# A Primer on Plant Hydraulic Physiology for Nursery Professionals

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## Abstract

Plant hydraulic physiology, the study of water movement through plants, offers mechanistic explanations for better understanding connections among nursery production regimes, seedling growth, and outplanting performance. Applying plant hydraulic physiology methods and concepts starts with an understanding of flow rates, conductance, and conductivity. Water flow and hydraulic failure in woody plants are affected by the size and arrangement of the xylem, the morphology and allometry of the plant, and the environmental conditions in which the plant is growing. Nursery professionals can predict and manipulate the complex and dynamic responses of seedlings to water stress with knowledge of the plant hydraulic traits. The application of plant hydraulic physiology will help with the efficient and sustainable production of seedlings that can survive in challenging outplanting environments.

## Introduction

Plant hydraulic physiology is the study of water movement through plants (McCulloh et al. 2019). From research outcomes in the field of plant hydraulic physiology, we can build mechanistic explanations of how woody plants respond to water availability and limitations (Venturas et al. 2017). This information can help explain the impacts of nursery production regimes on plant physiology and growth. The field's relevance to seedling nursery production has long been recognized (Carlson and Miller 1990). Advances in the last few decades make the potential takeaways and applications from plant hydraulic physiology into nursery science even more enticing.

Though relevant to nursery science, plant hydraulic physiology can be a complex topic to understand without first being introduced to the basic concepts and research methods. In this article, we explain the definitions and foundational ideas of water flow through plants and the intersection with plant anatomy, morphology, and physiology. We also provide examples of how a nuanced understanding of plant hydraulic physiology can lead to better decision making and planning in nursery production and outplanting (Lauri et al. 2011). With this improved understanding, researchers, nursery professionals, and foresters can leverage what is known through plant hydraulic physiology to ensure that high-quality, stress-resistant seedlings are grown in the nursery and planted in the field.

## Quantifying Water Movement

We will begin by describing the basics of water flow through plants and the units used to quantify water movement. For nursery professionals, the parallel to water flow through irrigation systems is a useful starting point. More technical definitions for water flow through plants and related equations can be found in plant physiology textbooks (e.g., Lambers et al. 2008, Tyree and Zimmermann 2002).

### Flow Rate

Flow rate, Q, is a volume of water per amount of time.

1) $Q = V/t$; e.g., gal min$^{-1}$ or L min$^{-1}$

In the nursery, we often consider flow rates such as the capacity of a well in gallons (or liters) per minute. Sprinkler emitters and hose nozzles are also typically classified by their flow rates (e.g., a mist head with a flow rate of 0.25 gal/min [1 L/min]). If the flow rate of a hose or sprinkler head is unknown, it could be approximated by timing how long it takes for the hose or sprinkler to fill a container of a known volume (figure 1).

The flow rate through a system is affected by the conduits through which the water flows, whether pipes or xylem. Much more water can flow through a 1-in (2.5-cm) pipe than a 0.25-in (0.6-cm) pipe at the same pressure. For very small conduits, like xylem, that have non-turbulent water flow, the flow rate is proportional to the fourth power of the radius of the conduit. Thus, a single xylem conduit with a diameter of 40 µm can move as much water as 256 xylem conduits with a diameter of 10 µm (Tyree and Zimmermann 2002). Small differences in xylem size can lead to large differences in the flow rate of water through the xylem.

