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Foliar water uptake: processes, pathways, and integration into plant water budgets

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Abstract

Nearly all plant families, represented across most major biomes, absorb water directly through their leaves. This phenomenon is commonly referred to as foliar water uptake. Recent studies have suggested that foliar water uptake provides a significant water subsidy that can influence both plant water and carbon balance across multiple spatial and temporal scales. Despite this, our mechanistic understanding of when, where, how, and to what end water is absorbed through leaf surfaces remains limited. We first review the evidence for the biophysical conditions necessary for foliar water uptake to occur, focusing on the plant and atmospheric water potentials necessary to create a gradient for water flow. We then consider the different pathways for uptake, as well as the potential fates of the water once inside the leaf. Given that one fate of water from foliar uptake is to increase leaf water potentials and contribute to the demands of transpiration, we also provide a quantitative synthesis of observed rates of change in leaf water potential and total fluxes of water into the leaf. Finally, we identify critical research themes that should be addressed to effectively incorporate foliar water uptake into traditional frameworks of plant water movement.

Despite being represented across numerous plant families and providing a notable water subsidy to plants, the process of foliar water uptake is still poorly understood. This review addresses the need for a cohesive synthesis of the processes that drive foliar uptake, the pathways of water movement, and the role of this water in plant water budgets. In addition to these components, we address the critical knowledge gaps needed for a more complete understanding of this nearly ubiquitous process.

Introduction

“...plants can plentifully imbibe moisture thro’ their stems and leaves as well as perspire it.” - Hales 1727

The direct uptake of water into leaves, commonly referred to as foliar water uptake (FWU), has been observed for at least 300 years (Hales 1727). Since then, FWU has been established as a common process that varies among individuals, populations, species, and ecosystems. At least 233 species spanning 77 plant families and 6 major biomes have demonstrated some capacity for FWU (Figure 1; Table S1). This does not include the more than 100 genera measured before 1942 (reviewed in Williams, 1942). The capacity for FWU also seems to be nearly universal, it has been observed in more than 85% of species studied (Goldsmith et al. 2013). This process has received increasing attention in the plant sciences, with rapid growth in both the number of peer-reviewed articles and the citation of those articles. Despite the considerable interest in research on FWU and increasing recognition of the role it may play in plant, community, and ecosystem functioning, our understanding of when, where, and how FWU occurs in leaves remains limited.

In the following review, we explore the physiology of FWU, with a particular focus on leaf and plant water balance. While several papers have demonstrated water uptake via bark (Katz et al. 1989, Mayr et al. 2014, Earles et al. 2016), this review focuses on leaf uptake. A more general review of the effects of leaf wetness and its effects on plant function at the community and ecosystem scales can be found in Dawson and Goldsmith (*In Press*). We begin by exploring the biophysical gradients required for FWU to occur, focusing on the physical and biological scenarios where FWU should be expected. We then review the relevant pathways of water movement into and through both the leaf and plant, highlighting where FWU fits into our current understanding of plant water movement. Finally, we contextualize FWU with whole plant water use by considering observed fluxes relative to known transpiration rates and changes in water potentials. Based on this synthesis, we identify the research questions that need to be addressed to accurately consider the processes and implications for FWU.

Physical and biological requirements of foliar water uptake

Water moves across gradients in chemical energy, often described in terms of “water potential”. Generally, the internal structures of a leaf are assumed to be nearly or completely saturated with water (high water potential; Cernusak et al. 2018) and the atmosphere is typically unsaturated (low water potential), resulting in a net efflux of water (i.e. transpiration). For water to flow into the leaf, the driving gradient of water potentials must be reversed, *i.e.*, the leaf water potential must be more negative than the atmosphere immediately surrounding the leaf (Rundel 1982). If water crosses the leaf boundary as vapor then it is instead driven by the vapor concentration gradient instead of water potentials. Atmospheric conditions are more typically measured as vapor pressure deficit, the difference in vapor pressure between saturation and ambient conditions for pure water at a given temperature. Comparing vapor pressure deficits (or relative humidities) with atmospheric water potentials can provide insights into the conditions necessary for FWU (Figure 2). The water potential of the surrounding air quickly becomes more negative than typical values for leaves at very low vapor

pressure deficits. For instance, at 25 °C, the water potential of the air drops below -4 MPa at 0.036 kPa vapor pressure deficit (97% relative humidity). Leaf temperature (relative to air) will also influence the leaf to air vapor pressure deficit. As leaves elevate above air temperature, the vapor pressure gradient increases which would result in greater FWU when leaves are wet. A reversal of this gradient leading to FWU can occur by increasing the vapor in the air surrounding the leaf surface or by reducing the water potential inside the leaf (Slatyer 1960, Simonin et al. 2009, Oliveira et al. 2014, Vesala et al. 2017).

The vapor pressure of the air reaches saturation (or near saturation) due to changes in weather conditions. Foliar water uptake has been demonstrated during periods when the air is saturated and liquid water forms on leaves, such as during rain and mist (Breshears et al. 2008, Steppe et al. 2018), fog (Burgess and Dawson 2004, Simonin et al. 2009), and dew (Munné-Bosch et al. 1999). However, there is also evidence of FWU of water vapor during periods where the air has not condensed to liquid water (i.e. water still in vapor form). Vapor uptake would be driven by vapor pressure and require the intercellular air space immediately within the leaf cuticle to have a lower vapor pressure than the vapor pressure of the air. This routinely occurs in leaf air spaces due to negative water potentials and the Kelvin effect reducing the vapor pressure (see Vesala et al. 2017 and Cernusak et al. 2018). However, any movement from intercellular air space into cells would require liquid water and would need to consider the resistance of a phase change from vapor to liquid.

Many studies over the last 60 years have detected water vapor uptake using a wide range of species and methods (Vaadia & Waisel 1963, Virzo De Santo et al. 1976, Mooney et al. 1980, Lange et al. 1986, Schmitt et al. 1988, Laur & Hacke 2013, Wang et al. 2016). Recent examples of FWU in high humidity conditions include *Picea glauca*, a temperate conifer (Laur & Hacke 2014), and *Reaumuria soongorica*, a desert plant from China (Wang et al. 2016). Many of these studies were conducted under high humidity conditions that may have resulted in some water condensation on the leaf surface, resulting in FWU of liquid water. Despite this potential artifact, it is apparent that FWU can ultimately occur in both liquid and vapor phases when a driving gradient for the entry of water into the leaf is present.

Leaf surface properties can affect the vapor pressure at the leaf to air interface (within what is referred to as the boundary layer) in ways that can also alter leaf wetness and FWU. Chemical structure of cuticular waxes, stomatal structure, trichomes, leaf hairs, and endophytes have all been shown to affect water retention on leaf surfaces (Smith & McClean 1989, Brewer et al. 1991, Brewer & Smith 1997, Wagner et al. 2003, reviewed by Rosado & Holder 2013). Thicker wax layers decrease leaf water retention by increasing the roughness of the surface (Koch et al. 2009, Taylor, 2011), while trichomes and leaf hairs also appear to decrease retention in a similar manner (Brewer et al. 1991, Pierce et al. 2001). However, these relationships are not always robust, as some succulent species with hydrophilic trichomes can actually increase retention and enhance leaf wetness (Grammatikopoulos and Manetas, 1994). Fernandez et al. (2017) highlights the diversity in the chemical and structural components of leaf surfaces and their potential implications for maintaining wet leaf surfaces. Cuticular properties that differ among leaves and across species will result in variation of boundary layer conditions that may promote differential fluxes of FWU.

