

**UC Davis**

**UC Davis Electronic Theses and Dissertations**

**Title**

Interactive Effects of Temperature and Water Potential on Whole-Plant Hydraulic Conductance

**Permalink**

<https://escholarship.org/uc/item/3wg154tm>

**ISBN**

9798189227998

**Author**

Rackson, Theresa Marie

**Publication Date**

2026-06-25

Peer reviewed|Thesis/dissertation

Interactive Effects of Temperature and Water Potential on Whole-Plant Hydraulic  
Conductance

By

THERESA MARIE RACKSON  
THESIS

Submitted in partial satisfaction of the requirements for the degree of

MASTER OF SCIENCE

in

Horticulture And Agronomy

in the

OFFICE OF GRADUATE STUDIES

of the

UNIVERSITY OF CALIFORNIA

DAVIS

Approved:

---

Thomas Norman Buckley, Chair

---

Megan Kathleen Bartlett

---

Lawren Sack

Committee in Charge

2026

## **Abstract**

Little is known about effects of temperature ( $T$ ) on whole-plant hydraulic conductance ( $K_{\text{plant}}$ ) in intact plants, due to the conflating influence of changes in water potential that often occur when temperature is changed, because of shifts in evaporative demand and/or stomatal conductance. This study aimed to isolate the effect of temperature on  $K_{\text{plant}}$  from that of water potential in intact plants. Whole plant transpiration was measured by mass loss, water potential was measured in transpiring leaves, and source water potential was estimated using plants that had been bagged for at least 24 hours to prevent transpiration.  $K_{\text{plant}}$  was then calculated from these measurements using Darcy's Law. We measured  $K_{\text{plant}}$  under the following conditions: (Condition 1) 20°C at ~40% RH (VPD = 1.4 kPa); (Condition 2) 30°C at ~75% RH (VPD = 1.06 kPa); (Condition 3) 30°C at 40-50% RH (VPD = 2.33 kPa). Conditions 1 and 2 were designed to vary temperature while minimizing changes in water potential. Conditions 2 and 3 were used to determine the vulnerability curve for  $K_{\text{plant}}$ , which was then used to correct for shifts in water potential between Conditions 1 and 2, enabling us to isolate the influence of temperature *per se* on  $K_{\text{plant}}$ . Our results showed that  $K_{\text{plant}}$  increased by an average of 1.4% per degree C in olives and 10% per °C in sunflowers; olive plants measured during winter dormancy showed reduced gas exchange rates and  $K_{\text{plant}}$  and weakly negative  $T$  responses. These results have implications for effects of  $T$  on  $K_{\text{plant}}$ , including as a possible mechanism driving stomatal opening in response to temperature.

## **Introduction**

Maintaining plant water status is essential for plant survival and productivity. Climate change is causing increasingly frequent and severe drought, heat waves, and higher temperatures overall, and both natural and agricultural systems are already being affected. In high temperatures, plants must navigate the tradeoff between keeping stomata open for CO<sub>2</sub> uptake and growth, vs losing too much water through transpiration. Whole-plant hydraulic conductance ( $K_{\text{plant}}$ , defined as the ratio of whole-plant water flow per unit leaf area to the difference between soil and leaf water potentials) has a large influence on leaf water potential, and indirectly on stomatal conductance. Temperature is thought to affect  $K_{\text{plant}}$  through both biological processes, such as changes in aquaporin activity, and physical processes, such as changes in water viscosity. Yet few studies have examined effects of temperature on  $K_{\text{plant}}$ .

$K_{\text{plant}}$  differs among plants of the same or different species in relation to growth environment temperature. Several studies subjecting young trees to different temperatures during growth showed different effects on xylem conduit size and hydraulic conductivity for different species. Angiosperm saplings (*Abies balsamea*, *Acer saccharum* and *Quercus macrocarpa*) grown in forests experimentally warmed by 3.4°C for 5 years had increased conduit diameter and higher specific hydraulic conductivity, but no significant difference in conduit size and conductivity were reported for two conifer species (*Picea glauca*, *Pinus strobus*) and *Populus tremuloides*, suggesting the effects depend on the location within the species' range (McCulloh et al. 2016). Another study that

grew ponderosa pine (*Pinus ponderosa* L.) seedlings 24 weeks in different temperatures (15°C nights, 25°C days vs. 20°C nights, 30°C days) found larger tracheid diameters in plants grown at elevated temperature, causing an increase in xylem-specific hydraulic conductivity (Maherali and Delucia 2000). However, a study on *Eucalyptus grandis* seedlings grown with a more dramatic temperature difference (10 and 35°C) found that xylem vessel size was smaller at high growth temperature, which was thought to be due to the decrease in water viscosity with higher temperature, making large conduits unnecessary to maintain the same  $K_{\text{plant}}$  (Thomas et al. 2004).

Many studies on the temperature effects on hydraulic conductance have focused on roots, shoots, or leaves, often excised and measured in isolation. These studies have generally shown that hydraulic conductance of individual plant organs increases with temperature (Newman and Jr 1988; Lopez and Nobel 1991; Öunapuu and Sellin 2013; Table 1 in Mills et al. 2026). Previous studies have speculated that changes in conductance at different temperatures may be caused by changes in water viscosity (Tsuda and Tyree 2000). Hydraulic conductivity for bulk flow of water, i.e., in the xylem, is inversely proportional to viscosity, and water viscosity decreases by about 2% per °C. For excised oak roots and shoots, hydraulic conductance increased between 15°C and 35°C, as predicted based on the effect of temperature on water viscosity (Cochard et al. 2000). Some studies have also measured the effect of root temperature on  $K_{\text{plant}}$ .  $K_{\text{plant}}$  increased in intact oak saplings when soil temperature was increased with air temperature held constant (Cochard et al. 2000), implying root  $K$  increases with  $T$ . In cotton seedlings,  $K_{\text{plant}}$  was high when root temperature was above 20°C, and decreased sharply approaching

15°C (Radin 1990). Most published data on leaf hydraulic conductance match or exceed the temperature response expected from viscosity (Matzner and Comstock 2001; Sack et al. 2004; Cochard et al. 2007; Sellin and Kupper 2007; Murai-Hatano et al. 2008).

Few studies have measured the effects of  $T$  on whole-plant  $K$ . A study on sunflower (*Helianthus annuus* L. cv. Russian mammoth) found that evaporative flux and high pressure flowmeter (HPFM) methods gave comparable estimates of  $K_{\text{plant}}$ , and HPFM measurements showed a 53% increase in  $K_{\text{plant}}$  with an 8°C increase in temperature (Tsuda and Tyree 2000). However, this temperature effect was not separated from diurnal effects (Tsuda and Tyree 2000). Data extracted from Schönbeck et al. 2022 showed that in young trees of *Fagus sylvatica* L., *Quercus pubescens* Willd. and *Quercus ilex* L.,  $K_{\text{plant}}$  actually declined with  $T$ . However, plants in that experiment had been left in the growth chamber at the target  $T$  for 5-15 weeks, so an acclimatory response may have been involved, in addition to any short-term response (Schönbeck et al. 2022).

