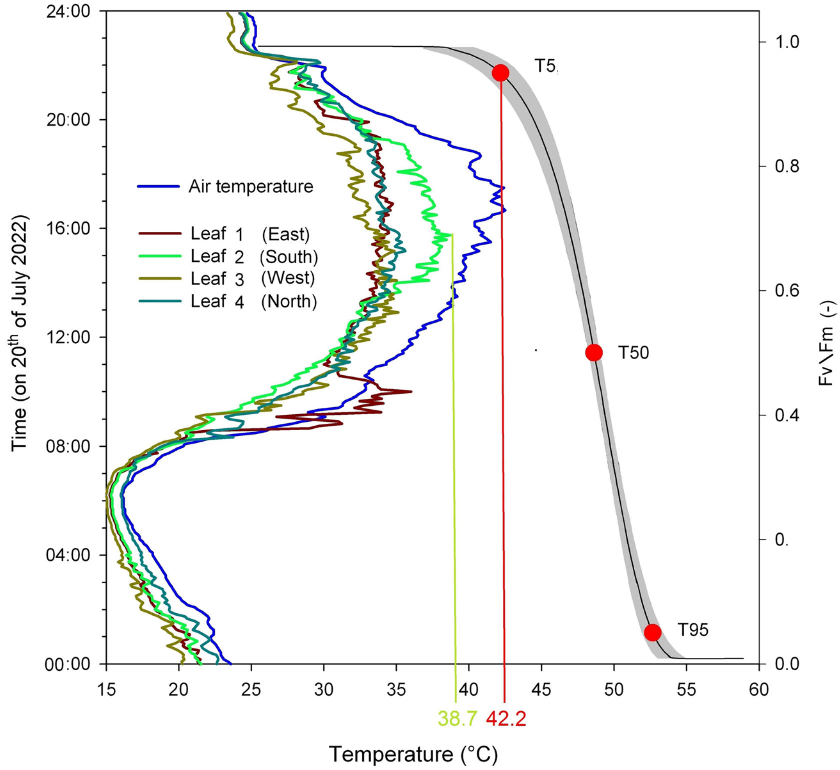

Fig. 1 Diurnal course of leaf and air temperatures measured on the 20th of July 2022. In vitro measured thermal tolerance of Austrian oak is indicated on the secondary y-ordinate (standard error of the temperature-depend photosynthetic decline function is highlighted in gray)

the pigment-protein complex is exposed to a critical temperature irreversible damage to the photochemistry can be assumed (Tiwari et al. 2021; Slot et al. 2021). The higher the degree of damage by extreme temperatures, the lower the photochemical efficiency of PSII which is expressed as the ratio between the variable and maximum chlorophyll fluorescence (Fv/Fm). A variety of thermal tolerance traits can be extracted from those measurements. The most important ones are T5, T50, and T95. T5 refers to the breaking point temperature or the temperature at which Fv/Fm declines by 5%. Analogously, T50 and T95 are the temperatures at which Fv/Fm declines by 50% and 95%, respectively (Tiwari et al 2021). The mentioned thermal tolerance traits have been estimated for a considerable variety of tree species in different climate zones (e.g. Tiwari et al. 2021; Slot et al. 2021; Kunert et al. 2021; Kunert and Hajek 2022), but have mainly been compared to maximum air temperatures of the focal regions. The comparisons of in situ measured thermal tolerance thresholds with air temperatures is also one of the main criticism as those traits should be related to actual leaf rather than air temperature (Tiwari et al. 2021; Kunert et al. 2021; Winter 2024). Existing measurements in temperate forests indicate that leaf temperatures vary largely among species (Guo et al. 2023) and can be within the range of the air temperature or even several degrees warmer when air temperature warms up to a moderate 25 °C (Leuzinger and Körner 2007). However, measurements and literature on leaf temperatures in forests measured during extreme heatwaves, are still rare and a direct comparison of critical leaf temperatures with thermal tolerance traits is absent in the literature. Therefore, I decided to run a spontaneous and preliminary case study with the available material when the formation of a heatwave was announced. Hence, this study presents a unique data set on leaf temperature measurements collected during the extreme heatwave in July 2022 in Germany. Leaf temperature measurements were conducted on an Austrian oak (*Quercus cerris* L.) and compared to in vitro measurements of the photosynthetic thermal temperature thresholds.