Leaf surface properties and structure will also affect water loss and leaf water potential, altering the driving gradient for FWU. For instance, cuticular composition and permeability can be affected by reductions in leaf water potential (Fernandez et al.

2017). These changes could be a function of the degradation of cuticular waxes or due to losses in turgor of cuticle cells. Thus, while reduced water potentials may enhance the water potential gradient into the leaf, there may be a simultaneous tradeoff with cuticle permeability that either enhances or offsets the flux of FWU. Foliar water uptake may be more important to leaf water balance in species with increased cuticular conductance at decreasing water potentials. The direction of this change and the water potential where changes to leaf conductance occur will be critical variables in understanding the temporal patterns of FWU fluxes and net effects on plant water balance. Structurally, the size and shape of the leaf cuticle, mesophyll cells, and air space will affect water loss and thus water potential. Gotsch et al. (2015) observed lower FWU in species with thicker leaves and a greater water storage capacity. In contrast, species with high FWU could withstand lower water potentials, but had lower water storage capacity. The storage capacity (i.e. capacitance) will also alter the duration of FWU; species with higher storage capacity should demonstrate lower FWU that is sustained for longer. This suggests that leaf water storage and foliar uptake may be linked such that they buffer leaves from drought.

The leaf (and wood) hydraulic capacitance will also affect the rate of water potential change, quantity of water, and the duration of FWU. Hydraulic capacitance buffers tension from negative water potentials by acting as a dynamic capacitor (Meinzer et al. 2013, McCulloh et al. 2014, Zeppel et al. 2014). Within the context of FWU, hydraulic capacitance will affect the rate of water potential increase. Species with higher capacitance will have slower changes in water potential. Where water for foliar uptake is available, the persistence of this water potential gradient would likely result in longer FWU durations. In turn, species with higher hydraulic capacitance should be able to absorb greater total quantities of water. One might expect a tradeoff between safety and efficiency in this regard, where species with high capacitance require high FWU fluxes to refill water storage and those with low capacitance would require only low FWU fluxes (McCulloh et al. 2014). The capacitance of wood and roots will also influence the redistribution of water in the leaf by buffering water potential gradients. Water from FWU could potentially provide a key subsidy to these critical pools that buffer plant water tension and losses of hydraulic conductivity.

Leaf water potentials change considerably on both diurnal and seasonal timescales and leaf water deficits can also increase the probability that the water potential gradient will reverse direction and result in FWU. For instance, Vesala et al. (2017) modeled transpiration and FWU as a function of leaf water and found that FWU fluxes measured in Coast Redwoods (*Sequoia sempervirens*) could be explained by leaf water potential. While the difference in water potential from the leaf to the air should explain FWU fluxes, no studies have quantified these fluxes experimentally. If the conductance of the leaf surface (cuticle or stomata) does not vary, then more negative leaf water potentials should lead to higher FWU fluxes (Limm & Dawson 2009, Goldsmith 2013). However, there is a potential tradeoff; when leaves have more negative water potentials, two processes may inhibit FWU. First, they will close stomata to resist water loss reducing the conductance of the leaf surface. If stomata are a pathway for FWU (discussed below), stomatal closure may limit FWU and several studies in water-stressed conditions have found support for this idea (Vaadia & Waisel 1963, Burgess & Dawson 2004). Second, water stress could alter mesophyll conductance, limiting the movement of water within the leaf (Zhou et al. 2013). While most (if not all) plants should experience water potentials that would allow for FWU, the frequency and magnitude of uptake will be driven by the atmospheric vapor

pressure deficit, the leaf water potential, the leaf hydraulic capacitance, and the conductance of the leaf surface to water vapor. Ultimately, in what physical environments will the requirements for FWU be met? The conditions for a driving water potential gradient into the leaf can be satisfied during all leaf wetting periods. It can also occur when there is a low vapor pressure deficit that results in a high atmospheric water potential, provided that there is a more negative leaf water potential. Evidence from Cernusak et al. (2018) suggests that the driving gradient should be frequently met due to the unsaturation of the intercellular air spaces. Foliar water uptake fluxes and quantities should be greater in plants with more negative leaf water potentials, such as those that occur later in the day, during dry periods between rain events, during dry seasons, or in water-limited ecosystems. Both leaf wetting and leaf water deficit undoubtedly occur across all major biomes, meaning that the conditions should be suitable for all species. The implications are significant: a reversal of flow largely contradicts the traditional conception of the Soil-Plant-Atmosphere Continuum (SPAC, Philip 1966). Recent work has called for a shift in this thinking to consider plant water movement in both directions (Goldsmith 2013). Yet some studies have observed species that do not carry out FWU co-occurring with species that do carry out FWU (Limm et al. 2009, Emery et al. 2016). Emery et al. (2016) suggested that stomatal crypts resulted in limited FWU, however, there remains no clear explanation for species-level variation in FWU. This suggests that suitable environmental conditions are not the sole explanatory variable in understanding the fluxes of FWU. While seemingly common, the extent to which FWU occurs or does not occur in conditions when the water potential gradient should be reversed is an area in need of further study.

Pathways of water movement

Entry points into the leaf

Water is routinely exchanged across the leaf surface by multiple pathways. In higher plants, stomata, cuticles, and specialized structures (e.g. trichomes, hydathodes, or scales) have all been hypothesized to serve as pathways for FWU (Figure 3). We explore the evidence for FWU through each of these structures and analyze the mediating factors that might lead to certain pathways over others.

The primary pathway for water loss from a leaf (i.e. transpiration) is stomata and due to the high conductance of water through stomata relative to other structures, it is intuitive that they could facilitate uptake. However, based on the assumption that droplet sizes or films on leaf surfaces typically exceed the size of stomata, stomata were generally thought to be impenetrable to water infiltration without external pressure (Schonherr & Bukovac 1972). More recent research using environmental scanning electron microscopy has demonstrated that stomata are a likely candidate for uptake of liquid water (Burkhardt et al. 2012). The process was mediated by salt ions in water (and potentially other molecules) that reduce surface tension (Burkhardt et al. 2010, 2012). Further studies have found that the combination of salt ions and sunken stomata in clefts of leaves of the tree *Chamaecyparis obtusa* var. *formosana* promotes leaf wetness while not directly blocking stomatal pores (Pariyar et al. 2017). Burkhardt (2010) proposed the “hydraulic activation of stomata,” stating that salt mediation allows for the creation of liquid water film that bridges the stomatal pore and enables bidirectional movement of water.

Both bacteria (Eichert et al. 2008) and endophytic fungi (Burgess & Dawson 2004) have also been suggested to facilitate FWU. In these cases, the presence of these other biota may reduce the hydrophobicity of the leaf surface and form “bridges” into

the leaf by which water can travel. It is well established that the leaf microbiome can affect leaf physiology and potentially water movement (Vacher et al. 2016). Additionally, studies on air pollutants applied in high humidity conditions lead to greater foliar uptake of both water and pollutants, primarily driven by the stomatal response to low vapor pressure deficit (McLaughlin & Taylor 1981, Norby & Kozlowski 1982). Facilitation by external biota and molecules could form bridges across stomata or crack the surface, leading to greater uptake through cuticular pathways. Abiotic and biotic facilitation of FWU may shift the particular uptake pathways in species, adding complexity to the physical determinants of FWU fluxes.