Additionally, most previous studies of  $K$  vs  $T$  have not controlled for variation in water potential that often accompanies variation in  $T$ , e.g., due to variation in VPD and thus in transpiration rate. Several studies have measured excised root  $K$  using methods that do not result in negative water potentials within the tissue, and thus do not require correction for possible  $K$  decline with dehydration (such as the HPFM or root pressure chamber (Bolger et al. 1992; Cochard et al. 2000; Wan et al. 2001; Muhsin and Zwiazek 2002; Murai-Hatano et al. 2008; Zuccarini et al. 2014)), but only two that we are aware of have done so on excised leaves (Sack et al. 2004; Cochard et al. 2007), and only one on shoots (Cochard

et al. 2000). No studies have measured the short-term (sub-diurnal) response of  $K_{\text{plant}}$  to  $T$  while attempting to correct for differences in water potential.

In this study, we aimed to isolate the effects of temperature on whole-plant hydraulic conductance from potentially conflating effects of  $\psi_{\text{leaf}}$ . We measured  $K_{\text{plant}}$  of potted plants at 20°C and 30°C using the evaporative flux method (EFM; computing  $K_{\text{plant}}$  as the ratio of steady-state water flux to soil-plant water potential difference). We also measured  $K_{\text{plant}}$  at high and low VPD holding temperature constant at 30°C to make a vulnerability curve (VC). This VC was used to correct for the effects of changes in water potential on  $K_{\text{plant}}$ , thereby isolating the effect of temperature *per se*. We repeated this for two species with divergent growth forms and water-use strategies: *Olea europea* (olive) Arbequina (a Mediterranean perennial adapted to sustained drought and extreme heat) and *Helianthus annuus* (sunflower) (a drought avoider with extremely rapid gas exchange and growth during brief wet periods). We hypothesized that  $K_{\text{plant}}$  would increase with temperature, due to the decrease in water viscosity and possibly changes in aquaporin function.

## **Methods**

### Plant Material and Growth Conditions:

*Olea europea* L. cv. Arbequina (olive) plants were purchased in 3.8-L pots, repotted into 7.6-L pots, and grown in a greenhouse under supplemental lighting, on the UC Davis campus (38.5381° N, -121.7820° W). We waited at least two weeks to use repotted plants. *Helianthus annuus* L. cv. Sunspot (sunflower) were planted from seed in 7.6-L pots and grown in a greenhouse under supplemental light (18-27°C, 65-80% RH). All experiments were run on mature nonflowering nonfruiting plants. Sunflowers were 4-8 weeks old at the time of measurement. For sunflower individuals that were flowering, we removed inflorescences and waited at least one week before conducting experiments.

### Measurements of hydraulic conductance:

We calculated hydraulic conductance as  $K_{\text{plant}} = E/(\psi_{\text{soil}} - \psi_{\text{leaf}})$ , where  $E$  is whole-plant transpiration rate and  $\psi_{\text{soil}}$  and  $\psi_{\text{leaf}}$  are soil and leaf water potentials, respectively. We measured  $E$  by mass loss,  $\psi_{\text{soil}}$  as the water potential of a leaf before the experiment (after the plant had been bagged and darkened for 24 hours to prevent transpiration and ensure equilibration between the leaf and soil), and  $\psi_{\text{leaf}}$  as the water potential of a leaf during steady-state transpiration. (Specific protocols for mass and water potential measurement are described further below.) Plants were kept in a growth chamber (BioChambers TPRB-74, Winnipeg, Manitoba, Canada), with light set to 90% (photosynthetic photon flux density at plant level  $\approx 1200 \mu\text{mol m}^{-2} \text{s}^{-1}$ ), and air temperature and relative humidity set to one of three conditions:

(Condition 1) 20°C at ~40% RH (VPD = 1.4 kPa)

(Condition 2) 30°C at ~75% RH (VPD = 1.06 kPa)

(Condition 3) 30°C at 40-50% RH (VPD = 2.33 kPa)

These three conditions were chosen to generate data that would enable us to isolate the influence of temperature *per se* on  $K_{\text{plant}}$ . Conditions 1 and 2 were designed to vary temperature while minimizing changes in water potential: we anticipated that stomatal conductance would increase at the higher temperature (e.g., (Mills et al. 2024; Mills et al. 2026)), and we sought to reduce the impact of that increase on transpiration rate (and hence on  $\psi_{\text{leaf}}$ ) by also reducing VPD. However, it was impossible to anticipate exactly how much VPD would need to be reduced to prevent any change in  $\psi_{\text{leaf}}$ , and as a result,  $\psi_{\text{leaf}}$  was never precisely equal at Conditions 1 and 2. To correct for the impact of those small changes in  $\psi_{\text{leaf}}$ , and thereby to isolate the effect of temperature itself on  $K_{\text{plant}}$ , we measured another point (Condition 3), which was designed to induce a substantial change in water potential by increasing VPD. Comparing the values of  $K_{\text{plant}}$  under conditions 2 and 3 (pooled across individuals to obtain a large enough sample to fit a “vulnerability curve” or VC) enabled us to quantify the effect of  $\psi_{\text{leaf}}$  on  $K_{\text{plant}}$  at constant temperature by fitting a linear least-squares model to log-transformed  $K_{\text{plant}}$  as a function of  $\psi_{\text{leaf}}$ , which we then used to correct for any small change in  $\psi_{\text{leaf}}$  between Conditions 1 and 2 for all experiments for that species. We varied the sequence of Conditions randomly among experiments, because previous authors have reported diurnal trends in hydraulic conductance (Tsuda and Tyree 2000; Nardini et al. 2005; Öunapuu and Sellin 2013); however, we did not notice

any influence of the sequence of the three Conditions on our results (one-way ANOVA,  $F(1,33) = 1.105$ ,  $p = 0.301$ ).

*Preparation and pre-equilibration of experimental plants.* Experiments were conducted between 2025-09-01 and 2026-03-25. For each experiment, plants were transported from the greenhouse to the growth chamber in the morning. Two stakes were placed at opposite edges of each pot, to protect the plant from getting damaged when bagged. A thermocouple was attached to one stake. Each plant was watered to field capacity and excess water was allowed to drain for 10 minutes while loosely covering the plant with a black plastic bag to stop transpiration. Following this initial watering, with the black bag still covering the plant, the pots were placed in an additional bucket and bottom watered, and the entire pot and bucket were sealed in a separate black plastic bag to prevent water loss via the soil surface. For experiments in September 2025, bottom watering was not used; instead, excess water was allowed to drain for 20 minutes before bagging. Trays were placed under pots inside the bags to prevent any possible water leakage. The bag covering the plant was then sealed around the whole plant and bucket. Bagged plants were kept bagged and in darkness for 24 hours to allow full equilibration with the moist soil.

In experiments conducted between 2025-09-01 and 2025-11-11, we used five plants in each experiment. For these experiments, measurements were only done with Conditions 1 and 2. This allowed us to measure four replicates in one day, with the fifth plant used to monitor soil water potential as described below. Experiments conducted

after 2025-11-11 used only one plant per experiment. This enabled faster stabilization of chamber temperature and VPD, making it feasible to measure each plant at all three Conditions.