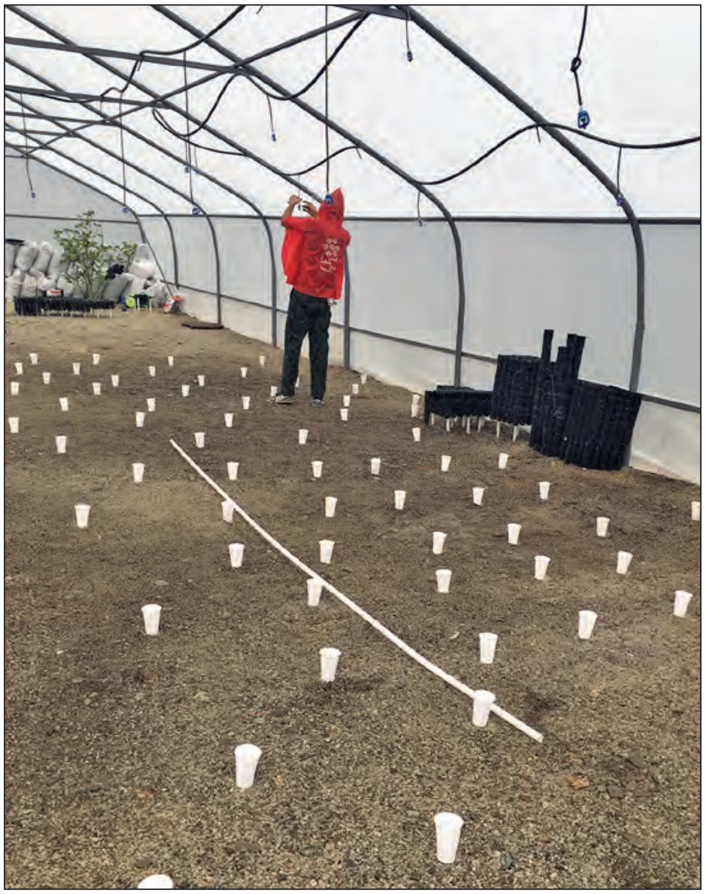


**Figure 1.** A cup test measures the amount of irrigation water that fills cups in a set amount of time. This test is used to determine the application rate of the irrigation system and accounts for the cumulative flow rate of multiple sprinkler heads across the growing area. (Photo by Rebecca Sheridan 2017)

## Conductance

In most nursery systems, pressure regulators are used to keep the water pressure constant, so we do not usually need to consider how pressure affects flow on a day-to-day basis for irrigation. With a pressure regulator, we assume the irrigation system is under a consistent pressure over time, allowing for even and predictable watering. When flow is considered in terms of the pressure gradient that drives water movement, this is conductance. Conductance, k, is given in units of water per time per pressure gradient.

2) $k = Q/\Delta\psi$; e.g., g $s^{-1}$ $MPa^{-1}$

In the next section, we will describe in more detail how conductance through a plant is impacted by xylem shape and arrangement.

## Conductivity

Conductivity, *K*, scales conductance to a length or an area.

3) $K = Q/(\Delta\psi \bullet area)$; e.g., g $m^{-1}$ $s^{-1}$ $MPa^{-1}$

This calculation allows us to compare capacity of different parts of the water movement system or water movement at different scales. Conductivity is not often used to describe irrigation systems, but in plants, we might be interested in comparing water flow through stems with different stem sizes and would therefore scale conductance by sapwood area to obtain a measurement of conductivity (Melcher et al. 2012). Across the breadth of work in plant hydraulic physiology, hydraulic conductivity is scaled in various ways such as sapwood area ($K_s$), leaf area ($K_L$), stem length ($K_l$), root mass, and so on. When reviewing a reported value of plant hydraulic conductivity, be sure to check how conductance is normalized to the plant's dimensions.

# Water Movement Through Plants

The metaphorical parallels between irrigation and water movement through plants start to break down when we consider the force of water movement in plants. Instead of being pushed by a pump or falling with gravity from a cistern, water in a plant is pulled by tension created when water evaporates from the leaf (evapotranspiration).

To explain this further, we can start by defining water potential. Water potential, ψ, is the potential energy of water within the plant's xylem or cells. Water potential is reported relative to the potential of pure water (ψ = 0). In plants, water potential is negative due to solutes, such as sugars, in sap and the tension created by evapotranspiration. While negative pressure is nonsensical for gases (the lower limit of pressure for a gas is zero, or a vacuum), liquids, such as water, can withstand tension, or negative pressure. The most often reported unit of pressure in plant hydraulic physiology is megapascals (MPa). For context, 1 MPa equals 9.85 atmosphere (atm) or 145 pounds per square inch (PSI). Plant water potential in leaves and stems is commonly measured using a Scholander-type pressure chamber (figure 2) (Tyree and Hammel 1972).

When water potential varies among different parts of the plant or between the plant and the growing environment, this results in a water potential gradient. Water moves from less negative to more negative water potentials, such as from a root in wet soil to the leaf surface, where water is evaporating into the ambient air. The pathway of water movement from the soil (or growing medium) through the plant and into the atmosphere is called the Soil-Plant-Atmosphere Continuum or SPAC. The water potential gradient created by evapotranspiration moves water against the gravitation gradient, allowing water to move up into even the tallest tree canopies.

## Xylem Function and Dysfunction

The bulk of water flow in a plant is through the plant's xylem. As with an irrigation system, the constraints and capacity of water movement are dictated by the size of the conduits through which water moves (xylem anatomy) and the arrangement of the system (plant morphology). Xylem is basically a modular system (figure 3). In conifers, xylem conduits are tracheids, and in angiosperms the conduits are vessel elements and tracheids. Water flow through an individual xylem conduit is determined by the inner diameter of the conduit (Hacke et al. 2017). The conduits are stacked end to end and connected via intervessel pits (Wason et al. 2019). The thickness of the xylem's cell walls, as well as the shape, size, and arrangement of vessel-to-vessel connections, also impact water movement. The width, length, and arrangement of the xylem conduits vary by species (Schenk et al. 2018). Classifications within wood as latewood and earlywood or ring-porous and