Some water uptake likely occurs across the cuticle (i.e. non-stomatal entry), even though they are highly resistive relative to stomata. Values of cuticular conductance are less than $0.1 \text{ mol m}^{-2} \text{ s}^{-1}$ and more commonly below $0.05 \text{ mol m}^{-2} \text{ s}^{-1}$, which is generally <5% of the sum of cuticular and stomatal conductance when stomata are open (Larcher et al. 2003, Riederer & Schreiber 2001). Cuticular conductance is often measured on intact and undamaged leaves. In damaged leaves, increased conductance may lead to increased FWU. Many studies have inferred that the cuticle is a primary pathway of water entry (Grammatikopoulos and Manetas 1994, Yates and Hutley 1995, Limm 2010, Goldsmith et al. 2013; reviewed by Kerstiens 1996). These come from situations where FWU occurs during periods when stomata are mostly closed (i.e. at night). Even when stomata are closed, there is evidence that water is still evaporated through the leaf surface and thus if the gradient is reversed, FWU will occur (Kerstiens 1996, Cavendar-Bares et al. 2007, Limm et al. 2010). Within the cuticle, there is a thin layer (termed the limiting skin) that is the main diffusion barrier for water molecules to cross (Slatyer 1960, Schonherr & Riederer 1989). The permeability of this layer may explain why cuticular thickness does not appear to affect water permeability (Kamp 1930, Becker et al. 1986, Schreiber & Riederer 1996).

Stomatal entry of water would allow for greater fluxes of FWU than entry through the cuticle due to the comparatively higher conductivity. Therefore, if stomata are open and there is a water vapor gradient into the leaf, stomatal flow should be the dominant pathway for FWU. However, the contribution of FWU via the cuticle should increase dramatically during periods when stomata are predominantly closed, as well as where there are relatively few stomata and large surface areas. Furthermore, stomatal aperture changes rapidly (as short as a few minutes), which would allow for rapid responses to environmental cues such as humidity or leaf wetness (Merilo et al. 2014). Therefore, evidence supports a strong role for stomata in the foliar absorption of water.

The cuticular composition will also influence permeability and the extent to which FWU occurs through stomata or cuticles. Certain compounds within cuticles, such as polysaccharide sugars, facilitate FWU (Kerstiens & Lenzian 1989, et al. 1992). Boanares et al. (2018) recently demonstrated that species with greater FWU fluxes had more pectins in their cell walls, while those with lower rates had greater quantities of cellulose. This study concluded that these molecules can alter the porosity and hydrophobicity by altering the linkages and surfaces on the leaf surface. Cuticular permeability also increases with leaf age due to cuticle damage and degradation and this may have implications for FWU (van Gardingen et al. 1991, Yates and Hutley 1995, Schreiber et al. 2001, Jordan and Brodribb 2007). For instance, old leaves of *Sequoia sempervirens* absorb more water than young leaves, possibly due to cuticular damage (Burgess & Dawson 2004). High relative humidity can also affect cuticular permeability by facilitating microbial growth (Lindow & Brandl 2003), increasing leaf wettability and

cuticle absorption (Bunster et al. 1989, Schreiber 1996, Knoll & Schreiber 1998, Schreiber et al. 2005). The role of cuticle structure and the exchange of water is reviewed extensively in Fernandez et al. (2017). Thus, while the predominant pathway for FWU may be the stomata, there is evidence that uptake through the cuticle may occur in some instances.

While less prevalent across taxa, specialized leaf structures can also play a significant role in altering leaf wetness and FWU. Trichomes, which are hair- or scale-like structures on leaf surfaces, are known to directly absorb water (Franke 1967, Benzing and Burt 1970, Benzing et al. 1978, Fernandez et al. 2014, Eller et al. 2016). Trichomes are particularly important for absorbing water in the largely epiphytic Bromeliaceae family (Benzing 2000; Crayn et al. 2004). These epidermal structures are highly variable in their morphology and function. As a result, they could play contrasting roles in FWU. Trichomes could facilitate water condensation on the leaf surface and promote FWU (Konrad et al. 2014) or, alternatively, increase leaf water repellency (Brewer et al. 1991) and reduce FWU. Evidence of water uptake has also been shown in hydathodes (specialized pores involved in guttation; Martin & von Willert 2000), porous surfaces in thorns (Schill and Barthlott 1973), and water-absorbing scales (Wang et al. 2016). While specialized structures likely play a significant role in water movement across the leaf surface in particular species, these specialized structures do not represent the primary pathway for FWU among all species.

Pathways inside the plant

Water entering the leaf through FWU first arrives in the intercellular air space or cells of the cuticle and continues to move along water potential gradients (potential pathways highlighted in Figure 3). While water potential gradients are generally understood for entire plants, driving forces and pathways of water molecules within the leaf are still poorly understood (Buckley et al. 2015). Water absorbed through FWU could continue to travel through intercellular air spaces or enter mesophyll (palisade or spongy) cells. In cells, water movement occurs apoplastically or symplastically; early research proposed that most movement was apoplastic (e.g. Byott & Sheriff 1976, Boyer 1977, Canny 1990). However, other studies have suggested that symplastic water movement could occur in certain situations, particularly when aquaporins are up-regulated to facilitate flow across the cell membrane (Chrispeels and Agre 1994, Tyree et al. 1999). Recent modeling experiments have suggested that apoplastic pathways should dominate (Buckley 2015). However, when there are internal temperature gradients from the mesophyll to the epidermis, vapor phase movement through the intercellular air space could contribute up to 44% of the flow (Rockwell et al. 2014, Buckley 2015, Buckley et al. 2015). This temperature gradient could be controlled through stomatal aperture, which influences leaf temperature through evaporative cooling. For FWU, it is likely that vapor phase water transport is a routine pathway of water movement inside the leaf and occurs in parallel with cellular pathways.

Ultimately, regardless of the pathway, there are three possible fates for water absorbed into the leaf by FWU: (1) entry into the mesophyll and use for photosynthesis or capacitance, (2) entry into the vasculature, or (3) transpiration back into the atmosphere. Transpiration will only occur if water potential gradients within the leaf are low and the gradient across the leaf surface is quickly reversed (i.e. short-lived wetting events). The pathway of water is governed by resistances across membranes, including across the epidermis, into mesophyll cells, and across the bundle sheath cells

into the vasculature. These resistances are also influenced by the architecture of these different tissues and whether the FWU water is in liquid or vapor phase (as all transport into cells will be in liquid phase). The net flux of water moving will be governed by the water potential gradient buffered by capacitance of individual tissues. Thus, flow should persist for longer to tissues with larger capacitance values. Below, we highlight evidence that water from foliar uptake enters mesophyll cells and vasculature.

There are three lines of evidence that water from FWU is incorporated into mesophyll cells. The first is evidence from fluorescence or radioactive tracer studies where water has been observed moving into palisade and spongy mesophyll cells, as well as epidermal cell walls (Munne-Bosch et al. 1999, Gouvra & Grammatikopoulos 2003, Ohrui et al. 2007, Eller et al. 2013). The second is the observation that leaf wetting and high humidity lead to up-regulation of aquaporin channels of mesophyll cells, increasing membrane conductivity and resulting in greater water flow (Ohrui et al. 2007, Laur & Hacke 2014). The third source of evidence for water reaching the mesophyll and being incorporated into photosynthetic pathways comes from research using stable isotopes of water as tracers (Lehmann et al. 2018). Oak saplings exposed to fog generated using water with a distinct oxygen isotope signature demonstrated a subsequent change in the oxygen isotope ratio of water in the leaf, as well as the oxygen isotope ratio of sugars observed both in the leaf and isolated from the phloem of the petiole.