Soil water potential ( $\psi_{\text{soil}}$ ). At the end of the 24-hour acclimation period, but with the plant still in the darkened chamber, the outer bag covering the plant was opened, a leaf was removed, immediately double-bagged in Whirl-Pak bags (Nasco, Baraboo, Wisconsin) with a wet paper towel in the outer bag, allowed to equilibrate internally (15 minutes in a cooler containing ice for olive, 10 minutes at room temperature for sunflower), and its water potential was measured using a Scholander Pressure Chamber (PMS Model 1505D, Albany, Oregon) and used as a proxy for soil water potential. During pressurization, a wet paper towel was placed inside the pressure chamber (olive), or the leaf was enclosed in a Whirl-Pak bag (sunflower). In some experiments, one plant was left bagged and covered with a cylindrical Reflectix shell to prevent transpiration during the rest of the experiment; this plant was used as a control to test whether water potential would continue to rise during the day, even after the 24-hour pre-equilibration (we found water potential to be stable; Figure 1). The bagged plant and the three other, unbagged plants were each placed in a corner of the growth room, with the corners chosen randomly.

Transpiration rate by mass loss ( $E$ ). To measure transpiration rate by mass loss, the outer bag covering the canopy was removed, while keeping the pot sealed in its bag to prevent soil evaporation and water leakage from the pot. The plant was placed on a

Sartorius CP | Gem<sup>plus</sup> Series balance (Göttingen, Germany) in the center of the growth chamber, with a cardboard shield over the balance to prevent noise in the mass measurement due to air circulation in the growth chamber. Temperature and relative humidity were set to given conditions to induce transpiration, and mass measurements were recorded continuously (0.2 Hz) by a datalogger (CR1000, Campbell Scientific, Logan, Utah) that was enclosed in an insulated box to maintain a steady temperature, and  $E$  was calculated from the rate of change of mass. Plants were left alone and monitored until environmental conditions and transpiration rate were both stable for at least 15 minutes at a given condition. For all datalogger data, the average of the last 15 minutes at each condition was used in subsequent analysis. For runs that were not bottom-watered, after each timepoint the volume of water lost was calculated for each plant, and that amount of water was added to the soil to bring it back to field capacity. Figure 2 shows the experimental setup. For experiments with five plants, at the end of the experiment each plant was defoliated, and leaf area was measured using ImageJ. Transpiration rate for the additional three transpiring plants was estimated from their total leaf areas, by assuming transpiration rate per unit leaf area was constant across all four transpiring plants at steady state; i.e.,  $E_{non-balance\ plant} = E_{balance-plant} \cdot (LA_{balance-plant} / LA_{non-balance\ plant})$ .

Transpiring-plant leaf water potential ( $\psi_{leaf}$ ). After transpiration had reached steady-state at a given temperature and humidity,  $\psi_{leaf}$  was measured as described earlier for  $\psi_{soil}$ . The height of leaves chosen for measurement was kept as consistent as possible within and across plants. For experiments with five plants,  $\psi_{leaf}$  was measured for each plant.

Air temperature, leaf temperature, and relative humidity. For each plant, a type-T thermocouple was placed on the underside of a young but fully expanded leaf. The height of leaves chosen for thermocouples was kept as consistent as possible across plants, and as close a height as possible to leaves chosen for  $\psi_{\text{leaf}}$  measurements. An additional thermocouple and an HMP50 relative humidity sensor (Vantaa, Finland) were mounted on a stick to measure the air temperature and RH, with a Reflectix radiation shield to minimize heat load from the chamber light source. All sensors were connected to the CR1000 datalogger and logged at 0.2 Hz. A dehumidifier was placed in the back of the growth room to improve humidity control. A box fan was also placed in the back of the room to improve air circulation for more consistent conditions throughout the growth room.

Correcting for changes in  $\psi_{\text{leaf}}$ . We adjusted each measured value of  $K_{\text{plant}}$  to a common value of  $\psi_{\text{leaf}}$ , namely,  $P_{50}$  – the value of  $\psi_{\text{leaf}}$  causing  $K_{\text{plant}}$  to decline by 50% relative to its value at  $\psi_{\text{leaf}} = 0$  and  $T = 30^{\circ}\text{C}$  – which we found from the VC for each species. Thus,

$$K_{\text{corrected}} = K(T, \Psi_{50}) = K(T, \Psi) * \frac{K(30, \Psi_{50})}{K(30, \Psi)}$$

$K_{\text{corrected}}$  was calculated for each  $K_{\text{plant}}$  measurement across experiments for that species.

The flow of measurements through the various calculations described above is shown diagrammatically in Figure 3.

Soil temperature. Additional experiments were performed to measure the soil temperature during the three conditions. Thermocouples were placed inside whirl-pak

bags and inserted into the soil at 2 cm and 10 cm depth. Plants were watered and pots were bagged the same way as previously described. Soil temperature was measured for 3 replicates of each species. Conditions were applied in randomized order (Olive: Condition 1, 3, 2; Sunflower: Condition 3, 1, 2). Olives conditions were set for 2.5 hours each, and sunflower conditions for 2 hours each, to roughly match the length of time transpiration typically takes to stabilize for the two species.

## Results

On average,  $\psi_{\text{leaf}}$  was slightly lower at high temperature (conditions 2 and 3) than at low temperature (condition 1) in both species, despite our attempts to prevent this by reducing VPD at the higher  $T$  (Fig 4), though these differences were not statistically significant ( $p = 0.093$ ). Nevertheless, we used relationships between  $K_{\text{plant}}$  and  $\psi_{\text{leaf}}$  measured at 30°C (Fig 5) to correct for these slight shifts in  $\psi_{\text{leaf}}$  with temperature.  $K_{\text{plant}}$  was positively related to  $\psi_{\text{leaf}}$  for both species, both overall and within most individual plants (9/13 for olive and 6/9 for sunflower) (Fig 5); all of the olive plants that showed a decline of  $K_{\text{plant}}$  with  $\psi_{\text{leaf}}$  were from December and January experiments, in which  $K_{\text{plant}}$  was very low under all three Conditions. The best-fit exponential vulnerability curves were  $K_{\text{plant}} / [\text{mmol s}^{-1} \text{MPa}^{-1}] = 0.223 \cdot \exp(0.371 \psi_{\text{leaf}} / \text{MPa})$  for olive, and  $K_{\text{plant}} = 18.4 \cdot \exp(3.67 \psi_{\text{leaf}})$  for sunflower, giving  $P_{50} = -0.727 \text{ MPa}$  and  $-0.582 \text{ MPa}$  for olive and sunflower, respectively. The sunflower VC was quite steep, consistent with the VC found by (Scoffoni et al. 2012).

$K_{\text{plant}}$  generally increased with  $T$  in both species, whether uncorrected for  $\psi_{\text{leaf}}$  or adjusted to a common  $\psi_{\text{leaf}} = P_{50}$  (Fig 6). For sunflower,  $K_{\text{plant}}$  increased with  $T$  in every experiment. For olive,  $K_{\text{plant}}$  (adjusted to  $\psi_{\text{leaf}} = P_{50}$ ) increased with  $T$  in 15 of 18 experiments conducted in the autumn, but in only 3 of 9 experiments conducted in the winter. We also expressed the change in  $K_{\text{plant}}$  with  $T$  in relative terms to enable comparison between species (and between seasons for olive), as a % change per °C (Fig 7). For sunflower, the mean and median % change per °C were 10.27% and 12.14%, respectively. For olive, the mean and median for autumn experiments were 1.4% and 0.96%, respectively; for winter experiments, these were -0.22% and -0.3%, respectively. As previously noted,  $K_{\text{plant}}$  was

generally lower for olive in winter (mean  $K_{\text{plant}}$  at 30°C and high RH: autumn = 0.4, winter = 0.24; t-test,  $p = 0.0074$ ), suggesting some broader phenological trend that may have been conflated with the effects of temperature per se on  $K_{\text{plant}}$ .

