Drought impacts on phloem transport

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Drought impacts on phloem transport have attracted attention only recently, despite the well-established, and empirically verified theories on drought impacts on water transport in plants in general. This is because studying phloem transport is challenging. Phloem tissue is relatively small and delicate, and it has often been assumed not to be impacted by drought, or having insignificant impact on plant function or survival compared to the xylem. New evidence, however, suggests that drought responses of the phloem might hold the key for predicting plant survival time during drought or revival capacity after drought. This review summarizes current theories and empirical evidence on how drought might impact phloem transport, and evaluates these findings in relation to plant survival during drought.

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Introduction

Predictions for future climate suggest an increase in drought frequency and severity especially in the mid-latitudes and low-latitudes [1]. This has brought up a concern about future agricultural and forest productivity. Reductions in productivity could be significant enough to have a major impact on human wellbeing [2,3]. Vegetation decline could also accelerate global warming through the altered carbon and water cycles [4]. These predictions are supported by a large number of observed ecosystem-scale forest mortality events during the past 20 years [5]. The scientific community has reacted by an increased interest in developing methods for predicting plant survival under drought [6–10]. The most commonly used concept in these models is based on the theories about xylem vulnerability to embolism [11•], and its connection to stomatal closure [12,13]. These theories suggest that during drought water tension in the xylem increases leading to embolization of xylem conduits. To prevent catastrophic loss of xylem conductivity plants close their stomata before a water tension threshold is reached. This threshold depends on plant species and is linked with xylem vulnerability to embolism [11•]. Even after stomatal closure, plants slowly lose water through the bark and cuticular tissue of leaves. Stomatal closure does not completely prevent additional embolism [14•,15•], but it significantly reduces water loss rates and embolism propagation.

The theories on xylem vulnerability to drought and its connection to stomatal closure point are robust and supported by a wealth of empirical evidence [11•,13,16,17], but the predictive power of this approach concerning plant survival time is limited [9,11•,18]. We lack knowledge on how to define the needed thresholds of catastrophic hydraulic failure [19,20]. Findings on a meta-analysis of 19 recent plant mortality studies on 26 species around the world suggests that 60% or higher loss of conductivity leads to mortality (defined as loss of leaves or cessation of respiration [21•]), while many other studies have used thresholds on 50–88% [19,20]. Other open questions include how fast plants would die once a threshold is reached [8], and how availability of new or stored carbohydrates, and their use impact these thresholds, and survival or revival capacity after drought [22,23].

Considerations of drought impacts on phloem transport and xylem–phloem interactions could be a key for resolving these challenges [24,25•]. Theoretically, limitations in phloem transport influence allocation and redistribution of carbohydrate reserves, possibly speeding up mortality via carbon starvation [24,26,30]. These limitations might feed directly back to stomatal closure during drought [27]. There is also evidence that reduction in carbohydrate reserves or turgor loss of the phloem tissue are best predictors of plant survival time during extreme drought [28–30], even if loss of xylem conductivity might be the final manifestation of death of the plant [30,31]. Phloem transport is also important for plant defenses against herbivore and pathogens [25•,31]. This might explain part of the high correlation of carbohydrate reserves with survival time ($R^2 > 0.9$) in datasets where mortality was facilitated by insects [8,29]. Therefore, understanding drought impacts on phloem transport and the role of xylem–phloem interactions during drought is essential for improving predictions of vegetation responses to environmental stress.

How could drought affect phloem transport?

Xylem and phloem are hydraulically connected, and they tend to be in hydraulic equilibrium at all relevant

time scales [32]. This implies that increasing xylem water tension during drought is sensed by the phloem tissue. To maintain functionality and avoid losing water to the transpiration stream during drought, phloem tissue water potential needs to be adjusted osmotically to match that of the xylem [27,33]. This osmotic adjustment could be obtained by increasing carbohydrate concentration in the phloem conduits and cells surrounding the conduits. But increasing carbohydrate concentration increases the solute viscosity exponentially [34]. For example, in pine, under severe drought when the xylem water potential drops below roughly −4 to −5 MPa (estimation made for pine anatomy using the FinnSim model [7]), the sugar concentration required to balance phloem and xylem water potentials increases to a level where fluid viscosity leads to significant increase in phloem flow resistance possibly blocking the conduits [33,35,36•]. If phloem osmoregulation is too slow or fails, water would flow from the phloem to the xylem resulting in turgor loss and collapse of the tissue (Figure 1) [35]. At the onset of drought, growth also often declines before stomatal closure [37,38]. This reduces the strength of carbohydrate sinks [39] slowing phloem transport down even if transport was not limited by any other mechanism. Instead of leading to phloem malfunction, mild drought might thus mostly affect phloem transport rates.

What do we know about drought impacts on phloem transport?