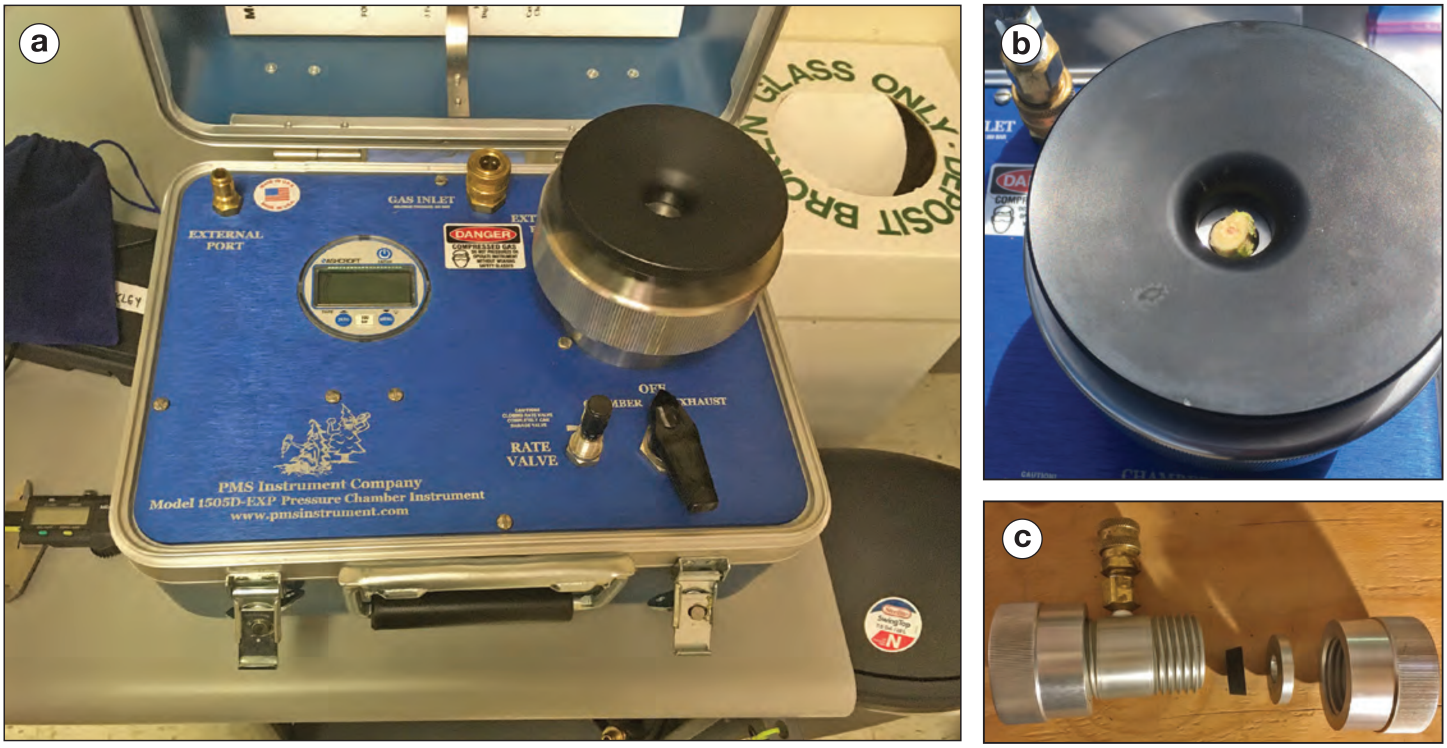


**Figure 2.** (a) A pressure chamber with a digital gauge to read pressure measurements is a useful instrument for plant hydraulic physiology measurements. (b) The plant stem segment is placed in the compression gland and pressure is applied to force water through the cut end. (c) A cavitation chamber is used to pressurize stem segments. Not pictured are the portable compressed gas tank and the pressure-resistant hoses that connect the tank, chamber, and accessories. (Photos by Rebecca Sheridan 2020)