Soil temperature (measured at 2 cm and 10 cm depths in the center of pots) responded slowly to shifts in air temperature, and as a result, generally did not reach equilibrium with the air during the measurement interval (Fig 8).

## **Discussion**

In this study we aimed to measure the effect of temperature on whole-plant hydraulic conductance ( $K_{\text{plant}}$ ) while controlling for differences in leaf water potential ( $\psi_{\text{leaf}}$ ) that may accompany temperature shifts. We isolated the effects of temperature by measuring  $K_{\text{plant}}$  of olive and sunflower using the evaporative flux method while varying both  $T$  and VPD to generate variation in  $K_{\text{plant}}$  and  $\psi_{\text{leaf}}$ , and used effects of  $\psi_{\text{leaf}}$  on  $K_{\text{plant}}$  at constant  $T$  to correct for slight shifts in  $\psi_{\text{leaf}}$  with  $T$ . Our results largely confirmed our hypothesis that  $K_{\text{plant}}$  should increase with temperature – by an average of 1.4% per °C for olive and 10.27% per °C for sunflower. However, olive plants measured in winter – when gas exchange rates and  $K_{\text{plant}}$  were generally low – exhibited a weak and statistically insignificant decline in  $K_{\text{plant}}$  with  $T$  (-0.3% per °C).

To our knowledge, this is the first study to isolate the short-term (~hours) response of  $K_{\text{plant}}$  to temperature in intact plants without the confounding effect of changes in  $\psi_{\text{leaf}}$ . Our results are consistent with previous studies that measured effects of  $T$  on isolated plant organs, including roots (Newman and Jr 1988; Lopez and Nobel 1991; Cochard et al. 2000), shoots (Cochard et al. 2000), and leaves (Öunapuu and Sellin 2013), as well as effects of root  $T$  on  $K_{\text{plant}}$  (Radin 1990; Cochard et al. 2000). One previous study (Tsuda and Tyree 2000) combined  $T$  responses of  $K$  in roots and shoots to compute the  $T$  response of  $K_{\text{plant}}$ , and also found a positive response of about 8.9% per °C; however, the  $T$  changes in that study were part of a diurnal cycle outdoors, and were thus conflated with other environmental factors. Most of these studies also did not attempt to control for the

potentially confounding effect of changes in  $\psi_{\text{leaf}}$  that often occur when  $T$  is changed, partly as a result of greater VPD at higher  $T$ .

One previous study (Schönbeck et al. 2022) reported measurements from which it was possible to isolate the effect of  $T$  on  $K_{\text{plant}}$  in *Fagus sylvatica*, *Quercus pubescens* and *Q. ilex*; our calculations from their data suggest, contrary to our findings, that  $K_{\text{plant}}$  decreased with  $T$ . However, those authors measured  $K_{\text{plant}}$  after plants had acclimated to different temperatures in a growth chamber for 5-15 weeks, so it is likely that broader acclimatory shifts had occurred, potentially including production of new conducting tissue that may have had different hydraulic properties. That would be consistent with prior literature showing that the effect of  $T$  on  $K_{\text{plant}}$  at longer timescales can be positive, neutral, or negative (Maherali and Delucia 2000; Thomas et al. 2004; McCulloh et al. 2016).

Olives had lower  $K_{\text{plant}}$ , and lower gas exchange rates overall, during the winter (December and January) than during the autumn (September and November), as well as opposite  $T$  response of  $K_{\text{plant}}$  (positive but insignificant in autumn and negative but insignificant in winter). Despite being kept in a greenhouse under supplemental light, lower  $K_{\text{plant}}$  suggests that the olives had gone dormant; indeed, the olive plants continued to produce new leaf growth throughout the autumn, but growth slowed in December. Other studies have found seasonal plasticity in  $K_{\text{plant}}$  (Zhang et al. 2025). Our findings complement those earlier results by suggesting that the impact of  $T$  on  $K_{\text{plant}}$  may itself also be seasonally plastic.

There are several mechanisms by which warming could increase  $K_{\text{plant}}$ . The most well-established of these is a decrease in the viscosity of water as temperature increases:

viscosity declines by about 20% from 20°C to 30°C, or 2% per °C. This should increase the xylem-lumen component of  $K_{\text{plant}}$  by the same proportion. Expressed as  $Q_{10}$  (the proportional increase in a property with 10°C warming), the viscosity response predicts a  $Q_{10}$  of 1.25 for xylem hydraulic conductance between 20° and 30°C. Our mean result for olive (1.4% per °C, or  $Q_{10} = 1.15$ ) is within a factor of 1.09 of the viscosity-based prediction. However, the effect of  $T$  on  $K_{\text{plant}}$  was far greater in sunflower, averaging 10% ( $Q_{10} = 2.0$ ).

Other studies have found temperature responses for organ-specific hydraulic conductances that matched or exceed the responses expected from viscosity (see Table 1 in Mills et al. 2026). For example, Cochard et al. 2000 found that between 15°C and 35°C root conductance of *Quercus robur* L. varied as predicted by the viscosity effect, only deviating from that below 15°C and above 35°C. In a study on leaves of sugar maple (*Acer saccharum*) and red oak (*Q. rubra*), Sack et al. 2004 found a temperature response that matched what is expected from viscosity for petiole segments and leaves with cut veins, but a temperature response higher than expected from viscosity for intact leaves ( $Q_{10} = 1.41$  for maple and 1.59 for oak). The authors attributed this result to the flow path including transcellular components, which is consistent with aquaporin activity increasing more strongly than viscosity with temperature (Sack et al. 2004; Murai-Hatano et al. 2008). Indeed, published  $Q_{10}$  mostly exceed 1.25 for leaf hydraulic conductance (e.g., 1.45 for *Oryza sativa* [Murai-Hatano et al. 2008], 1.51 for *Juglans regia* [Cochard et al. 2007], 1.64 for *Phaseolus vulgaris* [Matzner and Comstock 2001], 2.07 for *Tilia cordata* [Sellin and Kupper 2007]) and for root hydraulic conductance (e.g., 1.32 for *Phaseolus vulgaris* [Kuiper 1964], 1.45 for *Oryza sativa* [Murai-Hatano et al. 2008], 2.15 for *Hordeum vulgare*

[Clarkson 1976], and 2.24 for *Gossypium hirsutum* [Bolger et al. 1992]). Our results for sunflower fall within this range. It is perhaps unsurprising that dwarf sunflower would exhibit a stronger response of  $K_{\text{plant}}$  than olive, given that its short stature ensures that a disproportionately small share of its total water flow pathway occurs in axial stem tissues for which the viscosity effect should dominate.

Using vulnerability curves to correct for shifts in  $\psi_{\text{leaf}}$  with temperature enabled us to isolate the effects of temperature *per se*. Without these corrections, uncontrolled shifts in  $\psi_{\text{leaf}}$  systematically reduced the calculated sensitivity of  $K_{\text{plant}}$  to temperature (Fig 9), though the effect was not dramatic, perhaps because our use of a lower VPD at the higher temperature minimized shifts in  $\psi_{\text{leaf}}$  (Fig 4).