The study was carried out in a private orchard in the rural district of Fürth in Middle Frankonia, Germany (49°24′36.0"N, 10°49′39.3"E). With the weather prediction forecasting a heavy heatwave in July 2022, an Austrian oak (*Quercus cerris* L., DBH 15 cm and 5.7 m in height) was equipped with four leaf temperature sensors. Therefore, four thin film thermistors (TT6-10KC8-9–25, TEWA Sensors LLC, Lublin, Poland) were secured to the bottom side of four leaves in the upper canopy with perforated medical tape (Transpore™, 3 M™ GmbH, Austria). The sensors were attached to the abaxial mesophyll surface near the midrib but avoided any large veins (compare Fauset et al. 2018). The four leaves were positioned in the four cardinal directions in the tree crown and could be classified as the sun leaves that are not covered by other leaves. Thermistor output was recorded with a microcontroller (Arduino Mega 2560, Arduino, Italy) directly transferring the data to a desktop PC via the Parallax Data Acquisition tool (PLX-DAQ, Parallax

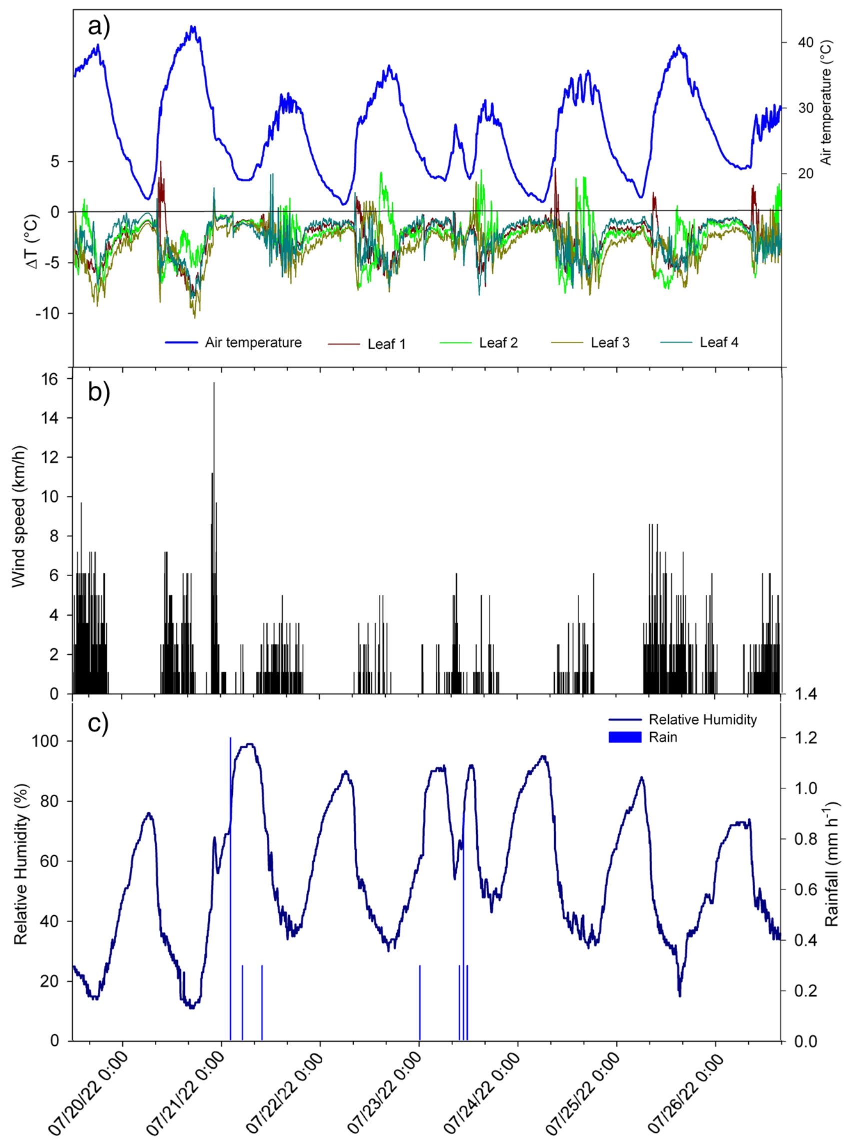

Fig. 2 Diurnal course of a) air temperature and the difference between air temperature and leaf temperature (ΔT) for several days. The wind speed during the same period is shown in b) and c) shows the amount of rainfall and the relative air humidity

Inc., Rocklin, USA). Leaf temperature was recorded every five seconds, however, 5-min averages were used for the analysis. Microclimatic parameters such as air temperature, rainfall, relative humidity and wind speed were measured continuously and recorded every 5 min with a professional weather station (PCE-FWS 20 Weather Station, PCE Inst., Durham, U.K.) in the orchard adjacent to the tree at a height of 2.4 m.

