

Commentary

Changing directions: the atmosphere–plant–soil continuum

‘Water moves from the soil, through a plant, out into the surrounding atmosphere.’

Nobel (2009)

This observation, often formally described as the soil–plant–atmosphere continuum (SPAC), has become the predominant framework used for thinking about the movement of water through plants (Philip, 1966). It is not incorrect. However, in this issue of *New Phytologist*, Eller *et al.* (pp. 151–162) provide compelling evidence that it is incomplete.

‘From the textbook perspective on plant–water relations, Eller and colleagues are describing water moving the “wrong way” through the plant: from the atmosphere, through a plant, towards the soil.’

The foundation of the SPAC lies in the movement of water through plants from areas of high (less negative) to low (more negative) water potential (represented by the symbol ψ). The uptake of water by plants from the soil occurs when there is a driving gradient for water loss by transpiration due to a large difference between the low water potential of the dry atmosphere and the relatively high water potential of leaves. This gradient is propagated through the plant along a continuous water column that is under tension, ultimately resulting in the uptake of water occurring at high water potentials in the soil (Nobel, 2009; Fig. 1a). Thus, in the framework of the SPAC, water moves unidirectionally from the soil, through a plant, out into the surrounding atmosphere. But what happens if water moves in the other direction?

Eller *et al.* add to a growing body of research demonstrating *foliar water uptake*, the movement of water coalesced on the leaf surface into the leaf. From the textbook perspective on plant–water relations, Eller and colleagues are describing water moving the ‘wrong way’ through the plant: from the atmosphere, through a plant, towards the soil. The study provides evidence for not only how this reversal of the continuum occurs, but also addresses the associated implications for plant, community and ecosystem functioning.

Atmosphere

The conditions in the atmosphere resulting in the movement of water into leaves require the presence of a driving gradient, where the leaves have lower water potentials than the immediate, surrounding atmospheric boundary layer (Rundel, 1982). Eller *et al.* demonstrate foliar water uptake tightly coupled to leaf wetting that results from cloud immersion occurring during the dry season in a tropical montane cloud forest. In doing so, the study also adds an important new perspective on how water enters the leaf and where it goes once it is wet, demonstrating that their particular study species has both a hydrophilic cuticle that could facilitate water entry, as well as hydrophilic tissues within the leaf that could serve to provide storage. A number of different pathways have been proposed for water entry, including the cuticle, hydathodes, and trichomes (Limm *et al.*, 2009). Although historically excluded from the list of possibilities, recent research also suggests the stomata as an additional pathway (Burkhardt *et al.*, 2012). Eller *et al.* have started to bridge the gap between historically distinct lines of research on foliar water uptake and foliar permeability. Whatever the means of entry, foliar water uptake is likely to be restricted to leaf wetting events; water potentials at a given temperature quickly become very low at anything < 100% relative humidity (RH) (e.g. -1.36 MPa for 99% RH at 20°C; Nobel, 2009). Thus, only when water has coalesced on the leaf surface and the leaf is experiencing a water deficit is the internal leaf tissue likely to have a lower water potential than the boundary layer. As with Eller *et al.*, the strongest evidence for foliar water uptake has originated from seasonally dry fog- and dew-affected ecosystems, where leaf wetting events are occurring when soil water availability is limited (Munné-Bosch *et al.*, 1999; Limm *et al.*, 2009; Goldsmith *et al.*, 2013). However, episodic dry season precipitation events leading to leaf wetness are prevalent in many ecosystems and there is no reason to expect that these events do not also lead to foliar water uptake (Breshears *et al.*, 2008).

Plant

The conditions in the plant resulting in the movement of water from leaves into the stem similarly require the presence of a driving gradient, where foliar water uptake results in a higher leaf water potential than that of the stem. Eller *et al.* demonstrate an increase in leaf water potential resulting from foliar water uptake, as well as the flow of water through the stem and away from the leaves. Although reverse water flow in stems has been observed (Burgess & Dawson, 2004; Nadezhdina *et al.*, 2010; Goldsmith *et al.*, 2013), little is known about the stem water potential gradients associated with rehydration by foliar water uptake (Simonin *et al.*, 2009). For instance, it is possible that a plant stem at less than its full water