As global temperatures rise, and weather becomes more sporadic, understanding the mechanisms behind plant hydraulics and stomatal response will be increasingly important. This study was inspired by a related project that sought to test the role of temperature-induced shifts in hydraulic conductance in the stomatal response to temperature at constant VPD (Mills et al. 2026). That study did not directly quantify  $K_{\text{plant}}$ , but instead used literature data for  $T$  responses of  $K$  in isolated plant organs to predict  $K_{\text{plant}}$  responses to  $T$ . Our results thus support the premise of Mills et al. (2026), albeit in different species, by demonstrating for the first time an increase in  $K_{\text{plant}}$  with temperature in intact whole plants and quantifying  $Q_{10}$  values within the range of published organ-specific values. Those authors found stronger responses of stomatal conductance to temperature in herbaceous species (*H. vulgare*, *Zea mays* and *P. vulgaris*) than in woody species (*Vitis riparia*, *Vitis vinifera* and *Eucalyptus polyanthemus*). Their finding is consistent with our

finding that the  $Q_{10}$  for  $K_{\text{plant}}$  was greater in an herb (sunflower) than a woody species (olive): if  $K_{\text{plant}}$  increases with warming, this should increase leaf water status, leading to stomatal opening (Buckley 2005, 2019).

The stronger responses of  $K_{\text{plant}}$  and stomatal conductance to  $T$  in herbaceous plants may also make sense from an ecological perspective. Woody plants can survive heatwaves by reducing gas exchange and thereby 'banking' water for future periods when lower temperature enable use of that water with a greater water-use efficiency; by contrast, herbaceous plants need to complete their life cycle in a fairly short period, and thus may benefit less from a conservative strategy, preferring instead to use enhanced evaporative cooling to reduce the immediate impact of high temperatures. Olives are traditionally unirrigated crops in Mediterranean climates, and must conserve water when under heat stress to reduce the risk of running out before the growing season is over. Differences in the sensitivity of hydraulic conductance to temperature may thus contribute to mediating broader ecophysiological strategies among plant functional types. Further validation of this idea awaits more extensive quantification of the direct effects of temperature on  $K_{\text{plant}}$  and stomatal conductance.

## **Conclusion**

We measured responses of whole-plant hydraulic conductance in intact plants for the first time, while correcting for the potentially conflating influence of changes in water potential.  $K_{\text{plant}}$  increased by an average of 1.4% per degree C in olives and 10% per °C in sunflowers; olive plants measured during winter dormancy showed reduced gas exchange rates and  $K_{\text{plant}}$  and weakly negative  $T$  responses. Our findings support and extend earlier work showing effects of  $T$  on hydraulic conductance in isolated organs, validate the premise of an hypothetical hydraulic mechanism for the response of stomatal conductance to temperature, and can contribute to improved process-based modeling of plant and ecosystem water fluxes in a fluctuating and changing climate.

## **References**

- Bolger TP, Upchurch DR, McMichael BL. 1992. Temperature effects on cotton root hydraulic conductance. *Environmental and Experimental Botany*. 32(1):49–54.  
[https://doi.org/10.1016/0098-8472\(92\)90029-2](https://doi.org/10.1016/0098-8472(92)90029-2).
- Cochard H, Martin R, Gross P, Borgeat-Triboulot MB. 2000. Temperature effects on hydraulic conductance and water relations of *Quercus robur* L. *J Exp Bot*. 51(348):1255–1259.
- Cochard H, Venisse J-S, Barigah TS, Brunel N, Herbette S, Guilliot A, Tyree MT, Sakr S. 2007. Putative Role of Aquaporins in Variable Hydraulic Conductance of Leaves in Response to Light. *Plant Physiol*. 143(1):122–133.  
<https://doi.org/10.1104/pp.106.090092>.
- Lopez FB, Nobel PS. 1991. Root Hydraulic Conductivity of Two Cactus Species in Relation to Root Age, Temperature, and Soil Water Status. *J Exp Bot*. 42(2):143–149.  
<https://doi.org/10.1093/jxb/42.2.143>.
- Maherali H, Delucia EH. 2000. Interactive effects of elevated CO<sub>2</sub> and temperature on water transport in ponderosa pine. *Am J Bot*. 87(2):243–249.
- Matzner S, Comstock J. 2001. The temperature dependence of shoot hydraulic resistance: implications for stomatal behaviour and hydraulic limitation. *Plant, Cell & Environment*. 24(12):1299–1307. <https://doi.org/10.1046/j.0016-8025.2001.00785.x>.
- McCulloh KA, Petitmermet J, Stefanski A, Rice KE, Rich RL, Montgomery RA, Reich PB. 2016. Is it getting hot in here? Adjustment of hydraulic parameters in six boreal and

- temperate tree species after 5 years of warming. *Global Change Biology*. 22(12):4124–4133. <https://doi.org/10.1111/gcb.13323>.
- Mills C, Bartlett MK, Buckley TN. 2026. The Stomatal Response to Temperature Is Enhanced by High Evaporative Demand, Consistent With a Partially Hydraulic Mechanism. *Plant, Cell & Environment*. 49(4):1958–1968. <https://doi.org/10.1111/pce.70347>.
- Mills C, Bartlett MK, Buckley TN. 2024. The poorly-explored stomatal response to temperature at constant evaporative demand. *Plant, Cell & Environment*. 47(9):3428–3446. <https://doi.org/10.1111/pce.14911>.
- Muhsin TM, Zwiazek JJ. 2002. Ectomycorrhizas increase apoplastic water transport and root hydraulic conductivity in *Ulmus americana* seedlings. *New Phytologist*. 153(1):153–158. <https://doi.org/10.1046/j.0028-646X.2001.00297.x>.
- Murai-Hatano M, Kuwagata T, Sakurai J, Nonami H, Ahamed A, Nagasuga K, Matsunami T, Fukushi K, Maeshima M, Okada M. 2008. Effect of Low Root Temperature on Hydraulic Conductivity of Rice Plants and the Possible Role of Aquaporins. *Plant Cell Physiol*. 49(9):1294–1305. <https://doi.org/10.1093/pcp/pcn104>.
- Nardini A, Salleo S, Andri S. 2005. Circadian regulation of leaf hydraulic conductance in sunflower (*Helianthus annuus* L. cv Margot). *Plant, Cell & Environment*. 28(6):750–759. <https://doi.org/10.1111/j.1365-3040.2005.01320.x>.
- Newman SE, Jr FTD. 1988. High Root-zone Temperatures, Mycorrhizal Fungi, Water Relations, and Root Hydraulic Conductivity of Container-grown Woody Plants. <https://doi.org/10.21273/JASHS.113.1.138>.

- Öunapuu E, Sellin A. 2013. Daily dynamics of leaf and soil-to-branch hydraulic conductance in silver birch (*Betula pendula*) measured in situ. *Plant Physiology and Biochemistry*. 68:104–110. <https://doi.org/10.1016/j.plaphy.2013.04.011>.
- Radin JW. 1990. Responses of transpiration and hydraulic conductance to root temperature in nitrogen- and phosphorus-deficient cotton seedlings. *Plant Physiol.* 92(3):855–857. <https://doi.org/10.1104/pp.92.3.855>.
- Sack L, Streeter CM, Holbrook NM. 2004. Hydraulic Analysis of Water Flow through Leaves of Sugar Maple and Red Oak. *Plant Physiol.* 134(4):1824–1833. <https://doi.org/10.1104/pp.103.031203>.
- Schönbeck LC, Schuler P, Lehmann MM, Mas E, Mekarni L, Pivovarov AL, Turberg P, Grossiord C. 2022. Increasing temperature and vapour pressure deficit lead to hydraulic damages in the absence of soil drought. *Plant, Cell & Environment*. 45(11):3275–3289. <https://doi.org/10.1111/pce.14425>.
- Scoffoni C, McKown AD, Rawls M, Sack L. 2012. Dynamics of leaf hydraulic conductance with water status: quantification and analysis of species differences under steady state. *J Exp Bot.* 63(2):643–658. <https://doi.org/10.1093/jxb/err270>.
- Thomas DS, Montagu KD, Conroy JP. 2004. Changes in wood density of *Eucalyptus camaldulensis* due to temperature—the physiological link between water viscosity and wood anatomy. *Forest Ecology and Management*. 193(1):157–165. <https://doi.org/10.1016/j.foreco.2004.01.028>.
- Tsuda M, Tyree MT. 2000. Plant hydraulic conductance measured by the high pressure flow meter in crop plants. *J Exp Bot.* 51(345):823–828.