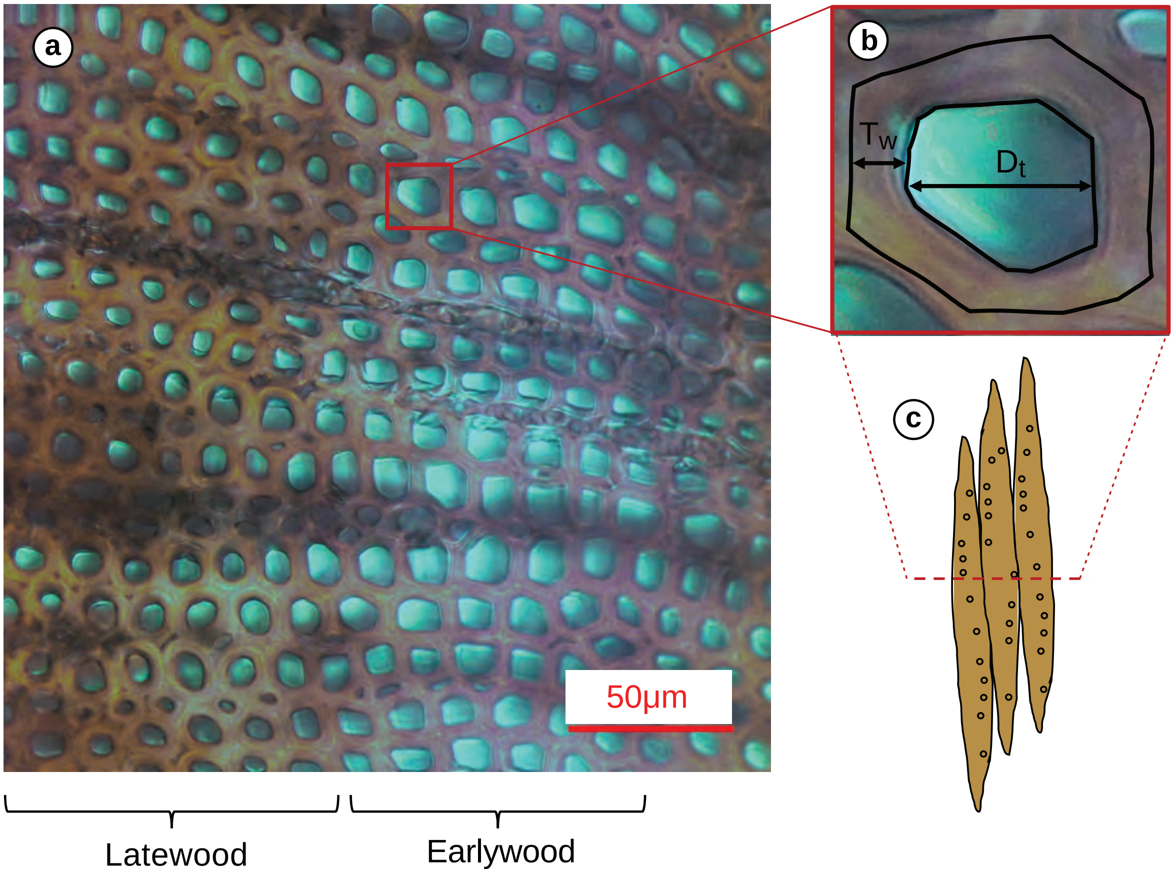


**Figure 3.** A cross-section of Douglas-fir xylem shows (a) individual xylem tracheids arranged with a notable transition in tracheid size from earlywood to latewood. (b) A close-up of an individual xylem element shows dimensions of inner diameter ($D_t$) and wall thickness ($T_w$) that impact water flow. (c) An illustration of tracheids with bordered pits (not to scale). (Photo by Rebecca Sheridan 2017)

diffuse-porous describe the way xylem elements of different sizes are arranged within the stem. This arrangement of xylem elements affects the efficiency of water movement through the stem (McCulloh et al. 2010). Dimensions of xylem conduits can change in response to environmental factors such as drought (Eilmann et al. 2009, Eldhuset et al. 2013, Fonti et al. 2013). Predictably, this variability impacts conductance at the xylem, organ, and whole-plant scales. In this way, plant structure and allometric relationships are also connected to plant hydraulic physiology (Mirabel et al. 2019).

So far, we have introduced concepts of water flow through plants when functioning in the absence of stress. When a plant is in water-limited conditions, such as drying soil, the plant experiences increasingly negative water potentials. With increasing stress on the water transport system through the SPAC, plants are at risk of xylem embolism or cavitation. Cavitation is the introduction of air into the water-filled xylem, which results in embolism, air-filled cavities within the xylem. As with xylem conductance, the mechanics of xylem embolism are related to xylem conduit size, arrangement, and interconnection (Gleason et al. 2016). Just as there is variety in the xylem system's function across organs, species, and environment conditions, there are also variable responses to water stress (Kavanagh et al. 1999, Stout and Sala 2003). Hydraulic failure due to water stress can reduce growth or cause dieback; the most severe consequence of water limitation to a plant is mortality (Hammond et al. 2019).

## Measuring Stem Conductance

Plant conductance and related hydraulic traits are measured in a wide variety of ways. Many techniques can be accomplished with relatively low-cost or lab-made equipment. Recent advances in x-ray microCT imaging technology allow water movement within plants to be measured *in vivo* in real time (Miller et al. 2020). We will not go into describing all the methods by which plant conductance can be measured, but several articles provide good starting points (e.g., Kolb et al. 1996, Li et al. 2008, Melcher et al. 2012). For purposes of this paper, we will focus on one commonly used metric within plant hydraulic physiology: stem conductance (figure 4). Stem conductance is the flow through a stem segment across a known pressure gradient and can be measured relatively easily in a lab setting using an elevated reservoir of ultra-pure, filtered water, tubing, and a pipette or microbalance to track output of water (Sperry et al. 1988). Most often, stem conductance measurements are scaled to the stem's length and diameter and reported as stem conductivity.

