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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?

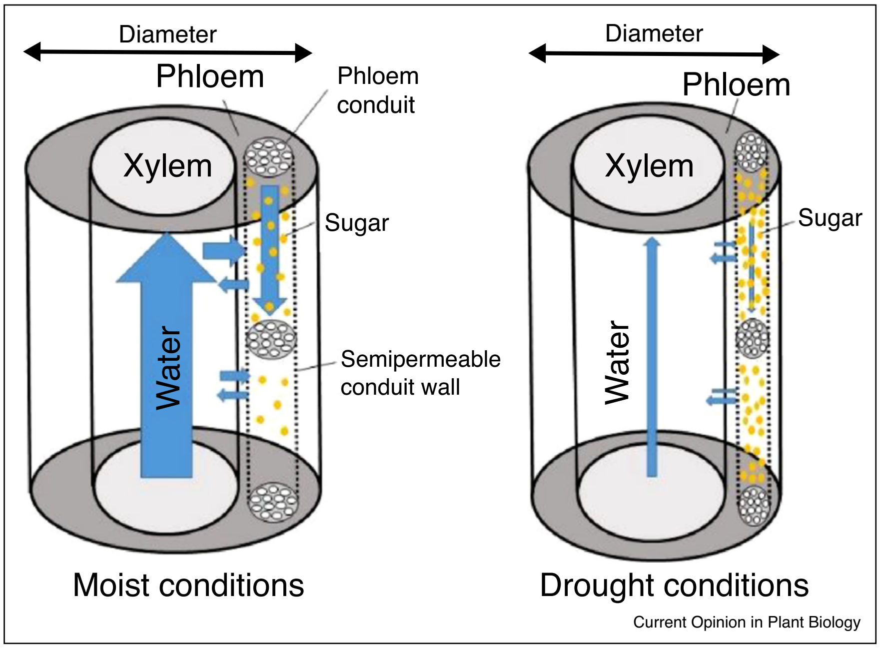
Xylem and phloem are hydraulically connected, and they tend to be in hydraulic equilibrium at all relevant time scales [32]. This implies that increasing xylem water tension during drought is sensed by the phloem tissue. To maintain functionality and avoid losing water to the transpiration stream during 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.