- Wan X, Zwiazek JJ, Lieffers VJ, Landhäusser SM. 2001. Hydraulic conductance in aspen (*Populus tremuloides*) seedlings exposed to low root temperatures. *Tree Physiol.* 21(10):691–696. <https://doi.org/10.1093/treephys/21.10.691>.
- Zhang Z, Guan H, Veneklaas E, Singha K, Batelaan O. 2025. Revealing seasonal plasticity of whole-plant hydraulic properties using sap-flow and stem water-potential monitoring. *Hydrology and Earth System Sciences.* 29(16):3975–3992. <https://doi.org/10.5194/hess-29-3975-2025>.
- Zuccarini P, Farieri E, Vasquez R, Grau B, Save Monserrat R. 2014. Effects of soil water temperature on root hydraulic resistance of six species of Iberian pines.

## Figures

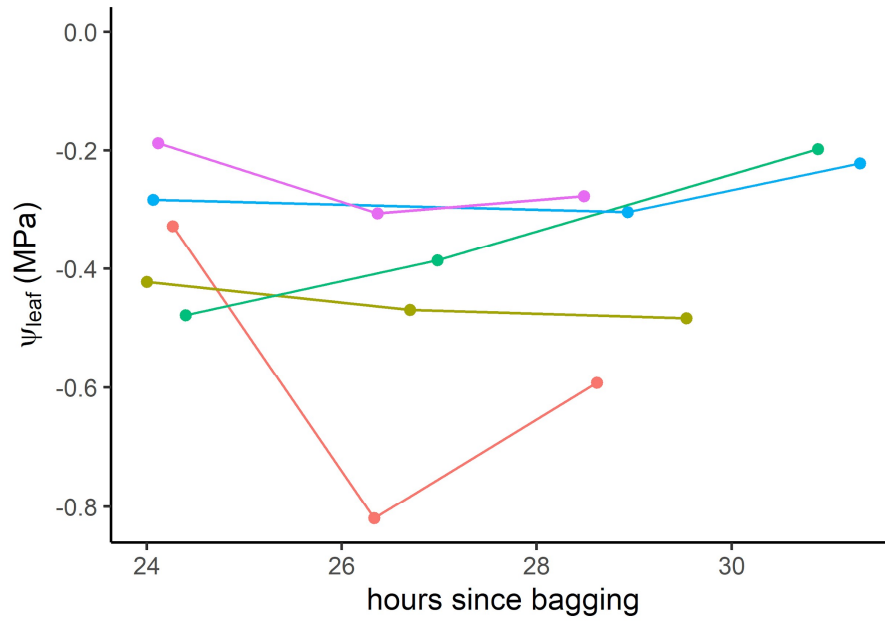


Figure 1.  $\psi_{\text{leaf}}$  for bagged olive plants vs. hours since bagging. Colors are individual plants.

Blue and purple were from bottom-watered plants.



Figure 2. Photo of system inside growth room during an experiment with five olive plants.

Calculate K from Darcy's law:  $K = \frac{E}{\Psi_{PD} - \Psi(T, \Psi)}$   $E$  = transpiration rate  
 $\Psi_{PD}$  = predawn leaf water potential = proxy for soil water potential

Condition 1:  $K(T_{low}, VPD_{low}) = K_{td}, \Psi_{td}, E_{td}$   $T$  = high temp  
 Condition 2:  $K(T_{high}, VPD_{low}) = K_{Td}, \Psi_{Td}, E_{Td}$   $t$  = low temp  
 Condition 3:  $K(T_{high}, VPD_{high}) = K_{TD}, \Psi_{TD}, E_{TD}$   $D$  = high VPD  
 $d$  = low VPD

$\begin{bmatrix} K_{TD} & K_{Td} \\ \Psi_{TD} & \Psi_{Td} \end{bmatrix}_{all\ plants}$

Make VC using Conditions 1 and 2:  $K_{TD}$  and  $K_{Td}$  vs  $\psi$  (Fig 5)

Use VC to correct for shifts in  $\psi$ . Adjust the measured  $K_{corrected}$  to a common value of  $\psi$  ( $\Psi_{50}$ , found from the VC) by multiplying by the ratio of  $K$  at  $\Psi_{50}$  to  $K$  at the actual  $\psi$

$$K_{corrected} = K(T, \Psi_{50}) = K(T, \Psi) * \frac{K(30, \Psi_{50})}{K(30, \Psi)}$$

$\begin{bmatrix} K_{Td} & K_{td} \\ \Psi_{Td} & \Psi_{td} \end{bmatrix}_{each\ plant}$

Plot  $K_{corrected}$  vs  $T$  (Fig 6)

Figure 3. Diagram showing logical flow of measurements and calculations.

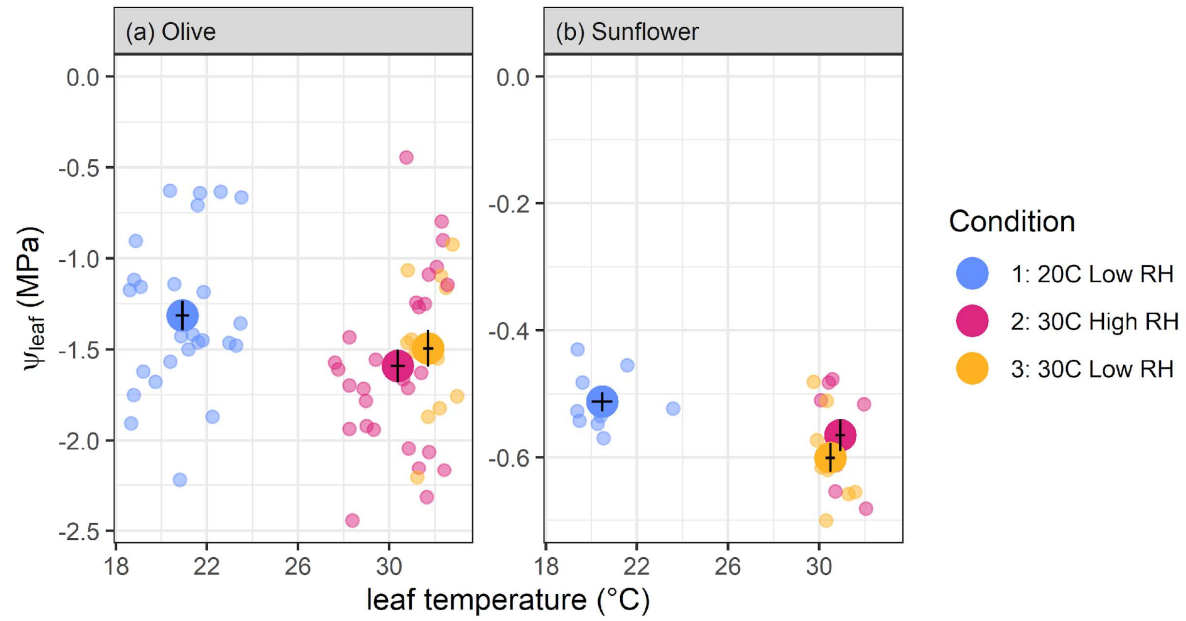


Figure 4. Raw  $\psi_{\text{leaf}}$  (MPa) vs. leaf temperature (°C) for (a) olive and (b) sunflower. Points are colored by condition. Large points represent the means of each condition, and error bars represent standard errors.