Water from FWU can also travel into the vasculature of a plant. In many species, bundle sheath cells are lignified, requiring water to enter through mesophyll cells. This greatly reduces the subsequent hydraulic conductance into the vascular bundle (North & Peterson 2005, Ohtsuka et al. 2017). To increase this conductivity, there can be upregulation of aquaporins in the bundle sheath, which leads to increased water flow into the xylem and phloem and the associated recovery of hydraulic conductivity (Mayr et al. 2014, Laur & Hacke 2014). Interestingly, Laur & Hacke (2014) found greater upregulation of aquaporins in phloem, suggesting that this water is initially transported to the phloem and then possibly the xylem. Sap flow (heat ratio method) has also been used to demonstrate that water from FWU is incorporated into plant vasculature (Burgess & Dawson 2004, Nadezhdina et al. 2010, Eller et al. 2013, Goldsmith et al. 2013, Gotsch et al. 2014, 2015 Darby et al. 2016, Steppe et al. 2018). Most recently, Steppe et al. (2018) demonstrated that FWU induced radial stem growth driven by changes in cell turgor. This evidence suggests that water from FWU may also serve to recharge wood capacitance. These studies demonstrate clear reversals of water movement through stems and trunks during leaf wetting periods. Together, the evidence supports the idea that water absorbed through leaves is routinely incorporated into plant vascular networks.

In some cases, the water absorbed in leaves can be released into the soil. Given a sufficient water potential gradient (including low soil water potentials), it is possible to observe a complete reversal of the Soil-Plant-Atmosphere Continuum (Goldsmith 2013). Early studies, such as Breazeale et al. (1950) and Breazeale & McGeorge (1953), isolated soil and plant compartments and found increases in soil moisture. More recent studies have used stable isotopes of water as tracers to detect the presence of water exchanged between the atmosphere and leaves as it moves into the soil. Both Eller et al. (2013) and Cassana et al. (2016) find evidence that water from FWU was transported to soil in seedlings of a tropical evergreen (*Drimys brasiliensis*) and a southern hemisphere conifer (*Araucaria angustifolia*) in Brazil. However, Limm et al. (2009) and Berry et al. (2014) conducted similar studies and did not find any signal of FWU water in the soil in

seedlings from temperate California Redwoods (10 herbaceous and tree species) and in Appalachian montane conifer forests (canopy conifers), respectively. Notably, recent research has demonstrated that stable isotopes of water alone cannot be used as tracers to establish the net uptake of water by FWU, due to the possibility of bidirectional exchange of water isotopes between the leaf and the atmosphere (Goldsmith et al. 2017). The extent to which FWU affects the flow of water into different parts of the plant and ultimately out of roots into the soil will require verification from additional methods. If this occurs routinely, single FWU events could improve soil water availability and whole-plant water balance at longer time scales.

The evidence presented here suggests that water absorbed through leaves can move considerable distances within the plant and potentially is utilized in distal leaves, wood vasculature, and roots. Quantifying and tracing the movement of water from FWU will require new methods capable of resolving higher resolutions and multiple dimensions. Imaging techniques such as microCT (e.g. Brodersen et al. 2011) and MRI (Zwieniecki et al. 2013), combined with assays of aquaporin regulation and new leaf hydraulic modeling (e.g. MOFLO, Buckley et al. 2017), could be particularly promising avenues of inquiry. Combining field-based methods such as sap flow, dendrometers, and stem psychrometry with mechanistic modelling will also expand our understanding of FWU in mature trees (e.g. Steppe et al. 2018). Further, research needs to consider the role of plant water status, hydraulic conductivity, capacitance, and soil moisture availability in driving the many pathways of FWU water through the plant. Reliably tracking the movement of individual water molecules from FWU would open doors for a unified three-dimensional model of water movement pathways.

Integrating FWU into plant water budgets

One critique of FWU is that it is assumed to be an insignificant quantity of water that is rarely relevant to plant processes. This perception has been driven by a diverse set of methodologies, which vary in scale from leaves to whole plants and result in incomparable values. Further, studies have not always considered FWU fluxes and quantities in the context of plant water budget parameters such as transpiration fluxes and leaf water potentials (Guzmán-Delgado et al., 2018). In this section, we compare what research is available on FWU fluxes, net quantities (inferred through sap flow data), and changes to leaf water potentials from FWU events with transpiration fluxes and leaf water potentials. We consider both the leaf and whole plant, as current methodologies are largely focused at these scales.

Determining fluxes presents a unique challenge for FWU. The movement of water is a function of the water vapor concentration immediately outside a leaf (w_a) and the water vapor concentration in the substomatal cavity (w_i)

$$E = (w_i - w_a) * g \quad (1)$$

where E is the transpiration (or net flux out of the leaf) and g is the stomatal conductance (Nobel 2005). For transpiration, the w_a term is smaller than the w_i term leading to a net loss of water from the leaf. When quantifying leaf-level transpiration, this gradient also remains relatively constant in sunny and high VPD conditions assuming a high boundary layer conductance. This gradient is maintained because the w_a of the air is so small relative to the leaf that small changes in w_a do not appreciably affect the gradient and transpired water largely equilibrates with the atmosphere. For FWU, this is not true. Due to the small volume of the leaf relative to the atmosphere, the

difference between w_i and w_a would decrease over time during an FWU event, slowing the net flux of uptake (Figure 4A). The actual rate of water potential improvement (Figure 4B) is then governed by the flux of FWU for that species. In species with a high FWU flux, the net improvement in leaf water potential would be much greater over the same time period compared to a species with a low FWU flux (Figure 4B). This concept assumes that the resistance of water entering the vasculature (and leaving the leaf) is very high relative to resistances within the leaf. If the flow into the vasculature is high, then a decline in flux would not occur until the entire plant reached equilibration, which is presumably a much longer time scale. Thus the duration and magnitude of the fluxes represented in Figure 4 would be greater if there is high conductivity into the plant vasculature. There may also be differences between species due to the maximum leaf water content capacity. Boanares et al. (2018) found that species with higher water content capacities (i.e. leaf capacitance) had slower uptake rates. Thus, integration of FWU fluxes over periods where the rate slows over time could yield lower average fluxes than the same species studied over short time periods that capture relatively constant FWU fluxes, depending on the leaf storage capacity.

Despite these limitations, FWU fluxes (integrated over any time period) can be compared to transpiration. To do so, we reviewed studies where we could determine the flux of water exchanged across the leaf per unit time through FWU. These typically came from studies where leaves were either experimentally submerged or misted and a change in mass was quantified over a defined time at a set leaf area ($\text{mmol H}_2\text{O m}^{-2} \text{s}^{-1}$). Among 24 species in this sample, values ranged from 0.004 to $0.390 \text{ mmol m}^{-2} \text{s}^{-1}$ (mean: 0.063 ± 0.085), highlighting high variability in this trait across species (Figure 5). Interestingly, the highest fluxes were observed in three temperate conifers: *Araucaria angustifolia* (Cassana et al. 2015), *Picea rubens*, and *Abies fraseri* (Berry & Smith 2013). Berry & Smith (2013) observed maximum transpiration fluxes of $1.5 - 2.0 \text{ mmol m}^{-2} \text{s}^{-1}$. Thus, in *P. rubens* and *A. fraseri*, FWU was approximately 10% of the maximum transpiration fluxes. This is similar to the results from Cassana et al. (2015) using sap flow methods. These values provide first approximations of FWU at the leaf-level relative to transpiration fluxes for canopy trees.