One way to quantify the impact of water stress on a plant is with the metric of stem conductivity. The relationship between water stress and conductivity is presented as a vulnerability curve (Tyree and Zimmermann 2002). Measurements made on a stem segment directly removed from a plant capture the conductivity of the stem under ambient conditions and the history of conditions the stem has encountered. If xylem conduits within the stem segment had embolized under ambient conditions, the embolism can be removed by putting the stem segment under water in a vacuum and pulling the air out. Stem conductivity measured after embolisms have been removed gives the maximum stem conductivity. Pressure can also be artificially imposed on a stem segment using a pressure chamber to replicate the stress a segment would face under drought or other water stress (figure 2) (Cochard

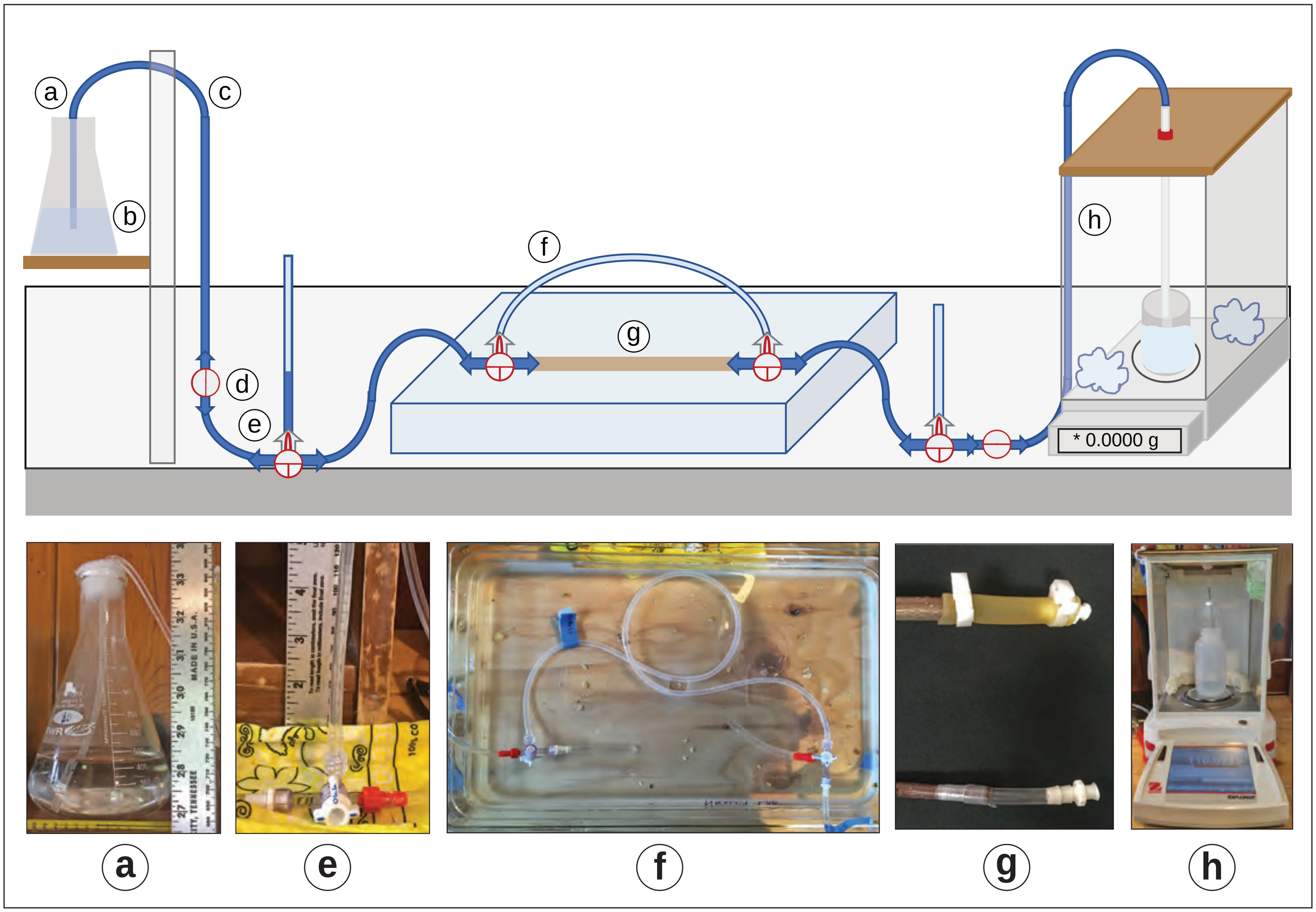


**Figure 4.** A stem conductivity apparatus consists of: (a) an elevated reservoir of water to provide a pressure gradient to induce flow through the stem, (b) a meter stick to measure height of the hydraulic head, (c) tubing through which water flows from the reservoir through the stem segment and onto the balance, (d) stopcocks that direct flow of water to the stem or to bypass tubing depending on the step within the method, (e) standpipe that allows pressure gradient to be equilibrated with the stem segment height, (f) bypass tubing, (g) stem segment plumbed into the system with rubber or tubing gaskets, and (h) an analytical balance that measures flow over time. With the flow rate onto the balance, the pressure gradient, and the length and diameter of the stem segment, stem conductance and conductivity can be calculated. The balance can be connected to a computer to automate the calculations. (Photos by Rebecca Sheridan 2020)

et al. 1992). The same stem segment can be measured multiple times with stepwise increases in water stress to create a response curve between water potential and conductivity (figure 5). Most often, changes in conductivity are reported relative to maximum conductivity, and subsequent values of conductivity are given in terms of the percent loss of conductivity (PLC).