In vitro*,* estimation of the thermal tolerance was performed two weeks after the heat wave. Therefore, the thermal dependency of Fv/Fm was assessed by following the protocol of Krause et al. (2010). Briefly, 40 healthy leaves were collected from a sun-exposed and rehydrated branch of the sample tree and leaf discs were cut from the leaves. Leaf discs were 3 cm in diameter. The leaf discs were wrapped in Miracloth (Merck, Darmstadt) layers and placed into water-tight Whirl–Pak bags. The bags were randomly assigned to one of eight temperature treatments and each bag was placed in a water bath at a given temperature for 15 min. The temperature treatments ranged from 25 °C to 60 °C, increasing the temperature in 5 °C steps. The temperature treatment followed a recovery period where leaf discs were kept under controlled moist conditions (20 °C, ~ 20 μmol m^{-2} s^{-1} light) for 24 h (Tiwari et al. 2021). After the incubation period leaf discs were dark-adapted for 30 min and the recovery of Fv/Fm was measured with a chlorophyll fluorometer (MINI-PAM, Walz, Effeltrich, Germany). A log-logistic curve was used to describe the Fv/Fm-temperature response (Kunert et al. 2021). Curve fitting was performed using the R program, version 4.2.1 (R Core Team 2022). The 'modelFit' function of the 'drc' package was used to test for the best fitting function and the ED function was applied to

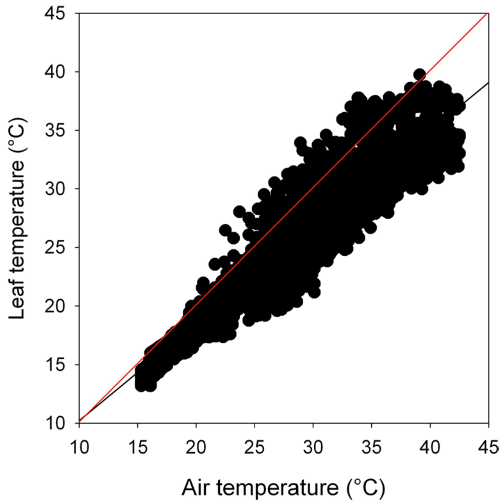

Fig. 3 Linear relationships between leaf and air temperature across all four leaves. ($y = 0.83x + 2.0$, $R^2 = 0.94$, $p < 0.001$). The red line indicates the 1,1 line to highlight the variation from the slope of the regression

calculate T5, T50, and T95 (Ritz et al. 2016). T5 describes the temperature at which Fv/Fm- declines 5% of the maximum. Accordingly, T50 represents 50% and T95 represents 95% of the maximum.

