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Article Addendum

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Abstract

Stomatal conductance directly modifies plant water relations and photosynthesis. Many environmental factors affecting the stomatal conductance have been intensively studied but temperature has been largely neglected, even though it is one of the fastest changing environmental variables and it is rising due to climate change. In this study, we describe how stomata open when the temperature increases. Stomatal conductance increased by ca 40% in a broadleaf and a coniferous species, poplar (*Populus deltoides x nigra*) and loblolly pine (*Pinus taeda*) when temperature was increased by 10 °C, from 30 °C to 40 °C at a constant vapor pressure deficit of 1 kPa. The mechanism of regulating stomatal conductance by temperature was, at least partly, independent of other known mechanisms linked to water status and carbon metabolism. Stomatal conductance increased with rising temperature despite the decrease in leaf water potential, increase in transpiration, increase in

intercellular CO_2 concentration and was decoupled from photosynthesis. Increase in xylem and mesophyll hydraulic conductance coming from lower water viscosity may to some degree explain temperature dependent opening of stomata. The direct stomatal response to temperature allows plants to benefit from increased evaporative cooling during the heat waves and from lower stomatal limitations to photosynthesis but they may be jeopardized by faster depletion of soil water.

Key words

Ball-Berry model; elevated temperature; evaporative cooling; global change; heat waves; photosynthesis; stomatal conductance

TEXT

Temperature is one of the most variable environmental factors. It changes diurnally, within the seasons of a year and, due to the climate change, it also has been gradually increasing over decades, a trend that is expected to continue through this century. Both mean temperature and temperature extremes are important to tree functioning and survival. Various tree species can withstand a wide temperature range, from temperatures well below zero °C to temperatures exceeding 50 °C. The high temperature limit is especially crucial and it is becoming ever more important: the frequency of extreme temperatures and the severity of heat waves have increased, and they are likely to increase further in the future.[1-3] Temperature affects most plant physiological processes, including photosynthesis (A_{net}) and transpiration (E). Both, A_{net} and E, are regulated by stomatal conductance (g_s) and they mutually affect each other.[4,5] Therefore, the effect of temperature on stomata is often considered indirect, through changes in plant water status, photosynthesis or vapor pressure deficit (*VPD*). Very little is known about the direct effect of temperature on stomatal conductance (g_s)[6] which may exist independently from indirect mechanisms.[7,8] Results of experiments that examined the direct dependence of stomatal conductance on temperature have not been consistent. Previous studies have reported a complete range of responses to increased temperature, including stomatal opening,[9–12] no significant response,[13–16] stomatal closure,[17–19] peaked response with maximum g_s at temperatures optimal for photosynthesis[20] or more complex responses.[21] One possible explanation for these inconsistent results is that to isolate the direct effect of temperature on g_s requires a well-controlled environment, particularly with respect to *VPD*, which is often hard to achieve.

Therefore, we have conducted a controlled experiment in the growth chambers on two tree species with contrasting anatomy and physiology: a broad leaved species, poplar (*Populus deltoides x nigra*) and coniferous species, loblolly pine (*Pinus taeda*).[22] We manipulated air temperature and *VPD* across large range (20 – 49 °C and 0 – 10 kPa, respectively) and we repeated the measurements under well-watered and droughted conditions and under ambient and elevated CO_2 concentration ([CO_2], 400 and 800 μmol mol^{-1}).

Photosynthesis and transpiration were measured on a leaf level at various levels of temperature and *VPD*

using a Li-Cor 6400. We addressed two questions: Does g_s change with temperature at the same *VPD*, and if

so, is it related to various indices of plant water status and photosynthesis?

We have observed that g_s increased with increasing temperature in both species in all tested environmental

conditions (Figure 1). For example, when leaf temperature increased from 30 °C to 40 °C, g_s increased by

42% in poplar and by 40% in loblolly pine, at a *VPD* of 1 kPa and [CO_2] of 400 µmol mol^{-1}. Change in g_s

occurred quickly. Faster than the 30 minutes required to change temperature and stabilize *VPD* in the growth

chamber. When *VPD* was high the effect of temperature on g_s was larger than when *VPD* was low. Increase in

[CO_2] or decrease in soil water content lowered g_s but even in at high [CO_2] or low soil water content g_s

increased with increased temperature.

We have tried to link this increase in g_s to several indices of water status and photosynthesis but none of them

could explain increase in g_s across the whole range of temperature used in this study, 20 to 49 °C. Trees often

regulate their stomatal conductance to maintain a specific transpiration rate across a wide range of *VPD*.[23]

Loblolly pine adjusted g_s in this manner but only at a given temperature. When temperature increased

transpiration increased as well. Plants, at least isohydric ones, adjust their g_s in response to leaf water potential.[24]