Maximum conductivity and vulnerability curve parameters vary by organ within a plant, environmental conditions, and species. Within a plant, it is thought that more expendable organs such as leaves and fine roots will experience hydraulic failure first, to protect the rest of the plant under drought conditions (Johnson et al. 2016). To compare among populations of interest, plant physiologists often report the water potentials at which 50 percent of conductivity is lost ($P_{50}$); $P_{12}$ and $P_{88}$ are also used to summarize key points on vulnerability curves. Thresholds for mortality have been identified for conifers at 50 percent stem PLC and for angiosperms at 60 to 88 percent stem PLC (Adams et al. 2017, Brodribb and Cochard 2009, Urli et al. 2012). The water potentials at which mortality-inducing losses of stem conductivity occur should obviously be avoided in nursery production.

## Other Physiological Responses

In the preceding sections, we have focused on stem hydraulic conductivity. However, plants draw on a suite of physiological traits and dynamic responses to avoid or mitigate water stress (Choat et al. 2018). In the context of seedling production, it is useful to also understand the physiological responses to water stress that occur before stem hydraulic failure and plant mortality. In the same way that a vulnerability curve is built for stem hydraulic conductivity, other hydraulic traits such as stomatal closure, leaf hydraulic conductivity, and leaf wilting can be mapped to changes in water potential. The response curves of multiple traits can be layered together, showing the sequence of physiological responses to increasing water stress (figure 6). For example, a plant may first respond to water stress by adjusting stomatal conductance, then leaf conductivity, before stem conductivity is impacted at more extreme water potentials. Sequential physiological responses have been mapped for individual species such as grapevine (*Vitis vinifera* L.) (Gambetta et al. 2020) as well as summarized for hundreds of species (Bartlett et al. 2016). Identifying, testing, and modeling sequences of physiological events may be useful for nursery professionals in operational contexts, such as identifying thresholds for irrigation.

## Application to Nursery Production

In nursery production, the goal is to produce seedlings with morphological and physiological attributes that are suitable for specific outplanting conditions, thereby

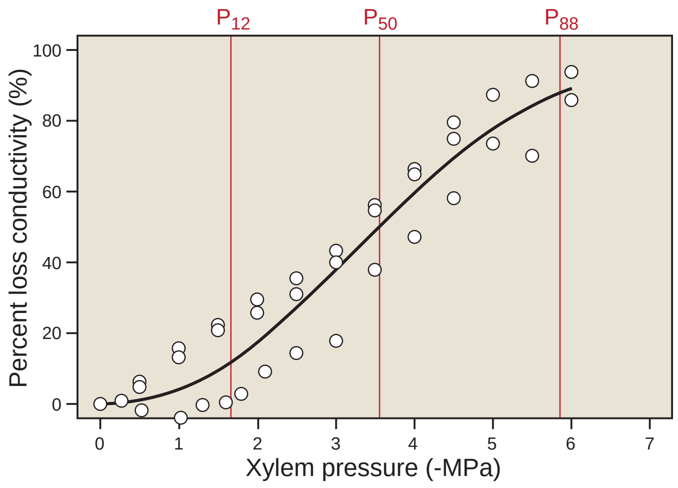
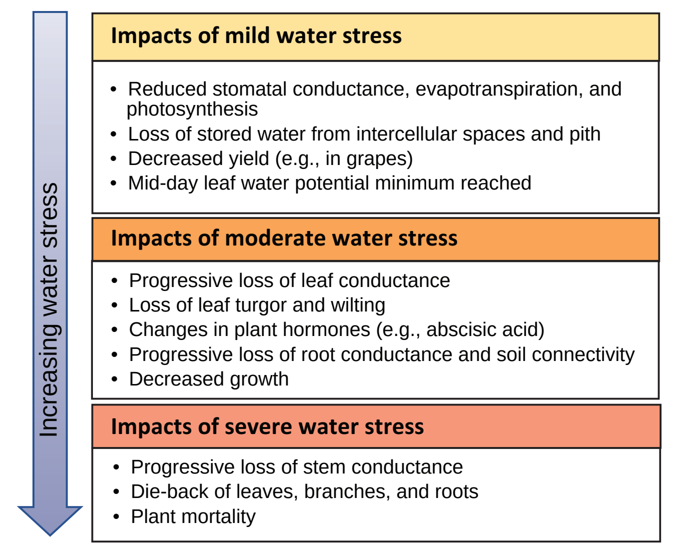