During the heatwave in July 2022, the hottest day was the 20th of July (Fig. 1). On this specific day, the air temperature reached a critical maximum of 42.5 °C (Fig. 1) and relative humidity went down to 11% with no air movement (Fig. 2). Several days later, on the 25th of July, maximum air temperature reached 39.6 °C (Fig. 2). Compared to the in vitro estimated thermal tolerance, air temperature surpassed the breaking point temperature (T5) by 0.3 °C (T5: 42.2 °C) on the 20th (Fig. 1), but did not surpass T5 on the 25th. Actual leaf temperatures were significantly below air temperature during the hottest 5 min on the 20th but were 0.2 °C higher on the 25th (leaf exposed to the south; 39.8 °C). In general, the maximum temperature reached by a leaf depended on its position within the canopy. The leaf positioned on the southern side and thus being the leaf directly exposed to the sunlight and strongly illuminated during the hottest time of the day was heated up most. The maximum temperature observed on the leaf surface facing south reached a maximum of 38.7 °C on the 20th and was only 3.8 °C below the maximum air temperature. The second warmest leaf was the leaf facing to the east, which heat up to 36.0 °C until 10 in the morning but was not directly exposed to the sun after this and cooled down to the temperature level of the not directly exposed leaves positioned in the north and west of the tree crown. Those two leaves reached a maximum temperature of 35.6 °C and 35.2 °C (west and north, respectively). This reflects the importance of a leaf's position within the canopy. Doughty and Goulden (2008) found that well-illuminated leaves can be warmed more than 2.5 to 3 °C higher than poorly illuminated leaves. In this tropical study by Doughty and Goulden (2008), poorly illuminated leaves remained near air temperature whereas sun-exposed leaf temperature could exceed the ambient air temperatures. In the current study, leaf temperatures also exceeded air temperatures in some cases, however only when the leaf was directly illuminated in the morning or afternoon and independent from the heat peak during the heatwave. In general leaf temperature was below air temperature (Fig. 3). The slope between leaf temperature and air temperature across all four leaves was 0.83, which is very similar to the slope value found in grassland species (slope = 0.88, Perera et al. 2019). Perera et al. (2019) concluded that this indicates a certain but limited degree of homeothermy. The investigated species showed the ability to buffer temperature variations to a certain extent. This ability of plants to buffer heat stress on leaf level seems to decline with increasing water stress (Siebert et al. 2014). For example, the canopy temperature was 2.7 °C lower than the air temperature on well-watered olive trees compared to naturally drought-stressed trees, however, air temperature did not reach critical values in this study (maximum air temperature of 35 °C, Akkuzu et al. 2010). I assume, that the investigated oak tree was not water stressed at the time of the heat wave even if the gravimetric soil water content in the top soil layer (0–15 cm) was below 1%. As Mediterranean species, the Austrian oak is most probably better adapted to dry and hot conditions than the native vegetation in Central Europe and could thus maintain transpirational cooling under the environmental conditions in July 2022. During the heatwave and the extreme temperatures, in vitro estimated thermal thresholds were not reached and leaves were accordingly not damaged by the high temperature. This was also reflected in the high quantum use efficiency (Fv/Fm > 0.78) of all four leaves after the heat period. Evaluating the species choice for the measurements in retrospect, I must admit that Austrian oak was somehow an unlucky choice as other species in the surrounding were suffering much more from this heat event and showed a clear decline in Fv/Fm (e.g. *Malus domestica*: Fv/Fm ~ 0.65, *Betula pendula*, Fv/Fm ~ 0.45). Here, I can only speculate that the leaves of apple trees and birch trees heated up much more. Regarding the species-specific heat resistance of Austrian oak, it is well-adapted to the current temperature extremes in Central Europe. However, it is a rather drought-prone Mediterranean oak (Manes et al. 2006) and might potentially suffer during future climate extremes.

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Author contribution NK conducted the study and wrote the manuscript.

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Data availability The data that support the findings of this study are available on request from the author.

Declarations

Conflict of interest I declare that I have no conflict of interest.

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