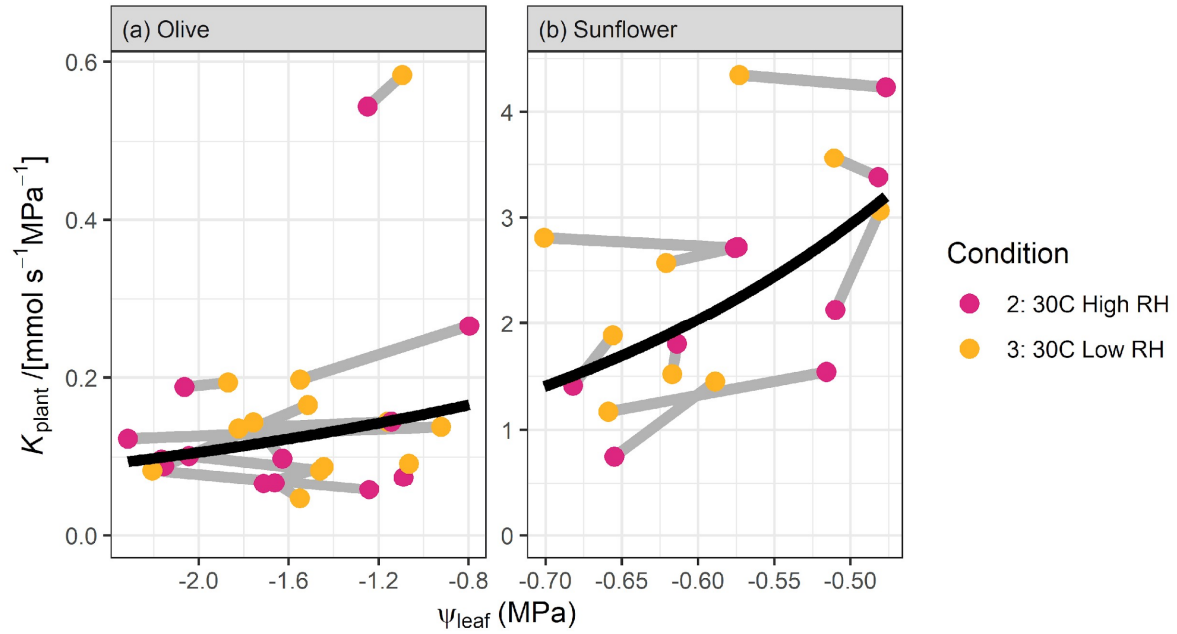


Figure 5. Vulnerability curves ( $K_{\text{plant}}$  vs  $\psi_{\text{leaf}}$ ) for (a) olive and (b) sunflower. Points are colored by condition. Points from the same plant are connected by gray lines. Black lines are linear least-squares models fit to log-transformed  $K_{\text{plant}}$ . The best-fit exponential vulnerability curves were  $K_{\text{plant}} / [\text{mmol s}^{-1} \text{MPa}^{-1}] = 0.223 \cdot \exp(0.371 \psi_{\text{leaf}} / \text{MPa})$  for olive, and  $K_{\text{plant}} = 18.4 \cdot \exp(3.67 \psi_{\text{leaf}})$  for sunflower, giving  $P_{50} = -0.727 \text{ MPa}$  and  $-0.582 \text{ MPa}$  for olive and sunflower, respectively.

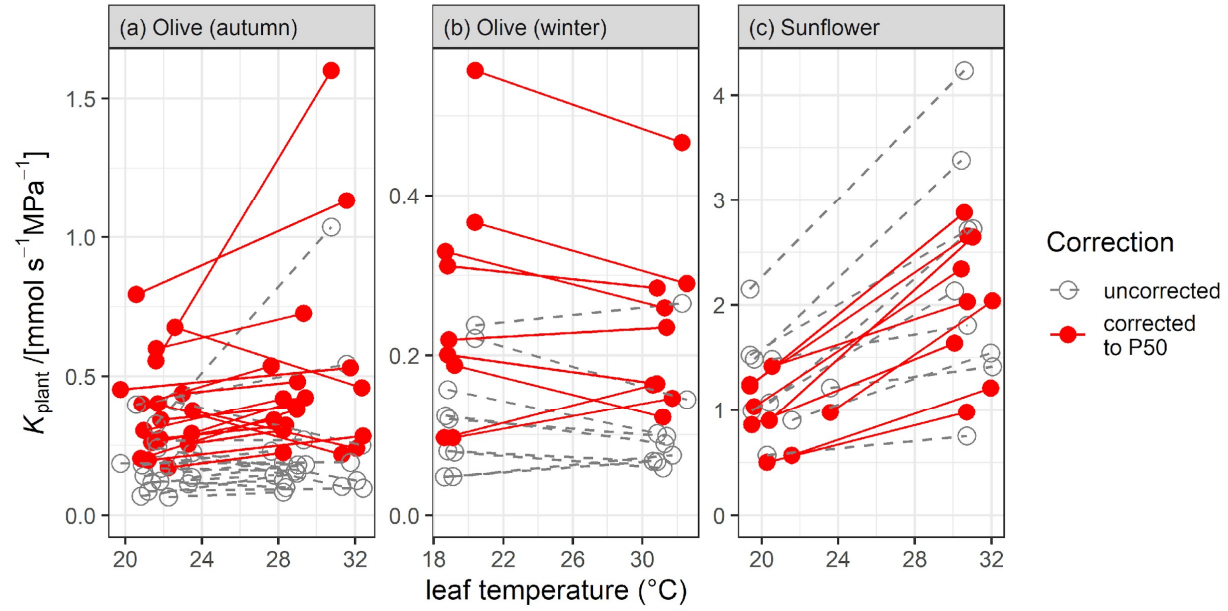


Figure 6.  $K_{\text{uncorrected}}$  and  $K_{\text{corrected}}$  vs leaf temperature ( $^{\circ}\text{C}$ ) for olive in (a) autumn and (b) winter and (c) sunflower. September and November olive experiments are grouped as autumn. December and January olive experiments are winter. Points from the same plant are connected by lines. Dashed lines and open circles are raw  $K_{\text{plant}}$  values, and solid lines and circles are  $K_{\text{plant}}$  values after correcting for effects of  $\psi_{\text{leaf}}$  using the vulnerability curve.  $K_{\text{corrected}}$  increased significantly with leaf temperature in sunflower (linear regression, slope = 0.096,  $p = 0.001$ ) but not in autumn olive (slope = 0.015,  $p = 0.17$ ) or winter olive (slope = -0.0008,  $p = 0.88$ ).

