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Commentary

Getting cold feet: tree productivity at the mercy of soil temperature

Killian Fleurial[1], Maryamsadat Vaziriyeganeh[1] and Janusz J. Zwiazek[1,2]

[1]Department of Renewable Resources, University of Alberta, 442 Earth Sciences Building, Edmonton T6G 2E3, Canada; [2]Corresponding author (jzwiazek@ualberta.ca)

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This scientific commentary refers to 'Negative effects of low root temperatures on water and carbon relations in temperate tree seedlings assessed by dual isotopic labelling' by Wang and Hoch (doi: 10.1093/treephys/tpac005).

In his pioneering 1868 *Lehrbuch der Botanik* (*Textbook on Botany*) Julius Sachs, often considered to be the father of plant physiology (Kutschera and Niklas 2018), noted that 'the absorption of water through the roots is also confined to certain limits of temperature... Tobacco plant and Gourd [sic] no longer absorb sufficient water to replace a small loss by evaporation in a moist soil of from 3 to 5 °C' (Sachs 1868). At the time, Sachs also noted that these low temperatures are limiting to other processes in plants such as the growth of green tissue or the exchange of oxygen and carbon dioxide. With considerable hindsight, we now know that water uptake is inextricably linked to turgor pressure and thus essential for cell expansion (Lockhart 1965). As such, turgor is a major limiting factor in tree growth and scaling-up its effects on forest biomass production is key to carbon sink and climate modeling (Friedlingstein et al. 2020, Cabon and Anderegg 2022). Yet, global models still overwhelmingly rely on ambient air rather than soil temperatures for their modeling even though soils show negative temperature offsets from recorded air temperatures from April to August in boreal and temperate zones, and nearly year round in the tropical forested regions of the globe (Lembrechts et al. 2022). These differences are highly dependent on both anthropogenic land use and climate-driven changes in ground cover (Lembrechts and Nijs 2020). Clearly, more attention needs to be given to the effects of low soil temperatures on plant roots and how they may impact these tree productivity models and, thus, projected climate change simulations.

Reductions in root hydraulic conductivity occur in cold soils even when water is readily available and air temperatures are warm (Running and Reid 1980, Wan et al. 2001, Kamaluddin and Zwiazek 2004). Although this effect has long been observed and reported, it can appear to run counter to the cohesion–tension paradigm under which plant hydraulics are most often viewed as a purely physical process with water pulled through a series of pipes along a water potential gradient stretching from the roots to the leaves (Dixon and Joly 1895). Although this simplified physical concept considers increased water flow resistance due to higher water viscosity at lower temperatures, it ignores important biological factors. Indeed, as Wang and Hoch clearly show in their paper published in the present issue of *Tree Physiology*, 'Negative effects of low root temperatures on water and carbon relations in temperate tree seedlings assessed by dual isotopic labelling', root water uptake is strongly reduced even at 7 °C. In their paper, Wang and Hoch used stable isotopes to show strong evidence of this reduction occurring at temperatures well above freezing and even in seedlings from cold tolerant species (*Alnus*, *Ulmus*, *Picea* and *Pinus* species), grown with water readily available, and in mild air temperatures of 24/18 °C (day/night). Where does the increased resistance come from? If water viscosity is the sole factor, the calculations of parameters such as the diameters of tracheary elements, vessel perforation plates, bordered pits, etc., would let us rank the species according to their low soil temperature tolerance levels. In this case, one would logically expect that conifer trees, due to their inherently less conductive hydraulic architecture, would be found at the bottom of the list, but many years of observations and research have proven that this is not necessarily the case.