More generally, we can also consider the fluxes of FWU we determined in the context of maximum transpiration fluxes reported in other studies. Transpiration fluxes vary based on growth form and biome but range from approximately $0.2 \text{ mmol m}^{-2} \text{s}^{-1}$ for plants in the tundra to values of $8 - 10 \text{ mmol m}^{-2} \text{s}^{-1}$ for herbaceous species in dry environments (e.g. deserts; Larcher 2003). More common values for tropical and temperate tree species range from $1 - 3 \text{ mmol m}^{-2} \text{s}^{-1}$. These transpiration ranges would support the idea that FWU fluxes are much lower than maximum transpiration fluxes. However, if FWU conditions occur more frequently or during midday periods when high transpiration fluxes would occur, the influence of FWU on plant water balance would increase. Further, simply because the fluxes may be small in relative terms, small changes to individual leaf water potential can have significant long-term effects on leaf photosynthesis and stomatal conductance (Simonin et al. 2009, Berry et al. 2014, Eller et al. 2016).

Several studies have also explored how FWU leads to increases in leaf water potentials. From these studies, we have derived rates of water potential improvement over time (Figures 4 & 5; Table S1). These values were collected for 75 species and range from very slow increases of $0.0007 \text{ MPa min}^{-1}$ to strikingly fast increases of $0.12 \text{ MPa min}^{-1}$ (mean: $0.014 \pm 0.003 \text{ MPa min}^{-1}$). The highest rate was observed in *Juniperus monosperma* shoots with an average starting water potential of -2.1 MPa and

integrated over a 5-minute period (Breshears et al. 2008). A net change of 0.6 MPa over a 5-minute period highlights the potential of FWU to alter water status with implications for long-term physiological functioning. The lowest rate observed ($0.0007 \text{ MPa min}^{-1}$) comes from a wetting study that integrated over 24 hours in *Quercus ilex* with an average starting water potential between -2.5 and -3.0 MPa (Fernandez et al. 2014). It is difficult to discern if this low rate is due to the long time period, water potential gradient, or a reduced FWU rate for this species. While we have highlighted that the rate of water potential change is likely not constant, extrapolating the mean rate ($0.014 \text{ MPa min}^{-1}$) suggests that noticeable changes of 0.1 MPa can likely be observed within 10 minutes. These improvements are dramatic and could lead to remarkable shifts in leaf water balance and serve to repair embolism. Future studies that explore this mechanism need to carefully consider integration over multiple time scales (e.g. Steppe et al. 2018) and the changing water potential gradient with environmental conditions in their experimental designs.

Finally, some fluxes and quantities of FWU have been inferred using whole tree studies with sap flow probes. These rates have been valuable estimates for understanding the influence of FWU at the scale of whole-plant water balance. It should be noted that these methods would integrate water absorbed through both leaves and bark (e.g. Earles et al. 2016). The rates cited in several studies suggest that reverse flow rates can be 5 to 26 % of maximum transpiration fluxes, which is consistent with leaf-level data (Burgess & Dawson 2004, Eller et al 2013, Li et al. 2014, Cassana et al. 2015, Steppe et al. 2018). What is unclear in these studies is the extent to which negative sap flow in wood presents a 1:1 relationship with water absorbed at the leaf surface. It is probable that some proportion of the water from FWU is utilized in mesophyll cells or stored in supporting cells in wood and therefore not be represented in sap flow data. Determining net FWU rates over longer time periods (e.g. days to weeks) is influenced by the temporal patterns of water potential of the leaf and soil further disconnecting leaf water uptake and negative sap flow in wood. Using sap flow probes on stems adjacent to leaves, Gotsch et al. (2014) measured dry season water use in small branches on canopy emergent trees in a tropical montane cloud forest and found that 9% of the water transpired was recovered through FWU. Darby et al. (2016) found that, in tropical montane cloud forest epiphytes, FWU accounted for ~30% of transpired water during the dry season and ~70% of transpired water during a wet season (Gotsch et al. 2015). Finally, Steppe et al. (2018) recently found that *Avicennia marina* had no radial growth in the absence of FWU, demonstrating that this water source is critical for wood development. Field-based whole plant studies provide tools that allow for continuous measurements allowing for greater integration of FWU into whole-plant water balance.

To consider the role of FWU in leaf and whole-plant water budgets, we have compared fluxes of FWU relative to transpiration and water potential values. While we demonstrate great variability across species, we also observe the potential for FWU to play a large role in leaf and plant water balance. The implications for this are significant, as FWU can quickly reduce water deficits (e.g. water potentials), as well as subsidize mesophyll cells or vasculature. However, more research is needed to elucidate the variation in these traits across environments and species, as well as to determine the net effects on long-term plant functioning and water balance.

Critical Knowledge Gaps

While FWU research has made significant progress in recent years, there are still many key knowledge gaps that limit a more complete understanding of water movement in plants. In this section, we elaborate on key questions surrounding the environmental scenarios when FWU is likely to occur, the precise pathways of water flow, and the net effects on leaf and plant water balance. Finally, we explore current methods and their limitations, as well as propose ideas to further our understanding of FWU and plant water movement.

When and where does FWU occur?

To assess when FWU occurs requires an accurate quantification of the spatial and temporal components of leaf wetting across canopies. It is well established that FWU can occur during leaf wetting events such as rain, dew, mist, or fog events. However, the spatial and temporal frequency of leaf wetting is often difficult to measure simultaneously to FWU. Complex canopies exhibit high spatial variability in microclimate, which can result in subcanopy leaves staying wet for up to 22 hours following rain events, more than double the time of canopy leaves (Dietz et al. 2007). While studies quantifying leaf wetness patterns are valuable, the complex dynamics of these patterns are just now being incorporated into canopy storage or plant water and carbon balance models (e.g. Steppe et al. 2018). Sap flow data during these periods demonstrate FWU during leaf wetting periods, but do not allow for separation of sunlit versus shaded layers of the canopy. Thus, FWU could continue to subsidize leaf water content in many sub-canopy locations well after a leaf wetting event ceases and the canopy dries. Further, the spatial patterns of leaf wetness on individual leaves may result in FWU only on certain areas of leaves which could not be captured in whole-plant methodologies. Quantifying the spatial and temporal components of leaf wetting will allow for predictive frameworks of when and where FWU occurs across forests and canopies.

The extent to which FWU occurs when the air is not fully saturated with water vapor also remains unresolved (i.e. low, but non-zero VPD). Some studies have demonstrated FWU in high humidity conditions (in the absence of physical leaf wetting). However, the physical process to reverse the water potential gradient when the air is not saturated will only occur when VPD is low and plants are experiencing more negative water potentials (Figure 2). While Vesala et al. (2017) has provided the modeling framework for understanding when these conditions occur, empirical support is still needed. Further, any water that enters as vapor would require a phase change to liquid for subsequent movement from the intercellular air spaces into mesophyll or vascular cells. Other studies, such as Darby et al. (2016), found that precipitation more accurately predicted FWU than vapor pressure deficit. Leaves that experience more negative water potentials, such as those in drier climates or during dry seasons, should experience more FWU in high humidity conditions. Determining the relationships between microclimate, water potentials and rates of FWU is complicated by the methods available to make continuous and precise measurements, but remains of interest.