There is little information about whether carbohydrate transport at tissue water potentials close to the viscosity limit occurs, even if the hypothesis about the importance of such transport for plant survival is plausible. This is because measuring phloem transport requires elaborate non-destructive techniques [40–42], and few studies have focused on transport under drought. Indirect evidence based on changes in non-structural carbohydrate pools during drought give ambivalent results. Shoot soluble sugar pools have been observed to increase after stomatal closure at −5 MPa leaf water potential in *Juniperus monosperma* [29]. But a comparable change in starch was observed suggesting that perhaps this change was due to local starch-to-sugars conversion rather than phloem transport. Studies on *Picea abies* saplings suggest that carbohydrates were not transported to the roots during a drought that lead to mortality [43,44], supporting the view of lack of phloem transport during severe drought. On the other hand, *Pinus edulis* trees that survived longest during a lethal drought consumed their carbohydrate reserves to a higher degree than trees that died faster supporting the view that access to carbohydrate reserves differs even within species and promotes survival [30].

Whether phloem sap viscosity increases to levels that might induce phloem blockage is also an open question.

Figure 1
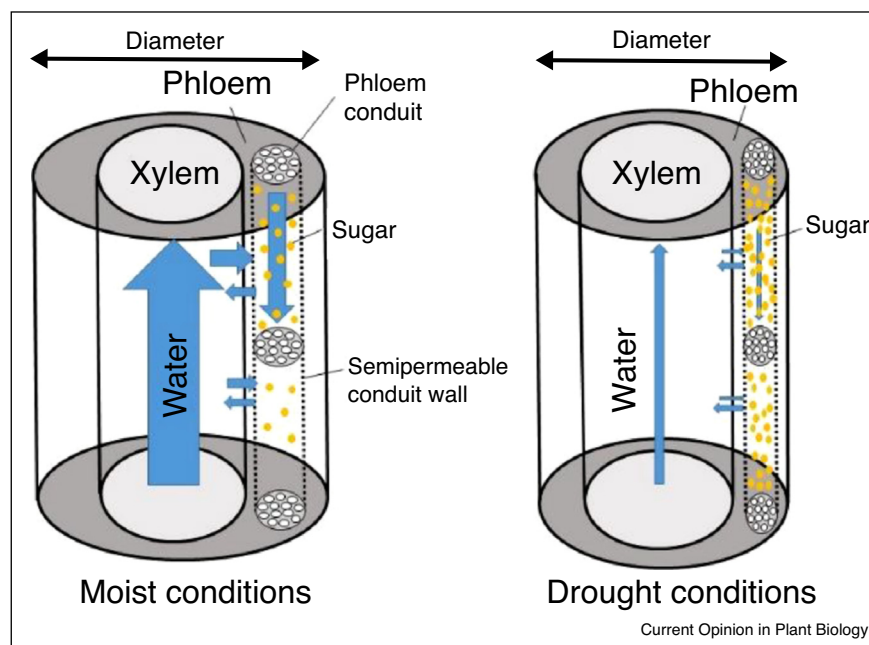
A schematic presentation on how drought impacts the whole stem, highlighting a phloem conduit. In moist conditions (left) even relatively low solute concentrations in the phloem can maintain hydraulic equilibrium with the xylem and pull water from the transpiration stream to the phloem. During drought (right), the tissues shrink, high solute concentrations in the phloem cells and conduits are needed to keep the water from flowing to the drying xylem.

For this to happen, and be relevant for plant survival during drought, the plant will need to transport carbohydrates at tissue water potentials close to or below −4 MPa (the threshold depending on phloem anatomy) [32,33]. Most desiccation avoiding (isohydric) plants never reach such tissue water potentials before stomatal closure. For these plants, the viscosity limitation may become important during redistribution of resources after stomatal closure [35]. Desiccation tolerant (anisohydric) plants that produce new carbohydrates at low leaf water potentials seem to reach such water potentials, but only in very arid conditions [29,45–48]. These plants may have different mechanisms for maintaining phloem transport or reducing the need for phloem transport. They could, for example store new photosynthetic products in the leaves [29] and release them in small quantities together with salt ions that do not increase fluid viscosity as much as carbohydrates [49]. The viscosity build-up also requires phloem conduits that are hydraulically relatively isolated from their surroundings. If the conduits are hydraulically well connected to their surroundings, phloem transport will be protected from effects of increasing viscosity by water readily entering and exiting the conduit and diluting the solution with increasing sugar concentration [34] as long as water is available. In that case, however, the risk for tissue turgor loss and requirements for fast osmoregulation would be higher than if the hydraulic conductivity between the xylem and the phloem was low [34,50,51].