Indeed, as also discussed by Wang and Hoch in this issue, although water is certainly slightly more viscous at positive temperatures nearing zero, its effect does not account for such large differences and much of the change in hydraulic conductivity in roots appears to be tied to changes in membrane water permeability that is mediated by aquaporins—small intrinsic membrane proteins that can act as water channels (Ionenko et al. 2010, Maurel et al. 2015). To illustrate this, in figleaf gourd (*Cucurbita ficifolia*) plants, when a cell pressure probe was used to gauge membrane permeability, low root temperature strongly reduced the hydraulic conductivity of root cortical cells and cotyledon midrib cells (Lee et al. 2008). Underlining these results, when high irradiance levels were further used to induce elevated transpiration, the permeability of the cell membranes did not change and was imperfectly compensated by a higher increase of water transport over the apoplastic pathway (Lee et al. 2008). In a subsequent study, it was then shown that overexpressing aquaporins in *Arabidopsis* increased root water uptake in cold conditions (Lee et al. 2012). The two key factors that can affect gating properties of water channels, and that can be affected by soil temperature, are phosphorylation of aquaporins and cytoplasmic pH. Many aquaporins must be phosphorylated to function as water channels (Maurel et al. 1995) and the channels close in response to cytoplasm acidification (Tournaire-Roux et al. 2003). Low root temperature reduces root respiration rates which, consequently, could deplete the energy required for protein phosphorylation and the maintenance of a proton gradient (Wan and Zwiazek 1999, Maurel et al. 2015). Maintaining root hydraulic conductivity despite low soil temperatures could, therefore, be key for plants to sustain growth and productivity if these conditions are to persist over extended periods of time, though it may not prove sufficient if plants are unable to avoid the oxidative damage that accompanies chilling (Aroca et al. 2005).

To further compound the reduction in water uptake, low soil temperatures impede root growth, even in tree species commonly distributed in cold climates (Landhäusser et al. 2001, Alvarez-Uria and Körner 2007), consequently reducing the root surface area that could be available for the uptake of water and nutrients. As such, the presence of an increased absorbing surface area brought about by certain mycorrhizal associations in roots could have a direct effect on water and nutrient uptake under low soil temperature conditions (Lehto and Zwiazek 2011). In addition, mycorrhizae are widespread throughout boreal zones of the world, and many are freezing resistant, persisting in the soil throughout the winter months. Some ericoid mycorrhizae may be able to maintain nutrient acquiring capacity at low soil temperatures through the secretion of cold active enzymes (Tibbett and Cairney 2007). Indeed, root hydraulic conductance (K_r, the extrinsic capacity of the whole root system to transport water) was enhanced approximately threefold at all root temperatures between 4 °C and 20 °C when the roots of American elm (*Ulmus americana*) seedlings were colonized by the mycorrhizal fungus *Hebeloma crustuliniforme* (Muhsin and Zwiazek 2002). Furthermore, fungal colonization resulted in approximately the same values of K_r at 4 °C as those measured in non-mycorrhizal seedlings at 20 °C (Muhsin and Zwiazek 2002). Large increases in K_r compared with non-mycorrhizal control were also reported for other northern tree species including white spruce (*Picea glauca*) and trembling aspen (*Populus tremuloides*; Landhäusser et al. 2002). However, the most significant impact of mycorrhizal fungi on root water transport may not in fact be through their increase of root area of roots but rather through an enhancement of root hydraulic conductivity (L_{pr}, the intrinsic capacity of the roots to transport water that is independent of their size; Muhsin and Zwiazek 2002, Siemens and Zwiazek 2008, Xu et al. 2015). Closer examination of the factors responsible for the effect of mycorrhizal fungi on root hydraulic conductivity revealed that both plant roots (Marjanović et al. 2005) and the associated mycorrhizal fungal aquaporins (Xu et al. 2015) may be responsible for this effect. The fungus increases gene expression of root aquaporins (Marjanović et al. 2005), through a yet undetermined process, and this, in turn, enhances cell hydraulic conductivity (L_{pc}) in plant roots (Lee et al. 2010, Xu et al. 2015).