In addition to understanding when FWU occurs, there is a similar need to understand where FWU occurs. Given that FWU has been demonstrated in at least 209 species, the implications are that it occurs in nearly every major biome (Figure 1). However, research on FWU to date has been biased towards cloud forest (60 species), Mediterranean (45 species), and crop (34 species) systems, limiting our ability to infer the prevalence and effects of FWU across a wide range of taxa and ecosystems. Further,

we infer that greater rates of FWU are expected in arid regions (e.g. Stanton et al. 2014), where a single wetting event may have a greater impact on plant water balance in arid regions. A recent analysis by Dawson & Goldsmith (*In Press*), using a conservative estimate of leaf wetness from global rainfall data, found that an average canopy spends ~ 120 days year⁻¹ wet. If the environmental conditions for FWU also extend beyond the leaf wetting event, then FWU is likely to be a routine process, not a rare occurrence. A strategic, systematic, and standardized sampling of FWU fluxes across major plant families and biomes should elucidate the role of FWU in biomes with different rainfall patterns and atmospheric moisture patterns.

Where does the absorbed water go?

While previous research has explored the pathways for water uptake into the leaf, methodological limitations have limited our ability to precisely determine the pathways of water inside the leaf and whole plant. There is clear evidence that some water enters both mesophyll cells (Munne-Bosch et al. 1999) and vasculature (Laur & Hacke 2014). Determining the proportion of the absorbed water that follows these pathways or is transpired remains unclear. Additionally, it is unknown if certain environmental scenarios dictate differential flows to each pathway. Whether FWU occurs in liquid or vapor phase could also influence the flow pathways inside the leaf. Once inside mesophyll cells, is water utilized for photosynthesis, stored, or incorporated into the vascular bundle? How is water that enters vasculature internally distributed (e.g. xylem or phloem) and where does it move? Many of these questions are just starting to be explored, but more work is needed to elucidate the fate(s) of water that enters from the leaf surface. Active work in plant hydraulics, *in vivo* plant imaging and sap flow combined with stem diameter variation could help address these questions. The pathways of the water from FWU will have implications for cellular processes and plant water balance at multiple scales.

What are the long-term effects on plant water balance, photosynthesis, growth, and survival?

Research has demonstrated that during leaf wetting events, significant quantities of water are absorbed, altering leaf and stem water potentials, improving branch hydraulic conductivity, and increasing leaf water content. However, quantifying the long-term effects of these improvements on net carbon and water fluxes has proven more difficult. Berry & Smith (2013) demonstrate that morning FWU improves net daily carbon gain as inferred from greater stomatal conductance during midday and afternoon periods. But to what extent do these daily gains occur across species and contexts and do they have net effects for days or weeks? For example, could the altered water potential values, stomatal conductance, and photosynthesis from one day of FWU be observed for days or weeks? Steppe et al. (2018) demonstrated that FWU was important for turgor maintenance and growth in *Avicennia marina*. Water from FWU could serve as an additional subsidy (similar to leaf capacitance) that buffers declines in turgor loss and hydraulic conductivity (Nguyen et al. 2017). Would these net effects allow for greater cumulative growth or carbon storage? Would daily water potential improvements keep plants above turgor loss points or significant losses in hydraulic conductivity? Does FWU result in water deposition into the soil that may improve long-term soil moisture availability? Will community-level variation in FWU result in species-specific responses to changing moisture availability (Goldsmith et al. 2013)? The answers to these questions are likely specific to the unique climatic conditions of a site,

as well as the species' capacity for FWU. Future research should consider both the short- and long-term effects on plant water balance based on the temporal patterns of FWU. Further, exploration of the linkages between FWU and hydraulic functioning, plant growth, and risk for mortality will enhance our ability to predict plant response to novel climates. Ultimately, understanding these linkages will allow for integration into ecosystem models that predict ecosystem hydrology and long-term vegetation dynamics.

Unifying Methods

The above questions require a new perspective and set of methodologies for quantifying reverse water movement in plants. In particular, a standardized method to accurately quantify fluxes and rates of FWU is urgently needed. Comparison among studies is currently complicated by the variety of methodologies (sap flow, isotopes, change in mass, change in water potential, dyes), time intervals (seconds to days) and environmental conditions used. These methods have value in addressing critical questions but limit the ability to standardize FWU into a unifying framework. Plant science researchers need to standardize these measurements to facilitate comparisons of FWU; recent research by Guzmán-Delgado et al. (2018) that utilizes methods for measuring leaf hydraulic conductivity may point towards a standardized approach for the future.

Additionally, the plant science community is steadily moving towards a more 3D view of plant water movement. Water can simultaneously move up, down, and laterally through leaves, wood, and roots (Lee et al. 2013). Incorporating FWU into this new 3D view is necessary to build a complete picture of plant water balance. However, visualizing these pathways will require novel methodologies. Microcomputed tomography and *in vivo* MRI imaging provide promising avenues for visualizing pathways of FWU in leaves and wood (e.g. Holbrook et al. 2001, Brodersen et al. 2011, Hochberg et al. 2016). To date, the use of these technologies remains limited and they have not explicitly been used in relation to FWU. The integration of these methods with continuous field measurements of whole-plant water balance will be needed to advance our understanding of FWU.

Conclusions

At the end of Stephen Hales' renowned publication, *Vegetable Staticks* (1727), he concludes that water absorbed through leaves is "...insufficient its small quantity is towards making good the great demands of perspiration." However, we demonstrate that FWU is prevalent across species and biomes, that the physical requirements for it to occur happen routinely, and that it can serve as a critical source of water for metabolic function. However, there are still many unanswered questions about FWU that require creative and interdisciplinary experiments. The undeniable ubiquity of this fundamental plant process highlights a need to understand FWU as intricately as we understand processes such as root water absorption, xylem flow and transpiration.

