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Threat from the sky – dry air puts plants under stress even when their roots have enough water

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RESEARCH ARTICLE

Hot and dry summers are not only a danger to human health but also to plants. Our goal in this study was to study the effects of warm and dry air conditions on the water transport in plants. We grew young trees of European beech, pubescent oak and holm oak in climate chambers with different temperature and humidity conditions, and with unlimited water in the soil. We measured several stem and leaf characteristics over a full growing season. We found damages in the water transport of trees that were well-watered, but experienced high temperatures and air drought. By showing that warm and dry air can stress well-watered plants, we found a new potential threat to future forest health in addition to the already known risk of soil drought by lack of precipitation. We conclude that it is very important to look how plants respond at a combination of both soil drought and atmospheric drought, posing a ‘threat from both sides’. Because only when considering all potential causes of plant drought stress, it is possible to make accurate predictions about the fate of our forests.

Hot and dry summers are not only a danger to human health but also to plants. Plants cannot function without water. Extreme droughts will become more intense, and last longer in the

future IPCC_2023. Recent examples include the extreme drought that hit central Europe in 2018. Such droughts can lead to crop failure and wide-scale forest mortality [C.D. Allen et al., 2015;[1] M.E. Olson et al., 2020;[2] V. Trotsiuk et al., 2021][3]. Many studies have focused on the consequences of soil drought (due to the lack of precipitation) on plants in nature and agriculture. However, a factor that has been less investigated is the effect of hot and dry air on plants [C.D. Allen et al., 2015;[1] C. Grossiord et al., 2020][4]. Over the last decades, average temperatures have increased worldwide. A rise in temperature means that the air can hold more water, which it sucks from the soil and plants [S.M. Vicente-Serrano et al., 2018][5]. This pulling force is called 'vapor pressure deficit' or VPD. A strong deficit, or a high VPD, can be referred to as 'atmospheric drought', as the air demands so much water that it dries out the plants and soil. It is essential to know how plants behave when the water demand of the air increases to such extreme values. Namely, we have the means to irrigate our plants, but it is more challenging or even impossible to lower the temperature or increase the relative humidity of the air to reduce this atmospheric stress.

Why is VPD important?

An increase in VPD means that the water demand from the air to the leaves increases, and thus leaves lose more water. When a plant loses more water than its roots can take, the tension on the water column in the water-transporting wood vessels (xylem) increases. Too strong tensions in the xylem can be dangerous to a plant, as water can pass from a liquid to a vapor phase forming air bubbles (a phenomenon called embolism). Vascular embolisms are dangerous, not only in humans stopping bloodflow, but also to plants, stopping water flow and blocking processes from photosynthesis to growth and transport of nutrients. Leaves have means to control water loss and prevent expensive and sometimes irreparable damages by controlling the opening of their stomata [J. Martínez-Vilalta et al., 2014][6]. Stomata are tiny pores on the leaves through which carbon dioxide is taken up from the atmosphere and water is lost. Research has shown that stomata close when VPD increases. This is a reaction mechanism that allows plants to avoid losing high amounts of water and reaching extremely strong tensions where embolism occurs. Some species are more vulnerable than others and thus close their stomata faster than others [F. Lens et al., 2011;[7] A. Tixier et al., 2014][8]. Plants adapted to drier conditions are less sensitive to this atmospheric pull than plants growing in wetter environments [J. Martínez-Vilalta et al., 2014;[6] K.A. Novick et al., 2016][9]. Furthermore, leaves are not always very efficient in closing their stomata and water loss also occurs through the epidermis, the outer leaf skin, in rather uncontrolled ways. So, during the night, or when stomata close due to low water supply, leaves may still lose water. This combined loss is called minimum leaf conductance [R.A. Duursma et al., 2019][10]. While the role of minimum leaf conductance was long underestimated, nowadays it is considered an important factor and final

step to plant desiccation under plant stress conditions.

Why is temperature critical?