There is little empirical information on the hydraulic conductivity between the xylem and the phloem. Some indirect measurements on temperate deciduous hardwood species suggest that the conductivity is of similar order of magnitude as has been reported for aquaporins (10^{-14} m s^{-1} Pa^{-1}) [52], but modeling studies often use values two or more orders of magnitudes larger than that [33,53]. Aquaporins have been found in phloem conduit cell membranes in some species [54••], and they are a very interesting solution to controlling the trade-off between viscosity build-up and turgor failure during drought. They can be readily formed and closed by the plant [55] allowing quick control of the hydraulic conductivity, and therefore also control of immediate osmoregulatory needs and phloem vulnerability to decreasing xylem water potential.

As of today, most studies on drought impacts on plant hydraulics, however, use plants that close the stomata at high leaf water potentials (desiccation avoiding plants) [21•], in which case no drought-induced limitation to phloem transport besides possible reduction in carbon sinks, should exist. Eventually, these plants will also reach low tissue water potentials that can block phloem transport [30], but few studies continue long enough to allow plants reach this point and test possible needs for phloem transport in these conditions. Many stud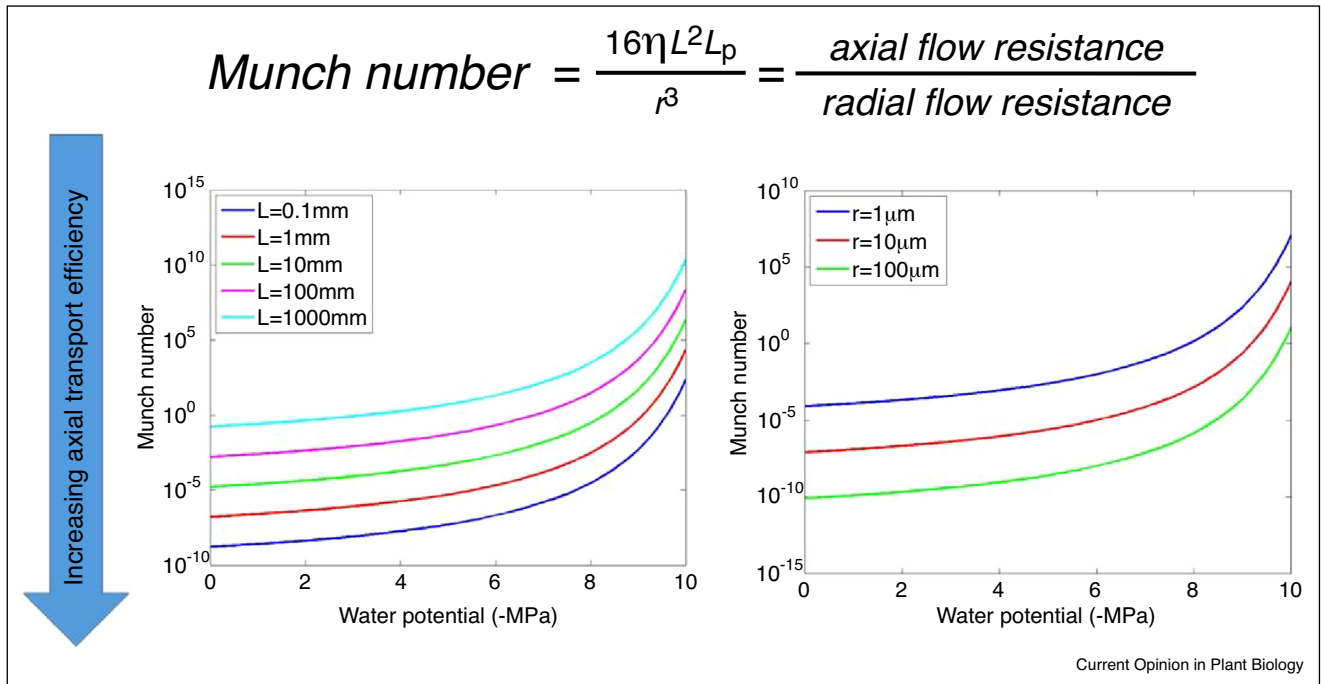ies also report an initial increase in leaf non-structural carbohydrate pools during drought, which is usually attributed to drought limiting growth before stomatal closure [24,26]. Interestingly, a study on desiccation avoiding *Pinus edulis* suggests that phloem transport limitations could also be involved. In that study phloem turgor collapsed (cells collapsed) two weeks before permanent stomatal closure during drought [30]. This study also shows that the rate at which carbohydrates are used after stomatal closure may depend on water availability. Some individuals can reduce the consumption rate with declining water availability increasing their survival time. If water is available, phloem transport will continue until carbohydrate reserves are consumed if stomata were forced to close, for example, by shading or CO_2 removal, [44]. In this case phloem turgor collapses even at relatively high xylem water potential [30] when osmoregulatory resources are consumed. At this stage, also the xylem embolizes even if the soil moisture content was at field capacity, indicating that the integrity of the phloem is important for maintaining xylem function [30]. This is a possible explanation to why phloem turgor collapse can predict plant survival time so well.