Typically, g_s lowers with a decline in water potential. In contrary, leaf water potential of both species

decreased with increasing temperature but the stomatal opening response continued. Indices related to carbon

metabolism also did not explain stomatal opening with temperature. Plants usually maintain a stable ratio

between intercellular [CO_2] (C_i) and atmospheric [CO_2] (C_a).[25] In our study, while C_i was relatively stable at a

given temperature over large range of *VPD*, it became highly variable with changes in temperature. For

example, in loblolly pine it ranged between 165 µmol mol^{-1} at 20 °C to over 400 µmol mol^{-1} at 49 °C which

was more than the ambient [CO_2] because photosynthesis became negative. One would expect a decrease of g_s

at this extreme temperature (i.e. to save water when it was pointless to keep stomata open for the

photosynthesis) but we observed the contrary response: stomata opened even more. Many models,[26] on the

scale from leaf through plant and ecosystem[27,28] and even global circulation models[29] rely on the correlation

between A_{net} and g_s. Their central assumption is that when g_s increases A_{net} increases as well and that this

relationship holds over the wide range of environmental conditions. This assumption worked in our experiment at the range of temperatures close to temperature optimum of photosynthesis. However, at temperatures of 40 °C or more A_{net} was decoupled from g_s and at the highest temperature (49 °C) it was apparent that g_s had become independent of A_{net} because A_{net} was negative. Some studies indicated that under extreme temperatures during heat waves, that the relationship between A_{net} and g_s was decoupled, and similar to our observations, A decreased, but g_s did not.[16,17,30] With heat waves becoming more frequent, for accurate predictions of trasnpiration we recommend introducing the decoupling of g_s from A_{net} at extreme temperatures into models.

The answer to why stomata opened with increasing temperature may be partly explained by a change in hydraulic conductivity of the pathway to the sites of evaporation.[31] When temperature increases, viscosity of water declines, roughly by 20% per each 10 °C, and at the same time, mesophyll conductance increases, which may improve the supply of water to sites of evaporation increasing guard cell turgor and stomatal aperture.[16,32] Resistance to water vapor and heat transfer among sites of evaporation and guard cells, which induce differences in temperature and VPD at these sites, may also regulate stomatal opening in response to transpiration and leaf temperature.[8]

So far, we have discussed only disadvantages of increased stomatal conductance at extreme temperatures. What about the possible benefits for the plant? First, there can be an increased rate of evaporative cooling. In poplar, transpiring leaves were by up to 9 °C cooler than non-transpiring which facilitated its survival and maintained positive rates of photosynthesis at most extreme temperature, dry air and wet soil. On the other hand, loblolly pine which maintained much lower transpiration rates than poplar was able to achieve only a 1 °C temperature difference. Furthermore, the cooling effect in both species was small when the soil was dry. The benefit for loblolly pine of increased g_s at higher temperatures may be lower stomatal limitations to photosynthesis at higher temperatures. Stomata are the largest barrier for diffusion of CO_2 into leaf mesophyll. Indeed, in loblolly pine at 30 °C and a high VPD (3.5 kPa) stomata limitation to the diffusion of CO_2 was by far the greatest restriction to photosynthesis, constituting 78% of the total of stomatal and

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mesophyll limitations combined. When temperature increased to 40 °C stomatal limitations fell to 23%. We did not see such a large change in poplar and stomatal limitations were low at all temperatures. Therefore, conifers may benefit more from a decrease in stomatal limitations more than broadleaves. That may be particularly advantageous for conifers as atmospheric [CO_2] increases in response to climate change because their stomata have much less response to CO_2 than broadleaves. In summary, increased stomatal conductance at higher temperatures may help trees to increase rates of photosynthesis and may help them survive short heat waves when there is enough water in the soil. However, it could have the disadvantage of quickly depleting soil water reserves during long heat episodes.

Acknowledgement

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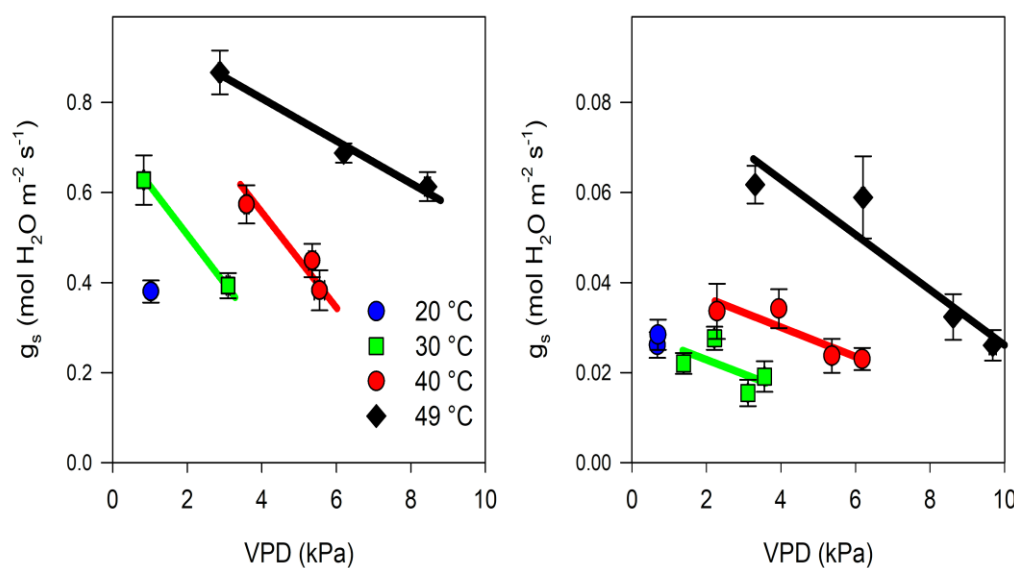
Figure 1

Figure 1

Stomatal conductance (g_s) of poplar (left panel) and loblolly pine (right panel) and its dependence on air temperature and vapor pressure deficit (*VPD*). Plants were measured in high soil moisture conditions and ambient [CO_2]. Error bars indicate standard error of the mean (n = 6). Linear regression was used to fit the data at the same temperatures.