Another reason for plants to regulate their stomatal opening is leaf temperature. Leaf photosynthesis operates best at certain optimal temperatures. By controlling the stomatal opening and the amount of water evaporating from the leaf, the leaf can be cooled relative to the air temperature, like sweating on a human body. Here as well, species differ in their tolerance to high temperatures with some that are adapted to higher temperatures needing less water to cool their leaves [C.A. Knight and D.D. Ackerly, 2002][11]. Drought and thermal tolerance are thus probably strongly related. However, higher temperatures and higher VPD might require contrasting stomatal behaviors, as higher VPD requires stomatal closure (to prevent embolism), and higher temperatures require stomatal opening (to regulate leaf temperature and avoid overheating). This leads to the question of how plants behave in a world where temperature and VPD are foreseen to increase in the coming decades.

While many studies focus on the effects of soil drought on plants – because of the extreme summers without sufficient rain – we wanted to know how temperature and VPD affect plants, even if they have enough water available in the soil. Such conditions could appear, for example, during a heatwave after a period of significant rain or could impacts vegetation that is artificially irrigated (e.g., agricultural systems or urban vegetation). If these air conditions can expose plants to stress, we know that irrigating vegetation might not be sufficient to ensure their survival in the future. Therefore, we tested this question on three European tree species from different climatic zones: European Beech (Fagus sylvatica), known for its preference for moist soils and cool temperatures; pubescent oak (Quercus pubescens), a relatively drought-tolerant species occurring in central Europe; and holm oak (Quercus ilex), a species native to the drier, Mediterranean regions [L.C. Schönbeck et al., 2022][12]. We expected that these species would show distinct responses to increasing temperature and VPD because of their evolutionary adaptation to warmer and drier, or cooler and wetter climates. We predicted that: increasing VPD and higher temperature, in the absence of soil drought, cause tension in the water transport system of the xylem. We expected this effect to be stronger in beech than in the two oak species.

How to measure plant stress and functioning?

We used climate chambers to test these hypotheses, because in nature, it is difficult to disentangle and individually manipulate temperature and VPD, as naturally, VPD increases when temperature rises. In the controlled environment of the climate chambers, we can ensure that the plant responses we measure are caused by the parameters we manipulate – temperature and VPD – and not by other drivers found in nature. For our study, we used six climate chambers that are temperature, humidity, and light controlled. In each chamber, we

placed several potted plants of the three species – European beech, pubescent oak, and holm oak, for a period of six months. The plants were three years old and approximately 50cm tall. We set three chambers to 25°C and three chambers to 30°C. The three chambers within each temperature level were then assigned to a low, medium, and high VPD level by adjusting the relative humidity of the air. In this way, we could measure the individual effects of VPD and temperature and their combined interaction on plant response, which would have been impossible to measure in a natural setting.

A range of measurements were carried out to monitor the status of the trees. For example, stomatal conductance, the water flow rate through the stomata, was measured using an infrared gas analyzer (Figure 1 A). For this, a leaf was clamped into a cuvette with controlled light, humidity, and temperature conditions. Using this approach, we slowly increased the VPD (by decreasing the air humidity) and measured the stomatal closure rate to increased VPD. Leaf water potential, i.e. the tension of the water column in the leaf veins, was measured using a pressure chamber that exerts positive pressure to push the water out of the leaf. It is assumed that the positive pressure that is needed to push water out, is equal to the tension the leaf veins experience. Minimum leaf conductance, i.e., the rate of water loss from the leaves when the stomata are closed, was measured by hanging individual leaves in a dark chamber for a few hours to mimic night conditions (to ensure the stomata are closed) and recording the weight over time to assess the water loss. Lastly, modern techniques using X-ray micro-computed tomography (µCT) allowed us to look at the vessels inside the stem and see which are were functional and filled with water vs. the ones that are were dysfunctional due to air bubbles inside (Figure 1, B and C). We then calculated the percentage loss of hydraulic conductance, the ratio of the embolized vessel area versus the total vessel area in the xylem.