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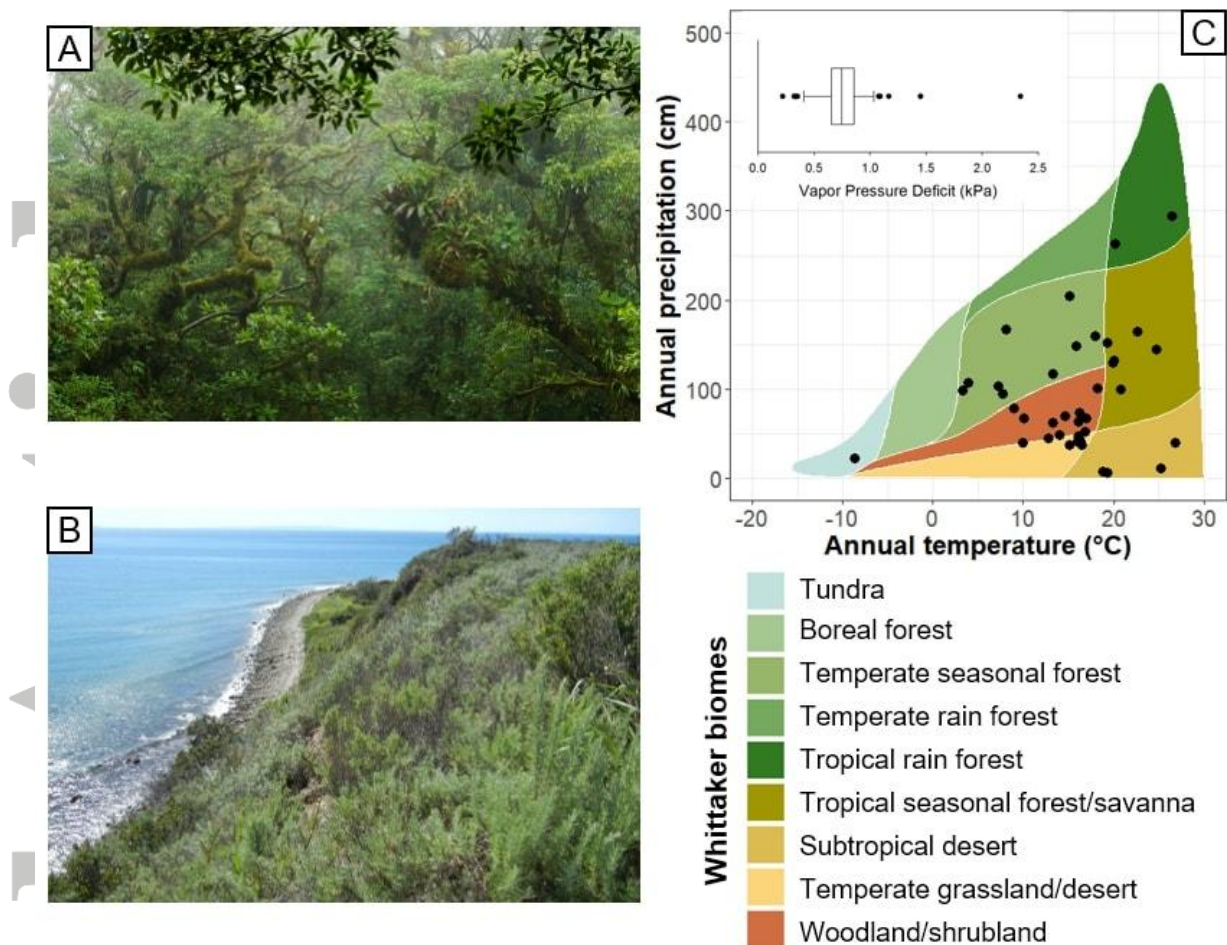


Figure 1. Foliar water uptake has been observed across a number of different biomes, ranging from A) tropical montane cloud forests in Monteverde, Costa Rica to B) coastal sage scrub ecosystems in Santa Barbara, California. The sites where foliar water uptake has been demonstrated are represented relative their location on a C) plot of classical Whittaker biomes (Whittaker 1962) using climate data from the TerraClimate database (Abatzoglou et al. 2018). The inset shows the distribution of average vapor pressure deficits for each site from TerraClimate.

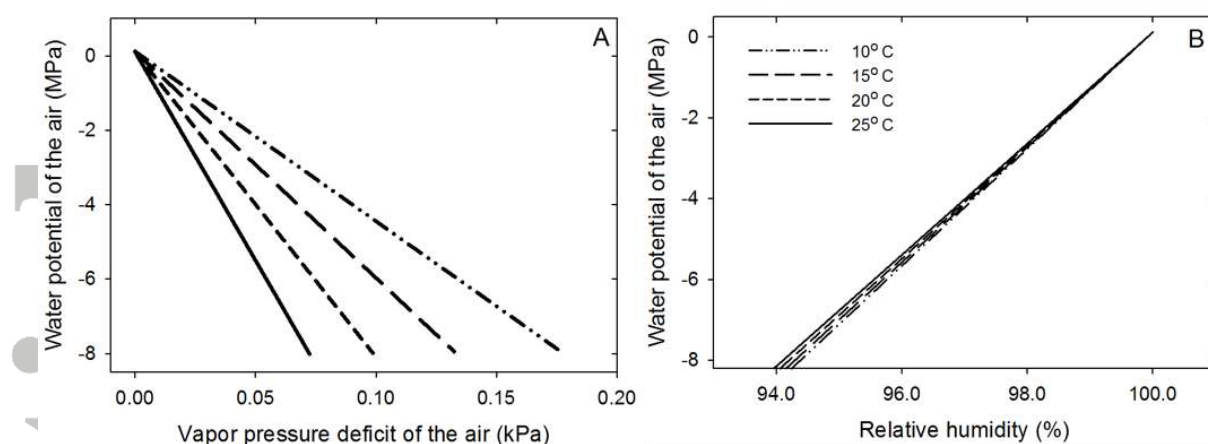


Figure 2. A low VPD (high relative humidity) is necessary for foliar water uptake. Water potential as a function of A) vapor pressure deficit (VPD) of the air and B) relative humidity at different temperatures.

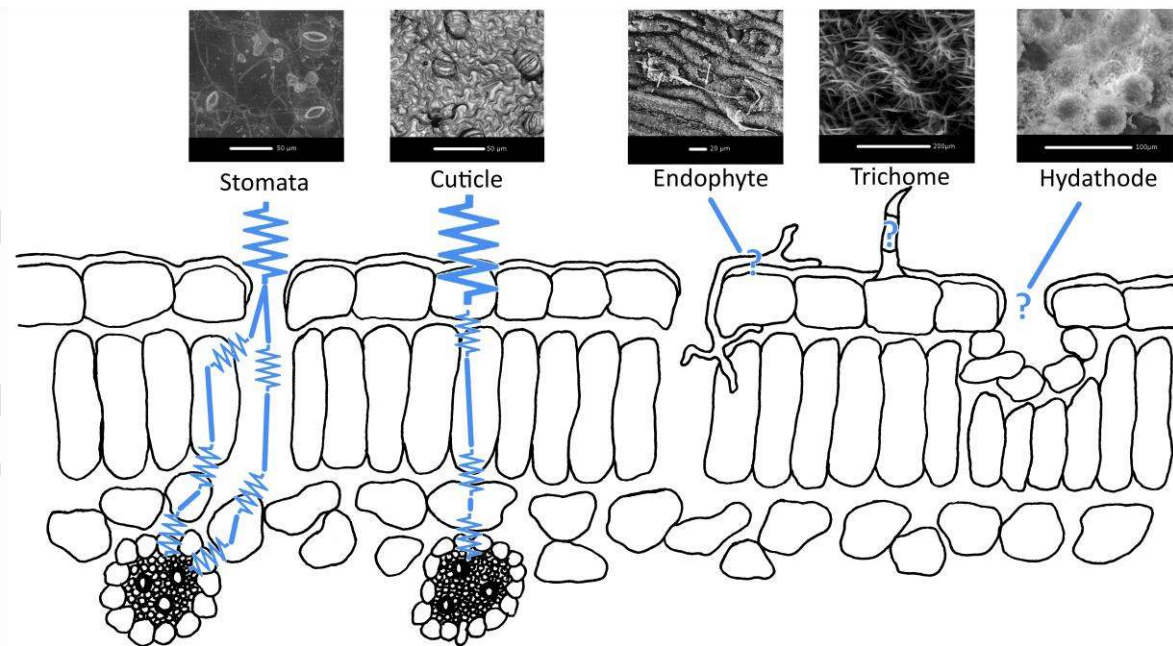


Figure 3. A number of leaf surface and internal structures have been implicated as pathways for foliar water uptake. Water faces resistance as it enters and moves through the leaf. Where known, relative size of resistors is based on values from Buckley (2015). Resistances provide illustrative examples but all these can vary significantly based on leaf anatomy and water gradients within the leaf. Example images of surface properties are taken from Burgess & Dawson (2004; endophyte), Martin & Von Willert (2000; hydathode), Goldsmith (unpublished; cuticle), and Emery (2016; stomata and trichome).