**Figure 5.** A vulnerability curve for *Malus* var. 'Prairifire' shows the percent loss of conductivity in response to more negative water potentials (n = 3). The vulnerability curve was built using measurements of stem conductivity from a stem conductivity apparatus with stepwise increases in stem water potential induced in the cavitation chamber. Vertical lines indicate 12 percent, 50 percent, and 88 percent loss of conductivity relative to maximum conductivity. (Adapted from unpublished data from Sheridan and Nackley)



**Impacts of mild water stress**

- Reduced stomatal conductance, evapotranspiration, and photosynthesis
- Loss of stored water from intercellular spaces and pith
- Decreased yield (e.g., in grapes)
- Mid-day leaf water potential minimum reached

**Impacts of moderate water stress**

- Progressive loss of leaf conductance
- Loss of leaf turgor and wilting
- Changes in plant hormones (e.g., abscisic acid)
- Progressive loss of root conductance and soil connectivity
- Decreased growth

**Impacts of severe water stress**

- Progressive loss of stem conductance
- Die-back of leaves, branches, and roots
- Plant mortality

**Figure 6.** Plant hydraulic physiology traits respond to increasing water stress in a predictable sequence. The precise water potentials at which these responses will be triggered depends on the species and population. (Adapted from Bartlett et al. 2016, Gambetta et al. 2020, and Miller et al. 2020)

optimizing survival and growth potential after planting, as stated in the Target Plant Concept (Dumroese et al. 2016). Plant hydraulic physiology can be a useful tool to develop nursery regimes to produce high-quality seedlings.

We often use proxy measurements to estimate water potentials within the SPAC for making decisions about when and how much to irrigate. This may be as simple as watching for visual signs of plant water stress, such as wilting (figure 7). A more precise method of irrigation scheduling is to track container weights, then irrigate at a target weight (Dumroese et al. 2015). Deciding to irrigate at a target container weight links the weight to the growing medium's water content which is linked to the growing medium's water potential and the assumed physiological response of the crop. To make a more direct connection between the decision to irrigate and the plant's physiological response, some investigators build response curves of photosynthesis to changes in water availability whereby irrigation is triggered before water limitations reduce photosynthesis (Fulcher et al. 2012, Nambuthiri et al. 2017). Controlling the irrigation in this way resulted in greatest plant growth under mild water deficits, more so than when containers were maintained at full saturation or when more severe water deficits occurred. Producing seedlings of similar or better quality with less water is important for improved water conservation in nursery production (Fulcher et al. 2016). This type of irrigation management system could be expanded to include the sequence of physiological responses to water stress described above, thereby shifting the framework from a focus on changes in container weights to a focus on plant hydraulic and physiological responses to water limitations.

**Figure 7.** Wilting is a sign that a plant has experienced moderate to severe water stress. Waiting to irrigate until wilting is observed can be a risky strategy for some species. (Photo by Rebecca Sheridan 2020)

Beyond irrigation scheduling, plant hydraulic traits can be used to proactively guide desirable plant attributes in nursery production. At an ecological scale, water deficits in one season have been found to impact plant growth in the following season (Kannenberg et al. 2019). Likewise, drought conditioning during nursery production exposes plants to mild water stress to prepare the seedlings for stressful outplanting conditions. Measurements of stem conductance, photosynthesis, and stomatal conductance, and imaging of stem segments identify which plant parts are impacted by drought conditioning, the amount of change, and how long the impacts persist. These measurements can help nursery growers tailor when, and to what degree, crops should be exposed to water stress for drought conditioning (Sloan et al. 2020). Further research is needed to explore how nursery practices, such as hardening off crops with water stress, can be guided by plant hydraulic traits.

As a final example, plant hydraulic traits can inform the day-to-day risk assessment that occurs during nursery production regimes. During the establishment phase of a nursery crop, there is a trade-off between frequent irrigation of the crop to avoid stressing very small seedlings and increased risk of root disease with saturated growing media (Dumroese and James 2005). However, even conifer seedlings less than 10 weeks past germination can withstand some risk of embolism, as determined using confocal microscopy to image xylem anatomy and calculate theoretical conductance and resistance to embolism (Miller and Johnson 2017). With precise estimates of water-stress levels that will reduce xylem function in young seedlings, irrigation and disease management can be balanced with more nuance.

