Commentary

Water in, water out: root form influences leaf function

One of the tenets of introductory biology courses is learning how the form or structure of any unit determines its function, and that form and function has long been used to understand patterns throughout the natural world (Grew, 1682; Wainwright, 1988; Díaz *et al*., 2016). Form predicts function at the cellular and organ level in plants; for instance, xylem cell diameter and pit pore size are great indicators of stem xylem hydraulic conductance and vulnerability to embolism (Pittermann & Sperry, 2005). Additionally, both theoretical treatments and experimental evidence indicate that root hydraulic function is coupled to leaf function (Cruiziat *et al*., 2002; Domec *et al*., 2009) but few studies have investigated how the anatomy and morphology of the roots may influence leaf function. In this issue of *New Phytologist*, Zhou *et al.* (2021; pp. 1481–1491) present results from a long-term precipitation experiment, showing that root form predicted leaf physiology. This study highlights that the form of one organ can have effects on function across the entire organism, providing a unique perspective in the study of form–function relationships.

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Root morphology and anatomy should influence leaf gas exchange through their effects on radial and axial hydraulic conductance. In the roots, radial flow is the transport of water from the soil matrix, through the cortex of fine roots and into the root stele/vascular tissue; the longer this tortuous pathway gets the more radial hydraulic conductance decreases (Tyree *et al*., 1994). Water transport in the stele occurs through the hollow, dead cells of the xylem (axial flow path), which compared to the radial path imparts a relatively high conductance pathway (Steudle & Peterson, 1998). Here, larger xylem cells, a higher density of cells per area, and larger stele diameters are all associated with higher rates of axial hydraulic conductance (Hacke & Sperry, 2001). The stele : root diameter ratio is a morphological feature that has been increasingly used to describe the balance between radial and axial hydraulic conductance, where roots with a higher ratio have relatively smaller cortexes and thus expected to have higher root hydraulic conductance (Valverde-Barrantes *et al*., 2016). Since the roots, stems, and leaves operate in a series, maximum whole plant hydraulic conductance is set by the portion of the pathway with the lowest conductance; roots with higher hydraulic conductance should support higher whole plant conductance (Passioura, 1982; Sperry *et al*., 1998). This begs the question; do these anatomical properties of the roots determine the ability of plants to respond to changes in water availability? If so, roots with higher radial hydraulic conductance (larger stele : root diameter ratio) should increase gas exchange rates more as water availability increases, compared to those with proportionately lower radial conductance.

Despite these seemingly straightforward expectations based on physics, drawing causality from the study of form–function relationships is complicated by the fact that plant form is strongly similar within groups of closely related species (Valverde-Barrantes *et al*., 2016; Zhou *et al*., 2018). Zhou *et al.* (2021) show that root morphology and anatomy were distinctly different between lilies, grasses, and forbs, effectively driving the form–function relationships they observed. This highlights the extremely difficult problem of disentangling the role of individual traits within the context of the complex evolutionary history of species (Caruso *et al*., 2020). In fact, many differences have arisen over evolutionary time, and the functional consequences of individual traits could differ across lineages; there are many ways to solve any physics challenge and the solutions employed will depend on the options available, i.e. species evolutionary history. Thus, there is much to be gained by the approach employed by Zhou *et al.* (2021) investigating the variation in plant form and function both within and across lineages.

Using this method, Zhou *et al.* (2021) found that lilies had large-diameter roots, large xylem vessels, an extensive cortex, and a relatively small stele; resulting in a low stele : root diameter ratio. Compared to lilies, all species of grasses and forbs had smaller-diameter roots, smaller xylem vessels, and thinner cortex. In forbs this was also accompanied by a much larger stele diameter, resulting in a dramatically higher stele : root diameter ratio compared to the grasses and lilies. Based on these anatomical features, lilies are expected to have the lowest root hydraulic conductance, whereas forbs should have the highest and grasses should be intermediate. Consistent with this idea, Zhou *et al.* (2021) found that rates of stomatal conductance were lowest in lilies, intermediate for grasses and highest for forbs. It should be noted that the grasses and lilies studied here showed very typical root anatomy compared to other monocots, but the forbs examined here are somewhat unusual, having a larger stele : root diameter ratio compared to other herbaceous eudicots (Wang *et al*., 2019) and woody plants (Gu *et al*., 2014). Thus, forbs in this study were more different from monocots than they would be on average. Regardless, the differences within monocots largely drove the form–function relationships observed by Zhou *et al.* (2021). Lilies were the most

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distinct when considered in a principal component analysis representing anatomical traits and physiological responses (Zhou *et al.*, 2021, Fig. 3), with the forbs and grasses being more similar to one another when all traits were considered simultaneously. Grasses showed the greatest within-group variation in principal component scores, suggesting that they should show the most variation in their response to a change in climate conditions. Zhou *et al.* (2021) did not detect a physiological response in the leaves of grasses to increased precipitation, however they also did not find a root anatomical response for any of the clades examined. By contrast, the leaves of lilies and forbs did respond by increasing stomatal conductance and transpiration under higher precipitation (Zhou *et al.*, 2021, Fig. 4). Low variation in measured root traits, accompanied by large variation in leaf physiological response to increased precipitation, suggests that leaf responses to precipitation change was largely determined by factors not measured in this study.

By taking advantage of a water addition manipulation that spanned 10 years to investigate how morphological and anatomical traits of roots impact the leaf function across different lineages of herbaceous plants, this study adds much-needed perspective to the literature on plant water transport. The field of plant hydraulics has been dominated by drought studies on woody plants growing in un-manipulated natural settings or short-term laboratory experiments (Allen *et al.*, 2010), and largely without considering the evolutionary history of study species (although see Pittermann *et al.*, 2012; Ramírez-Valiente *et al.*, 2020). The unique approach of Zhou *et al.* (2021) reveals that rates of instantaneous water use efficiency (WUE) (carbon assimilated/transpiration rate) were correlated with leaf gas exchange and stele : root diameter ratio, while long-term WUE was correlated with root anatomical traits (Zhou *et al.*, 2021, Fig. 3). This may reflect the fact that long-term WUE is the result of many correlated traits acting together, all of which ultimately depend on the combined water and nutrient uptake functions of roots, whereas short-term WUE more closely reflects the ability of roots and stomata to respond rapidly to a change in environmental conditions (Renninger *et al.*, 2015). Zhou *et al.* (2021), thus implicate variation in stele diameter and stele : root diameter ratio as important factors driving leaf responses to climate change. Lastly, these novel findings were based on an easy-to-measure root trait that has been less-investigated in terms of plant hydraulics, root cortex thickness. This ease of measurement opens the possibility to understand how radial vs axial conductance contributes to water uptake and use across many species, lineages and ecosystems, providing new opportunities to disentangle the complex roles of plant traits, environment and evolutionary history in form–function relationships.

Zhou *et al.* (2021) illustrate how important root anatomy can be for understanding aboveground plant physiology. It has long been recognized that roots should have a critical impact on whole-plant hydraulic conductance due to the limitations of radial flow where water enters the roots. Despite this, when compared to hydraulic measurements of stems and leaves, there is a paucity of studies including root hydraulics, and the number of studies using phylogenetic comparative approaches are even fewer. While root traits are often included in hydraulic process models, we need more empirical studies of root form and function that account for evolutionary history if we are to accurately represent the true contribution of roots to whole-plant hydraulics, to ecosystem-scale processes, and to the evolution of plant–environment interactions (Iversen *et al.*, 2017).

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