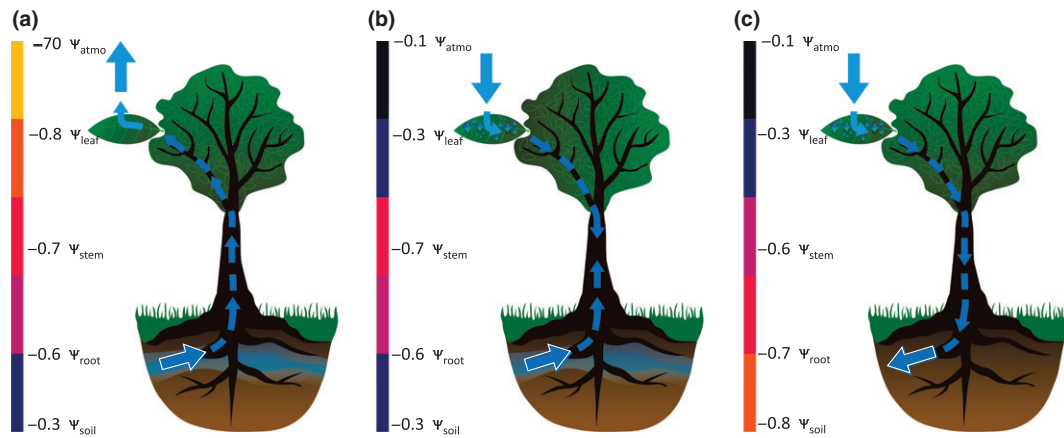


Fig. 1 Three potential scenarios for the movement of water through plants based on gradients in water potential (ψ in MPa). In scenario (a), water moves from higher ψ_{soil} to lower ψ_{atm} by transpiration. In scenario (b), water moves from higher ψ_{atm} (during a leaf wetting event) to lower ψ_{stem} by foliar water uptake, while also simultaneously moving from higher ψ_{soil} to lower ψ_{stem} , thus refilling the plant from two directions. In scenario (c), water moves from higher ψ_{atm} (during a leaf wetting event) to lower ψ_{soil} by foliar water uptake. Note that additional scenarios, such as the hydraulic redistribution of water from one soil layer to another by roots, are not included. Hypothetical values of ψ based on Nobel (2009). Illustration courtesy of F. van Osch.

storage capacity has a water potential such that when foliar water uptake begins, water is simultaneously moving towards the stem from both the roots and the leaves (Fig. 1b). In principle, the stem refills from both directions until no driving gradient exists. Such a scenario raises the critical need for temporal measurements of stem rehydration kinetics under the unusual, nonsteady state conditions imposed by foliar water uptake (Scholz *et al.*, 2011).

Ultimately, given an increase in water availability within the plant, Eller *et al.* demonstrate a resultant increase in photosynthesis and growth for saplings in a glasshouse experiment; foliar water uptake is likely to be particularly valuable with respect to early life history stages, where access to soil water may be more limited. While some questions remain regarding whether this translates to more than transient effects for plants in the field, the study points the way for the next steps in measuring and defining the frequency and effects of the reverse flow of water on whole plant functioning.

Soil

The conditions in the soil resulting in the movement of water from plants into the soil along a driving gradient have previously been observed only in the relocation of water by roots from a wetter to a drier soil layer (i.e. hydraulic redistribution; Neumann & Cardon, 2012). However, Eller *et al.* now demonstrate that water derived from foliar water uptake in the plant canopy is being redistributed to the roots, if not the soil itself (Fig. 1c). Given the number of species and the number of ecosystems where foliar uptake has already been demonstrated, these striking results should provide the basis for compelling new research questions. Hydraulic redistribution between soil layers has been demonstrated to have a host of effects, including positive impacts on the plant, the surrounding above- and below-ground biotic community, and the ecosystem's biogeochemical cycles (Prieto *et al.*, 2012). Although the frequency with which foliar water uptake leads to increased water below-ground remains unknown, the results provide the

impetus for considering how we define hydraulic redistribution and demonstrate the complete reversal of the SPAC.

New and changing directions

Foliar water uptake has now been identified in at least 70 species representing 34 plant families in seven different ecosystems (Goldsmith *et al.*, 2013). It provides a means by which the movement of water through plants is not always unidirectional or even bidirectional; rather, it is possible that it can simultaneously be moving in more than one direction at once (Fig. 1). As such, the SPAC is likely to best be described, both conceptually and mathematically, as the movement of water occurring as a function of all potential water sources (Simonin *et al.*, 2009).

The framework provided by the SPAC has provided significant advances in the field of plant–water relations and contributes to our thinking across every possible scale of organization, from the flux of water through a single plant leaf to an entire ecosystem (Manzoni *et al.*, 2013). The study provided by Eller *et al.* should serve as a call not only to reconsider how we employ it as we move forward, but also to look far and wide for the consequences of doing so.

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