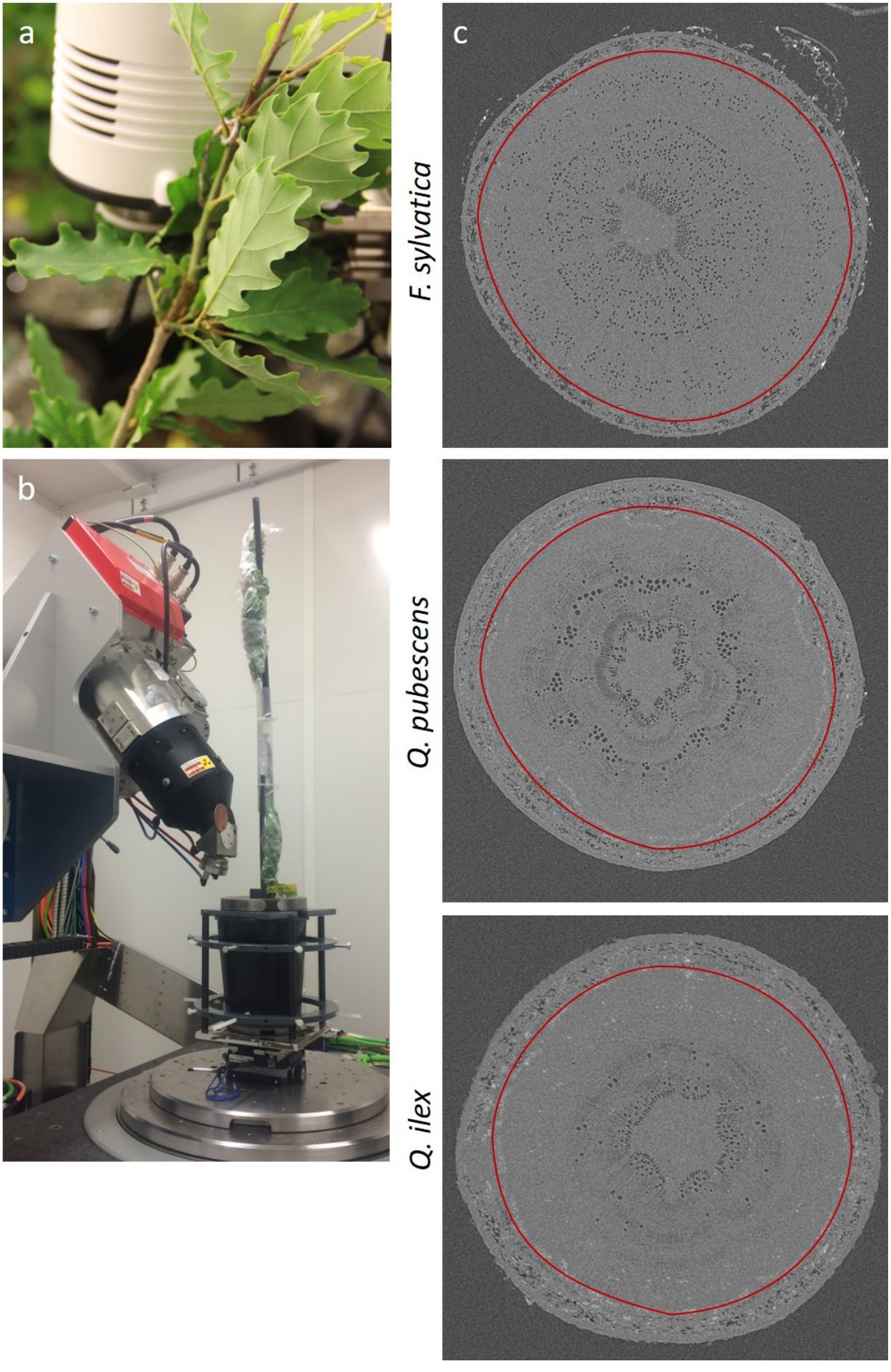

a
b
c
F. sylvatica
Q. pubescens
Q. ilex

Figure 1: A) A leaf of a pubescent oak tree is measured for stomatal conductance using a gas exchange device. B) A young tree is fixed to a stable frame and placed in the X-ray micro-computed tomography scanner. C) Images from the X-ray micro-computed tomography scans of the three used species: European beech (F. sylvatica), pubescent oak (Q. pubescens) and holm oak (Q. ilex). The light grey area shows wood and water filled vessels, while the dark grey dots indicate vessels that have air in them.