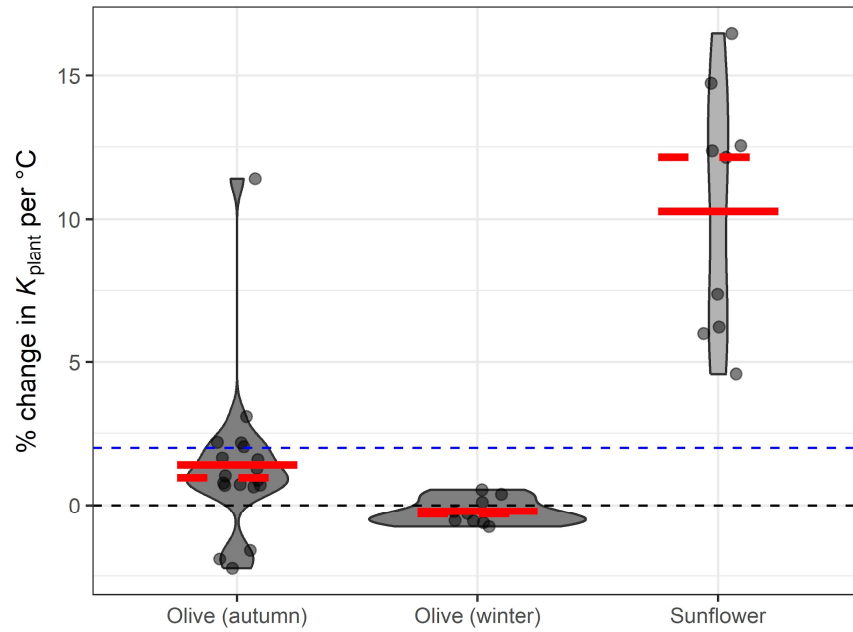


Figure 7. Percent change in  $K_{\text{corrected}}$  per degree C increase in temperature for olive in (a) autumn and (b) winter (dark grey) and (c) sunflower (light grey). September and November olive experiments are categorized as autumn. December and January olive experiments are winter. Solid red lines are means, thick dashed red lines are medians. The blue dashed horizontal line is the predicted effect on  $K_{\text{plant}}$  of decreases in viscosity with temperature.

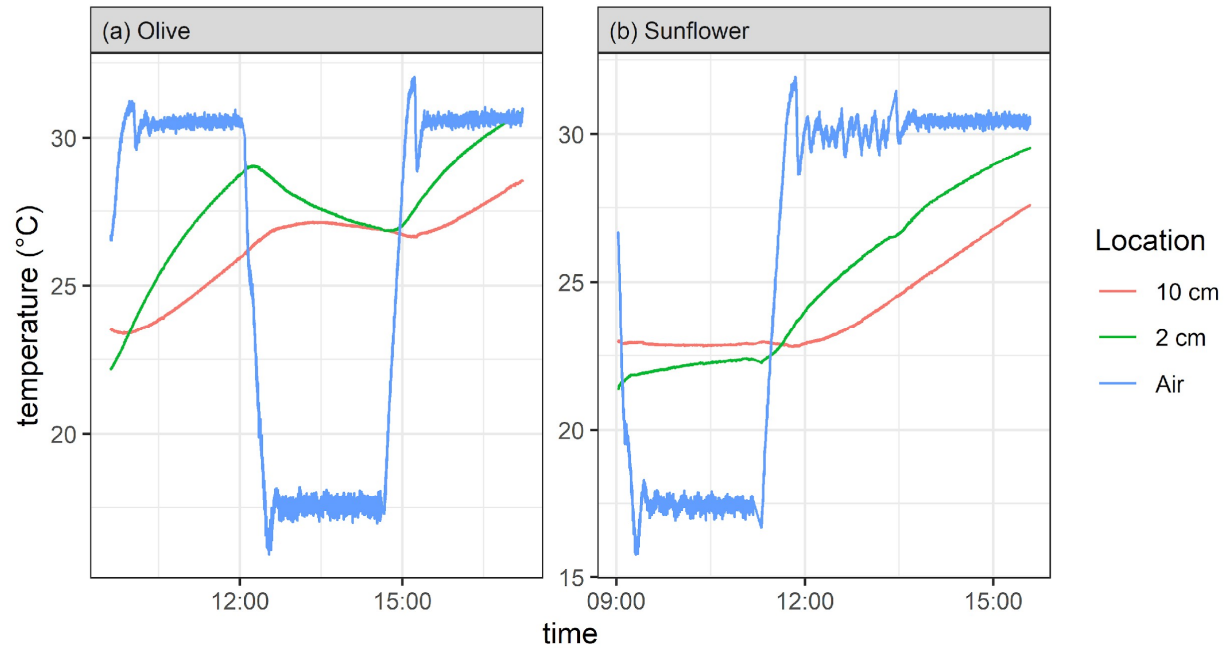


Figure 8. Soil temperature vs. time at 2cm, 10cm and air, in pots containing (a) olive and (b) sunflower plants. Soil temperatures are averages across three pots. Chamber conditions were applied in the following orders: olive: Condition 1, 3, 2; sunflower: Condition 3, 1, 2.

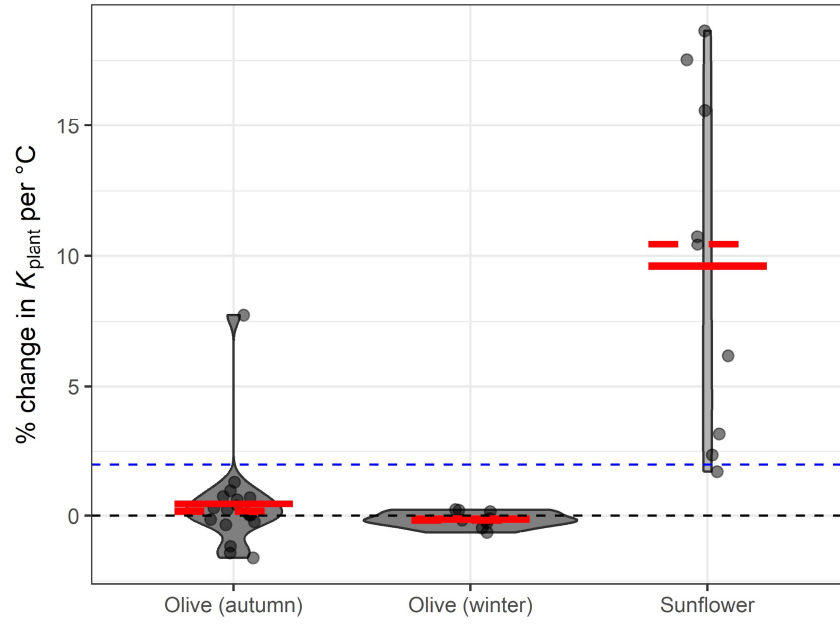


Figure 9. Percent change in raw  $K_{plant}$  (i.e., before adjustment to a common  $\psi_{leaf}$  value to correct for uncontrolled changes in  $\psi_{leaf}$  with  $T$ ) per degree C increase in temperature for olive in autumn and winter (dark grey) and sunflower (light grey). September and November olive experiments are categorized as autumn. December and January olive experiments are winter. Solid red lines are means, thick dashed red lines are medians. The blue dashed horizontal line is the predicted effect on  $K_{plant}$  of decreases in viscosity with temperature.