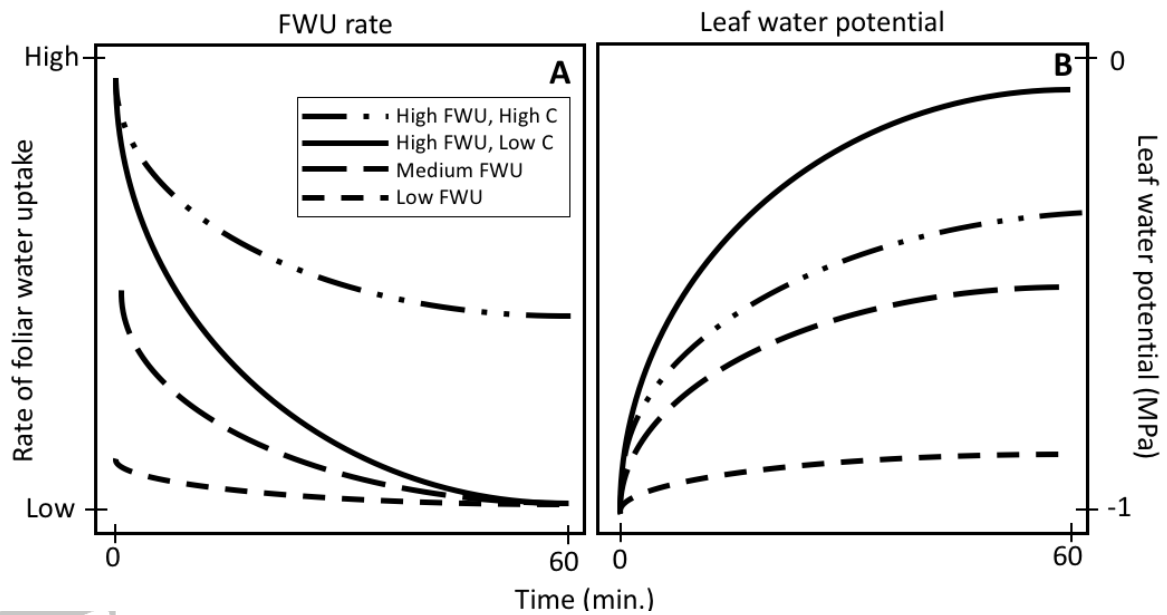


Figure 4: The A) rate of foliar water uptake should decrease exponentially as a function of time with B) the decreasing change in leaf water potential as a function of time. However, these relationships should differ in plants with high (solid line), medium (dash) and low (short dash) rates of foliar water uptake. Additionally, capacitance of the rehydrating leaf (C) should modulate the rate of water potential change such that a leaf with a higher C (dash-dot line) will take longer to reach equilibrium than a leaf with lower capacitance but the same initial FWU rate (solid line). Individuals with high rates of foliar water uptake improve leaf water potential as much as 0.9 MPa in 60 min, while individuals with low rates only changed water potential 0.09 MPa over 60 min. All data are constrained by rates taken for species in the database where FWU was quantified over 1 h.

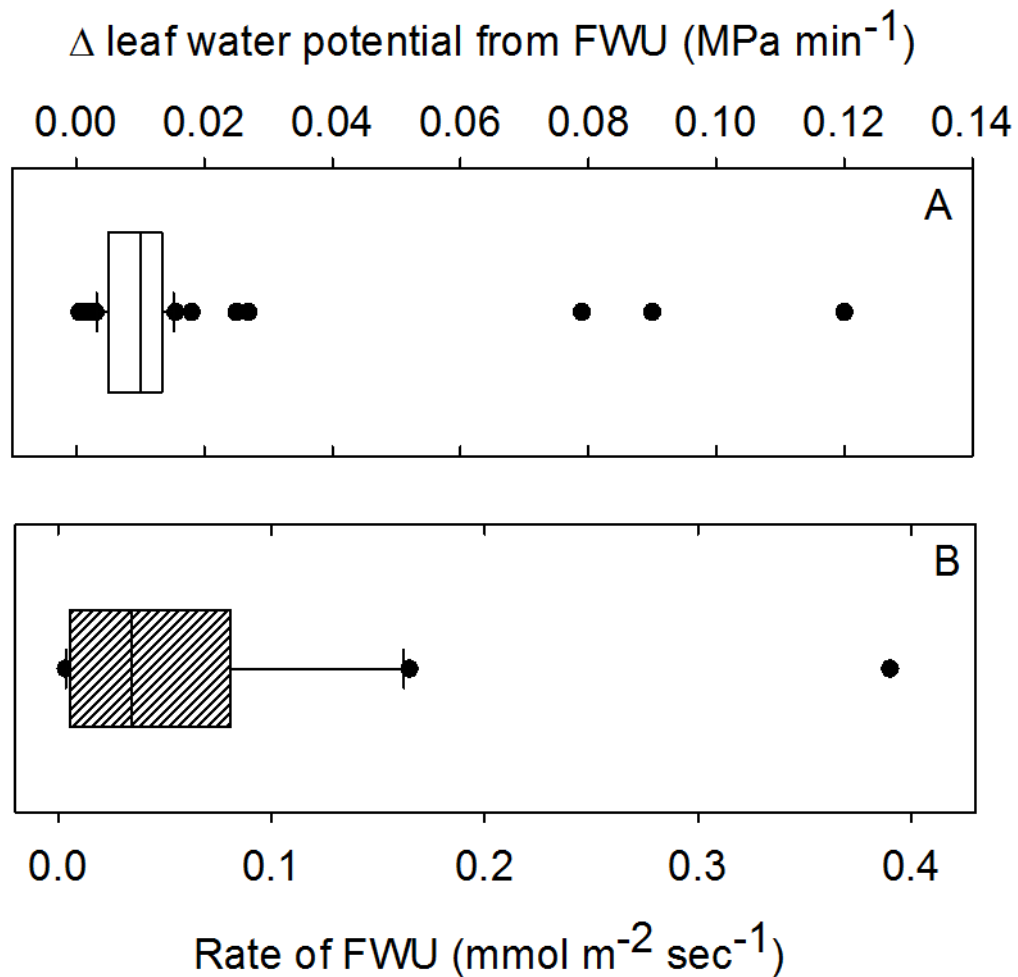


Figure 5. A summary of data from studies reporting A) the change in leaf water potential as a function of foliar water uptake ($n = 75$ species) and B) the rate of foliar water uptake ($n = 24$). In studies with changes in water potential, all values were standardized per minute, even if the study measured uptake for a different duration. Rates of uptake were converted to $\text{mmol m}^{-2} \text{s}^{-1}$ for comparison with transpiration rates, which typically are reported in these units