In parallel, low temperatures also affect phloem transport. As early as in 1919, Child and Bellamy reported a blockage of translocation in the phloem induced by chilling a small part of a stem, petiole or runner to 3–6 °C (Child and Bellamy 1919). Similarly, in this issue Wang and Hoch reported a 60% reduction in the phloem transport of carbon to the roots at just 7 °C (Wang and Hoch 2022). This loss of phloem conductivity due to chilling may also be partly due to the decreased fluidity of the cytoplasm and the plasma membrane (Alonso et al. 1997). In cow thistle stems, it was hypothesized that aquaporins or other transport molecules in the sieve element plasma membranes are disrupted by the low temperature (Gould et al. 2004). Nevertheless, after localized chilling a rapid aquaporin upregulation was shown in balsam poplar sieve cell membranes (Stanfield and Laur 2019). This dynamic response may serve to counteract the reduced passive permeability of the plasma membrane, as the water released from the sieve tubes consequently adjusted pressure allowing flow to resume (Stanfield and Laur 2019). At a larger scale, there is evidence of a greater use of whole-tree non-structural carbohydrate pools in boreal rather than in temperate paper birch populations (*Betula papyrifera*) (Fermaniuk et al. 2021). These differences are primarily driven by the branch pools for spring growth (Fermaniuk et al. 2021) and could partly help avoid the impact of a potentially slowed root phloem transport in cold springtime soils. Furthermore, the role played by the conversion of starch to soluble carbohydrates for cold protection has long been documented (Sakai and Yoshida 1968). However, it was shown that carbon assimilation and, thus, its transport may not be the limiting factor for productivity

