Biotic and abiotic factors act in coordination to amplify hydraulic redistribution and lift

The possibility that water can flow from roots to the soil has been a major focus of attention for well over 70 yr in ecology and agronomy (Kramer, 1933) and much effort has been devoted to demonstrate its existence and to quantify its magnitude (Molz & Peterson, 1976). When the root-xylem tissue interfacing the soil has a hydraulic conductivity ($K$) well in excess of the soil hydraulic conductivity, the flow of water from a root to adjacent soil pore spaces can occur provided that the root water tension is smaller than the adjacent soil water tension. However, the idea that this mechanism may be part of a water-redistribution network induced by the rooting system as a plant strategy to buffer against prolonged droughts emerged later. It was shown that some species delay the onset of water stress by preferentially transporting soil water from the upper soil layers into deeper layers after rainfall and then releasing water from the deeper layers into the upper soil layers, where needed, via this rooting network (Mooney et al., 1980). Hydraulic lift (HL), which occurs primarily at night, was coined to describe the latter mechanism (Caldwell et al., 1998), while hydraulic redistribution (HR) is used to emphasize that the rooting system can distribute water passively within the soil profile from wet to dry soil layers. With the proliferation of sap-flow and stable isotope measuring techniques over the last two decades (Emerman & Dawson, 1996), evidence of HL has been reported for shrub, grasses and tree species, and for temperate, tropical and desert ecosystems (Caldwell et al., 1998; Horton & Hart, 1998; Oliveira et al., 2005). Despite the widespread evidence and voluminous data on the occurrence of HL and HR, three inter-related topics have resisted rigorous treatments to date: to what extent HR and HL confer advantages to the entire ecosystem in terms of carbon (C) gains (Emerman & Dawson, 1996); to what degree biotic and abiotic processes work in coordination to ‘amplify’ HR or HL; and given the reported magnitudes of HR and HL, how their effects can be represented in future generations of large scale C–water transport models, a topic now receiving attention in climate systems (Lee et al., 2005). The study by Domec et al. (pp. 171–183), in this issue of New Phytologist, considered the first topic for a loblolly pine stand during months of normal and below-normal precipitation and ‘fingerprinted’ the effects of HR on tree transpiration, ecosystem water use and the key components of the C balance. Using combinations of long-term...
sapflow, soil moisture and eddy-covariance flux measurements, they showed that HR was amplified most at intermediate soil-moisture states during the drought period. They also showed that the understory species was dependent on the HR induced by the deeper rooting system of the overstory pine trees for water supply during the drought. These long-term measurements further showed that in the absence of any HR benefit, gross ecosystem productivity and net ecosystem exchange were reduced by as much as 750 g C m\(^{-2}\) yr\(^{-1}\) and 400 g C m\(^{-2}\) yr\(^{-1}\), respectively. With these estimates, Domec et al. unequivocally calls into question the current treatment of root-water uptake in models and necessitates novel theoretical tactics to begin tackling the second and third topics raised here, the compass of this Commentary.

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Any progress on these two topics must separate HR induced by the rooting system from the soil-moisture redistribution mechanism across soil layers (Fig. 1). In the absence of any rooting system, water movement occurs from regions of wet- to dry-soil layers based on matric potential gradients and Darcy’s law, with magnitudes dictated by the soil water-retention and hydraulic-conductivity functions. This soil-induced redistribution mechanism occurs at all times and is not restricted to nocturnal conditions. Fig. 1 presents the modeled time evolution of the soil-moisture-content profile for a 1-m uniform bare soil column where soil evaporation is censored and water is only allowed to drain from the 1 m base. After 100 d, the upper 30-cm layers experience increases in soil moisture that can only originate from the deeper layers. These soil-moisture increases are commensurate with values reported by Domec et al. However, Domec et al. (Fig. 1b in their paper) were able to show that HL was recharging the top layers at much faster rates (c. 0.6 mm d\(^{-1}\)) than the calculations in Fig. 1 would suggest (c. 0.15 mm d\(^{-1}\)), especially in the summer months of the drought and only during nocturnal conditions. When comparing the results in Fig. 1 with those of Domec et al., one question that can be raised is whether biotic and abiotic factors are acting in coordination to amplify HR well beyond the soil-distribution mechanism highlighted in Fig. 1.

To address this issue, the interplay among soil-moisture redistribution, the structure of the rooting system and its hydraulic properties, soil type and the transpiration rate required to satisfy the plant C demands were analyzed using a numerical model (Siqueira et al., 2008, 2009). In this model, two flow patterns simultaneously occur – the first is at scales comparable to the root zone depth (c. meters) and the second is at length scales inversely related to root densities (c. millimeters), taken here to represent the radial distance between rootlets (Mendel et al., 2002). The scale separation between the two flow patterns justified the computation of each independently