What kind of phloem would be best for facilitating transport during drought?

Structurally, to maintain transport capacity of the phloem at low tissue water potentials, it would be beneficial to have the conduits surrounded by living cells that can control their water content and serve as a water reservoir relatively independently of the xylem. These kinds of structures seem to be common in leaves and stems of many angiosperms [56]. Many plants also show bands of fibers between rows of phloem conduits [56] that could provide mechanical resistance against phloem collapse. Maintaining phloem turgor under drought would be easier if the xylem and the phloem were hydraulically relatively isolated. But at the same time, even in non-drought conditions, the only source of replacement water for the phloem tissue (including conduits and other cells) is through the xylem, and some hydraulic connection is thus essential. One could hypothesize that a system with lowest possible hydraulic conductivity between the xylem and the phloem that does not lead to viscosity blockage of flow at low tissue water potentials would be optimal.

The combined impacts of conduit anatomy and wall permeability on sugar transport in conduits with semi-permeable walls can be summarized by considering the ratio of flow resistance in axial and radial direction, the Münch number (Figure 2) [53,35]. If the flow resistance in axial direction increases to the order of magnitude of the resistance in radial direction, efficiency of axial transport would be severely impacted. The axial resistance increases with increasing viscosity, and conduit length (Figure 2), while radial resistance decreases with increasing wall permeability. Axial flow resistance is also lower in

Figure 2

$$\textit{Munch number} = \frac{16\eta L^2 L_{\mathrm{p}}}{r^3} = \frac{\textit{axial flow resistance}}{\textit{radial flow resistance}}$$

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The Münch number describes the ratio of axial and radial flow resistance in cylindrical conduits with semi-permeable walls. It is the ratio of fluid viscosity (η), conduit length (L) squared and wall permeability L_p to conduit radius (r) cubed. At low Münch numbers axial transport in phloem conduits is efficient. At low tissue water potentials, having low wall permeability, and short and wide conduits would be a benefit.

Figure 3

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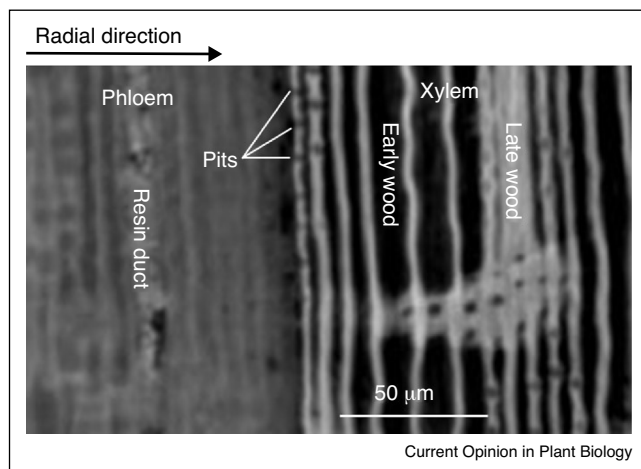
An X-ray tomography image of the xylem–phloem boundary in *Pinus edulis*. Bordered pits are found at the last cell wall of the xylem connecting it to the first cell layer of cambium connecting the xylem and the phloem.

wide than narrow conduits. Based on these arguments it looks like that at a set conduit wall permeability, short and wide conduits would be better for maintaining phloem transport at low tissue water potentials than long and narrow conduits. There is, however much unknown about phloem transport and anatomy [57]. Even the effective transport length of conduits is somewhat unclear because of the observations that sieve plates or other obstructive-looking structures may not obstruct the axial flow [58]. Therefore, accurate estimates of flow limitations during drought are still challenging. New evidence on phloem anatomy of two coniferous species that have become the model species of drought responses of desiccation avoiding and tolerant plants (*Pinus edulis* and *Juniperus monosperma*, respectively) also indicates that the xylem and the cambial layer can be connected by bordered pits (Figure 3), and there is an abundance of sieve pores connecting the phloem conduits to form a conduit network rather than a tissue of single conduits (S. Sevanto, unpublished data). If these findings are verified by future studies, our current views of how plants control drought impacts on phloem transport might change dramatically.

Conclusions

Theoretical work on drought impacts on phloem transport indicates that the hydraulic conductivity between the xylem and the phloem, and between phloem conduits and their immediate environment determines how and when phloem transport becomes impaired during drought. Whether these predictions match the reality requires more experimental work on phloem anatomy

and function, especially under drought conditions. In the few studies that have addressed phloem transport during drought, integrity of the phloem seems to be essential for plant survival and it comes out as one of the best predictors of plant survival time. However, more studies on whether and how plants might promote or control phloem integrity during drought are needed before the true impacts of phloem transport on plant survival during drought can be assessed.

Acknowledgements

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