Warm and dry air can cause damage to trees even with their roots hydrated

Using the X-ray micro-computed tomography images, we found that well-watered trees experiencing higher temperature and VPD had more vessels filled with air bubbles (Figure 1 C). This means the water transport in those vessels was blocked due to too strong tension on the water inside the vessel. These damages were primarily seen in European beech, a species that has suffered from large-scale mortality in recent years. In line with these results, the leaf veins experienced stronger tensions on the water in response to higher temperature and VPD. As expected, the more drought-tolerant holm oak did not show damages due to higher temperature or VPD tolerance, while pubescent oak was found in the middle of these two. This was in line with our expectations that there would be a gradient in the response to VPD from drought-adapted towards less drought-adapted species. We also found that the minimum leaf conductance, the amount of water lost after stomata closed, could be an important cause of these damages. We found a positive correlation between minimum leaf conductance and percentage loss of conductivity, meaning that plants with higher water loss through leaves would have a higher risk for air bubbles in the xylem during stress.

We can explain these results using a commonly used theory in plant biology: the safety-efficiency trade-off [C. Grossiord et al., 2020][13]. Plants either invest energy in safety, i.e., strong, tough leaves and strong, dense wood that can withstand strong tensions. But with that comes a reduction in the efficiency of water transport. On the other hand, plants can invest in efficiency, leading to high water transport, high photosynthesis rates, and faster growth, but with the trade-off that they are less protected against drought stress. European beech is an excellent example of a species that has invested in efficiency. Its large crowns with thin leaves lose a lot of water, and the soils in which the trees grow are generally moist. Furthermore, other researchers showed how European beech has a strategy to keep its stomata open and lose water rather than preventing water loss [L. Walthert et al., 2021][14]. This may result in leaf shedding when water loss is so severe that damages occur. Such patterns were observed in the 2018 drought in Europe, where many beech trees lost their leaves much earlier than expected in late summer [M. Arend et al., 2022][15]. While this might be a successful strategy for individual extreme years, repeated droughts could reduce the vitality of such trees because they cannot utilize their leaf function long enough. Therefore, the carbon investment in new

leaves is less efficient.

While oak is generally seen as drought-tolerant, the variety of oak species is very large [A. Vilagrosa et al., 2012][16]. The two oak species included in this study have very distinct characteristics: Holm oak is an evergreen species with tough and resilient leaves, while pubescent oak is shedding its leaves in autumn and regrowing in the next spring. The wood of the holm oak also consists of smaller vessels, which give more strength at the cost of efficient water transport. The wood thus is expensive to make, in terms of carbon-investment, but in turn provides protection against stress. These characteristics enable it to be very adapted to dry environments, and it has been demonstrated that it is able to cope with a wide range of extreme conditions, from colder to warmer, and wetter to drier [J.I. Garcia-Plazaola et al., 1999][17]. Pubescent oak likely has a slightly more risk-taking strategy. It has wood and leaves that allow more efficient water transport at the cost of safety. The differences between these species were well visible in this study. Holm oak adjusted leaf gas exchange and even adjusted the drought-tolerance of its leaves, in a rapid response to the changing environmental conditions. Herewith it prevented damages to its xylem vessels. Pubescent oak showed a lower active response and in turn had higher losses of water conductivity in the xylem. That being said, both species showed much lower stress responses than the beech in this study, indicating that the conditions that the trees were exposed to in this study, were not at a level to push the oak species to a threshold for survival yet, showing their general well-drought-tolerant characteristic.

Implications of these findings

By showing that high atmospheric drought (higher VPD) can stress well-watered plants, we identify its potential threat to future forest health, in addition to the already well-known risk of soil drought by lack of precipitation. Even more striking is that these results were found at not even very extreme temperature and VPD. This is important because while researchers are quite confident in their predictions of future temperature changes, there is much more uncertainty about the future patterns of air humidity [S.M. Vicente-Serrano et al., 2018][5]. Therefore, predicting how forests will respond to future climate change is still challenging. Nevertheless, we show how species that are not adapted to soil drought like beech, are also at risk for hydraulic damage when air drought increases. These findings are very important for accurate plant productivity, health, and mortality predictions.

One can say that an experiment in such climate chambers represents far from real-world conditions. This is partly true, but the work done in climate chambers is a vital contribution to the fundamental understanding of how plants may respond to future climatic scenarios in the real world. Future work should continue working on these VPD and temperature factors and try to confirm the results from this study in an actual natural area. In addition, it is very

important to look at the combined effects of soil drought and atmospheric drought on plants, which poses a ‘threat from both sides’. Because only when considering all potential drivers for plant hydraulics and functioning is it possible to make accurate predictions about the fate of our forests.

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