![Fig. 1](image-url)  Illustration of the hydraulic lift (HL) induced by the rooting system and how it differs from soil moisture-induced distribution (soil HD) quantified using the boxed one-dimensional Richard’s (1931) equation. Here, \( t \) and \( z \) are time and depth from the ground surface, respectively; \( q \) is the water flux along \( z \) given by Darcy’s law; \( k(\theta) \) and \( \psi(\theta) \) are the soil hydraulic conductivity function and soil water pressure potential, respectively, at a given soil moisture, \( \theta \), approximated by power-law functions, with \( k_0, \psi_0, b \), and \( b \) varying by soil type. In these runs, the hydraulic properties employed are presented elsewhere (Oren et al., 1998). The assumed initial soil moisture content is shown in dashed lines, and the solid line represents the soil-moisture profile after 100 d. Notice the accumulation of water in the top layers (referred to as soil HD).
at fine time steps and recoupling them through a mathematical homogenization technique in space. This model can account for many known features of root uptake, including diurnal hysteresis in canopy conductance, HL and HR (Siqueira et al., 2008). The model assumes that root absorption is driven by pressure differences between the root–soil interface and root xylem tissue characterized by $K_r$. In essence, the model neglects osmotic transport that can be significant for near-saturated soil conditions (Siqueira et al., 2008). The model calculations also neglect pressure losses within the root xylem, which have been considered in other recent models (Amenu & Kumar, 2008). Order-of-magnitude analysis shows that the root pressure is in a quasi-hydrostatic state and primarily adjusts in time to maintain the transpiration demand of the plant, the latter being driven by photosynthesis. This argument simplifies the modeling of water flow inside the rooting system. The assumption becomes more realistic as the soil dries because the soil hydraulic conductivity decreases dramatically compared with $K_r$. The model further assumes horizontal homogeneity for the root area distribution. In addition, gravitational effects are neglected in the radial domain, making the rootlet orientation immaterial. The higher gradients and faster dynamics in the radial direction justify this assumption. Model calculations were performed (assuming both high and low $K_r$ values to regulate the strength of HR) for: three types of root-density profiles (constant, linear and power-law; Fig. 2a inset) in a silt clay soil; and three soil types (sand, silt clay and clay) for a linearly distributed root-density profile. All the plant physiological attributes related to leaf-level physiological traits and to radiative and aerodynamic parameters are identical across model runs. Also, the diurnal environmental forcing variables, including incident short- and long-wave radiation, mean wind speed, and air and dew-point temperatures, were assumed to be periodic so that all space–time variations in soil moisture are the result of the interaction between biotic and abiotic factors. These calculations have shown that, in all cases, the HL delays the onset of soil-moisture stress within the 1-m rooting zone by some 20–40 d (Siqueira et al., 2008). Moreover, it is amplified most for intermediate soil-moisture states, consistent with Domec et al. Based on the data shown in Fig. 2, the soil type and the root-density distributions appear to have comparable effects on HL.

To ‘encode’ these findings in larger-scale C–water cycling models, the reductions of transpiration with soil moisture for the soil-moisture states below field capacity are presented in Fig. 2(a,b). This representation, often the basis of the so-called loss function, is now routinely used in ecohydrological applications (D’Odorico & Porporato, 2004) to reproduce plant response to water stress. It is safe to state that the effects of elevated HL are to shift the onset of transpiration reductions to lower root-zone soil moisture, thereby allowing the ecosystem to sequester more C, as found in Domec et al. Moreover, the effects of HL for intermediate ranges of soil moisture are commensurate to those reported by Domec et al. Moreover, the effects of HL for intermediate ranges of soil moisture are commensurate to those reported by Domec et al. Fig. 2 further demonstrates that for a uniform rooting-density profile, HL confers minor benefits to the plant. We have conducted a number of model calculations similar to the ones shown in Fig. 2, with all combinations of soil types and root distribution, and have concluded that the effectiveness of the HL is mainly controlled by the root vertical distribution, while the soil-moisture levels at which HL is most effective appear to be dictated by the soil hydraulic

![Fig. 2 Loss function from model runs](https://www.newphytologist.com/content/187/1/3-6/fig/2)

**Fig. 2** Loss function from model runs comparing plant response to root-zone soil moisture ($\theta$) with high hydraulic lift (HL) (high $K_r$ value) and low HL (low $K_r$ value). (a) Responses with different root-density distributions in a silt loam soil, and (b) responses to different soil types with a linearly distributed root-density profile. The inset in panel a, shows the three different root-density ($\lambda$) profiles used in the runs. The rooting zone is only 1 m deep.
properties and the atmospheric water-vapor demand (Siqueira et al., 2008).

To conclude, Bonner (1959) stated that some of the problems pertaining to water movement in plant physiology are becoming increasingly amenable to mathematical analysis and called for the creation of a branch in plant physiology titled ‘Phytobiophysics’. This call was made in 1959 – and the occurrence of phenomena such as HL and HR simply reinforce this call today.

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References


What’s good for you may be good for me: evidence for adaptive introgression of multiple traits in wild sunflower

Interspecific hybridization has long been considered an important evolutionary mechanism in plants (Arnold, 2004). In particular, the transfer of adaptations among related taxa mediated by interspecific hybridization has received considerable attention from theoretical and empirical points of views. This process, often called ‘adaptive introgression’, involves the transfer of fitness-increasing alleles and their phenotypic effects from one taxon to another (Whitney et al., 2006; Fig. 1). Although many empirical examples of this process have been proposed (Rieseberg & Wendel, 1993; Table 1), and some of them convincingly demonstrated using appropriate empirical approaches (e.g. Martin et al., 2006; Whitney et al., 2006), it remains difficult to evaluate the overall importance of this process between related taxa. Moreover, even in documented cases, it is typically unknown whether multiple traits are involved in adaptive introgression, and which traits are more likely to introgress. Theoretical studies indicate that under heterogeneous environments, a single allele that is at an advantage in the alternative environment and genetic background is expected to introgress readily (Barton, 2001). However the transfer of multiple traits in introgressed populations, possibly with complex epistatic interactions, is not straightforward and depends heavily on conditions such as the rate and duration of hybridization and the detailed genetics of hybrid fitness (Barton, 2001). In this issue of New Phytologist, Whitney et al. (pp. 230–239) specifically address the issue of adaptive introgression of multiple traits by comparing phenotypes and fitness of natural and synthetic hybrids of two wild sunflower species, Helianthus annuus and Helianthus debilis. Together with the results obtained in a previous investigation (Whitney et al.,