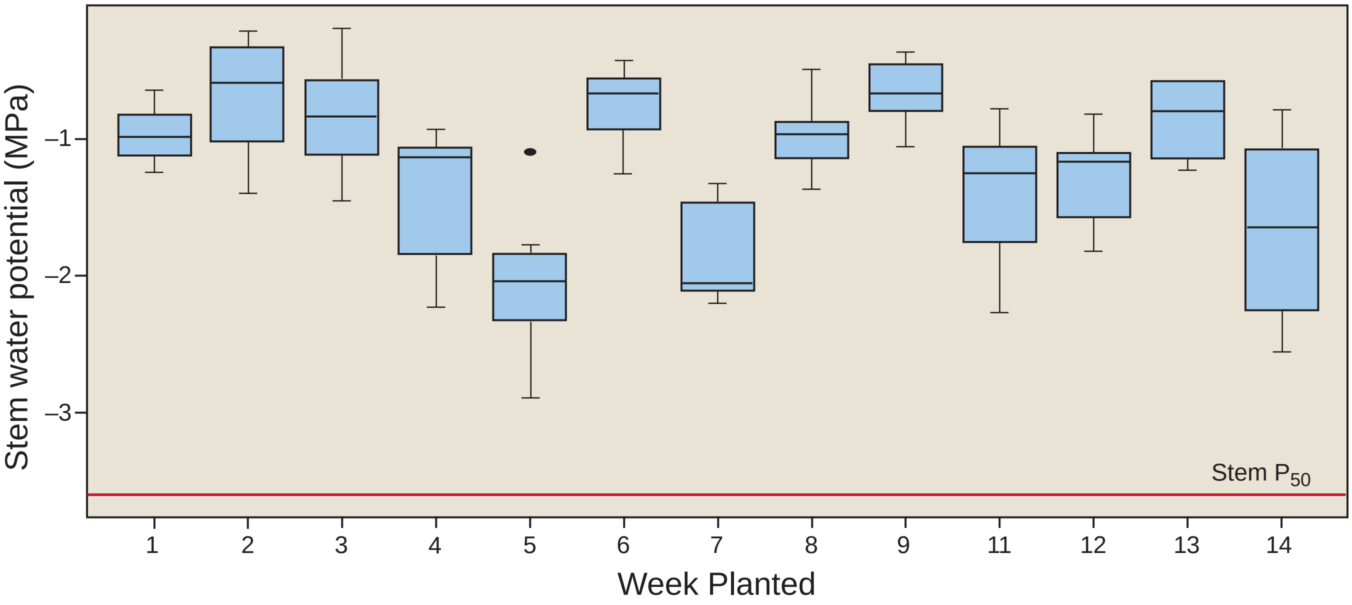


**Figure 8.** Stem water potential of *Malus* 'Prairifire' seedlings at the time they were removed from cold storage for outplanting (n = 7). Week 1 is the first planting date on March 19, 2020; the seedlings had been in cold storage since late 2019. The water potential at which stem $P_{50}$ (water potential at which 50 percent of conductivity is lost) occurs is indicated with a red line. Given that none of the stem water potentials were near stem $P_{50}$, the seedlings were not likely to suffer from hydraulic failure through the stem after extended cold storage. (Adapted from unpublished data from Sheridan and Nackley)

At the other end of the production cycle, seedlings kept in cold storage could be at risk of desiccation if stored too long, yet the timeframe for planting is often constrained by environmental conditions at the outplanting site. When nursery-grown seedlings were outplanted from storage each week through the spring season, however, the seedlings kept in storage longer did not show increasing symptoms of hydraulic failure as the season progressed, indicating seedling quality can be maintained for a time even if planting is delayed (figure 8). At many points within a production cycle, nursery professionals often face less-than-ideal circumstances in which information about plant hydraulic traits can help guide decisionmaking.

## Conclusion

Nursery production is a logical application of plant hydraulic physiology, though there is still much work to be done to leverage the science more widely into practice. Still to be bridged are the differences between nursery environments and the natural systems in which most foundational hydraulic physiology work has been done. In the nursery, we control plant water status through irrigation, medium type, and container choices, and we control water demand by adjusting air flow, temperature, humidity, and shade. Additionally, seedlings and saplings respond to water stress differently than mature individuals (Augustine and Reinhardt 2019, Medeiros and Pockman 2010, Sperry and Saliendra 1994). Despite these challenges, the current research and potential advances in plant hydraulic physiology can be useful to nursery production. The field offers tools and knowledge to ensure that we can efficiently and sustainably produce seedlings that are well suited to survive in challenging outplanting environments.

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