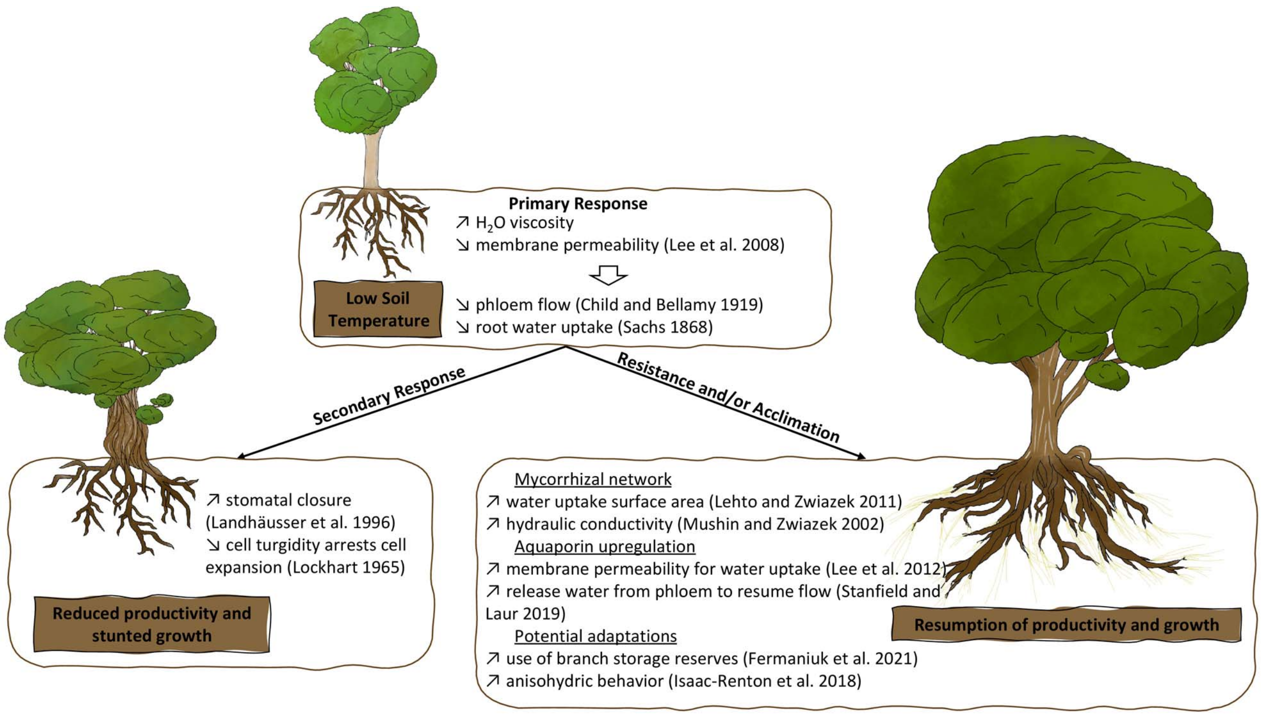

Figure 1. As soil temperatures decrease, the viscosity of water increases. In plant roots a primary response to lower temperatures is a reduction in membrane permeability (Lee et al. 2008). The combination of these effects leads to a reduction in the flow of photosynthates in the phloem (Child and Bellamy 1919) and water uptake (Sachs 1868). This apparent reduction in available water to the roots leads to two notable secondary responses, stomatal closure (Landhäusser et al. 1996) and a drop in turgidity affecting cell expansion (Lockhart 1965). In time, these secondary responses reduce productivity and stunt growth. Nevertheless, resistance or acclimation to non-negative low soil temperatures likely occurs in certain species or populations. Certain mycorrhizal associations in the roots can significantly increase water uptake by providing a greater surface area (Lehto and Zwiazek 2011) and increased root hydraulic conductivity (Muhsin and Zwiazek 2002). The upregulation of certain aquaporins can increase membrane permeability not only for water uptake (Lee et al. 2012), but also for water release from the phloem to resume flow (Stanfield and Laur 2019). We also suggest that the greater dependence on branch carbohydrate reserves and anisohydric behavior observed in certain northern tree populations (Isaac-Renton et al. 2018, Fermaniuk et al. 2021) may help trees resume and maintain productivity and growth at lower soil temperatures.

in cold soils as Norway spruce trees growing in soil cooled by pockets of permafrost maintained high levels of carbon despite their severely stunted growth (Körner and Hoch 2006, Hoch 2008).

Indeed, although low temperature effects and restrictions on productivity are often discussed in terms of cell growth with respect to limitations in nutrients and reduced photosynthesis, with studies like the one presented by Wang and Hoch in this issue, evidence is now mounting that root water uptake may be the most important limiting factor. As cold soils immediately lead to an apparent restriction of the water supply in plants (Figure 1, Primary Response), growth is rapidly reduced leading to reduced productivity and stunted growth (Figure 1, Secondary Response; Wan et al. 1999, Landhäusser et al. 2001). As such, low soil temperature stress is often considered to elicit a drought-like stress, a dual adaptation to both types of stress could plausibly be expected to occur. Coastal Douglas-fir in the Pacific Northwest from populations subjected to lower winter temperature gradients have been recorded to be more drought resistant than those from provenances with milder winters (Bansal et al. 2016). However, contrary to expectations, Arctic tree populations were reported to be physiologically maladapted to drought (Isaac-Renton et al. 2018). In their provenance trial, in addition to thinner cell walls, Isaac-Renton et al. (2018) observed consistently poor stomatal control in lodgepole pine from northern provenances. Considering that a common response to low soil temperatures is an immediate closure of the stomata due to decreased water delivery (Figure 1, Secondary Response; Landhäusser et al. 1996, Wan et al. 2004), anisohydric plants should be better adapted to prolonged low soil temperatures in terms of maintaining their productivity. Further research is undoubtedly needed, but when viewed from this prism, the results observed in Douglas-fir and lodgepole pine would no longer seem so contradictory. An adaptation to withstand seasonal lower temperatures is different from an adaptation to grow at low soil temperatures where maintaining productivity could be crucial. The first could confer drought resistance and the other drought vulnerability. More research is also needed to better understand the effects of plant and fungal aquaporins and their associations on root transport dynamics in trees exposed to low soil temperatures. It seems likely that all these factors may contribute to make certain species or populations more productive at low soil temperatures (Figure 1, Resistance and/or Acclimation).

Conflict of interest

The authors declare no conflict of interest.

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