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Hydraulic lift: a potentially important ecosystem process

Jonathan L. Horton and Stephen C. Hart

It is well known that water availability influences plant geographic distribution[1]. Globally, water availability in terrestrial ecosystems is the most important factor limiting CO_2 fixation and growth of individual plants, as well as ecosystem net primary productivity[1–3]. This is true in arid and semi-arid regions, as well as in mesic regions that are prone to short-term seasonal water deficits[3–5].

When plant demand exceeds water supply, plants must find other sources of water or make more conservative use of available water to minimize water stress and meet metabolic requirements[5]. Mooney and co-workers[6] suggested that *Prosopis tamarugo*, a shrub growing in the Atacama Desert in Chile (an area with an average annual rainfall of 0.3 to 0.7 mm), reduced water stress by transporting ground water into its deep roots and then releasing it, from its roots, into the upper soil layers where it can be utilized later. This process of taking water from deeper, moister soil layers and transporting it through plant roots to upper, drier soil layers has been termed hydraulic lift[7]. Hydraulic lift has been proposed as a mechanism that can buffer plants against water stress during seasonal water deficits[8].

Hydraulically lifted water (HLW) can benefit the plant that lifts it but might also benefit neighboring plants[5,8]. The volume of HLW can be such that it might influence seasonal water balances of individuals, communities, or even ecosystems[5,7,9] (Table 1). If this phenomenon is widespread, it should be

Hydraulic lift is the process by which some deep-rooted plants take in water from lower soil layers and exude that water into upper, drier soil layers. Hydraulic lift is beneficial to the plant transporting the water, and may be an important water source for neighboring plants. Recent evidence shows that hydraulically lifted water can promote greater plant growth, and could have important implications for net primary productivity, as well as ecosystem nutrient cycling and water balance.

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incorporated into models of competitive interactions[5], as well as ecosystem process models and water budgets[10].

Evidence for hydraulic lift

Mooney and co-workers[6] found that *P. tamarugo* possessed a dense root mat about 1 m under the surface. This mat was located in a moist soil layer that could exceed field capacity (Box 1), even though the soil above and below was much drier. The authors attributed this to hydraulic lift. The mechanism used to explain this phenomenon is based on passive movement of water down a water potential (Ψ) gradient. During the day, if a plant is transpiring, the Ψ gradient is from the ground water into the plant's roots and out through stomata to the atmosphere. At night, when the stomata close, water moves into the shoots until shoot Ψ is equal to the Ψ in the deep soil. The Ψ gradient is now from both the deeper soil and the plant shoot into the drier surface soil around the root mat. Water moves from the roots into this soil layer where it can be used for transpiration the next day[7].

In the semi-arid Great Basin of Utah, USA, Richards and Caldwell[7] observed significant diel fluctuations in soil water potential (Ψ_s) in areas around the sagebrush (*Artemisia tridentata*). Soil water potential decreased during the day, as plants were actively transpiring, but increased in the upper soil layers at night, when plants were no longer transpiring (Fig. 1). The nocturnal increase in Ψ_s was several orders

of magnitude greater than that expected from simple capillary water movement from deep to shallow soil. In fact, when transpiration was suppressed during the daytime, by placing plastic bags over the plant shoots, the Ψ_s increased during both day and night. Each deep-rooted (2.2 m) shrub could hydraulically lift up to 1 L m^{-2} of water each night, a substantial fraction of what the shrub transpired the next day. Hydraulic lift has been observed in other semi-arid shrubs as well[11,12].

Dawson[5] reported similar diel fluctuations in Ψ_s under sugar maple (*Acer saccharum*) in a mesic forest in central New York, USA, during an extended dry period. These were also attributed to hydraulic lift. In addition, he compared the hydrogen stable isotope ratios (δD) of ground water and soil water from samples taken under large trees and at different distances from the tree trunks. Soil water δD within 2.5 m of the trees was found to be indistinguishable from ground water. At greater distances from the main trunk, isotope ratios showed a mixing of ground water with soil water, until the soil water isotope ratio at 5 m away from the main trunk was indistinguishable from that in the precipitation that fell before the dry period. This analysis provided further evidence that large *A. saccharum* trees hydraulically lift water from deeper soil layers, and release it into the upper soil layers.

Additional evidence for hydraulic lift comes from experiments with agricultural plants grown in split-root culture[13,14]. In such experiments, a layer of perlite, or some other substance that does not transmit water, separates two soil layers, both of which contain plant roots. Water is added to the lower soil layer, and any increases in water content in the upper soil layer are attributed to transport through plant roots[15]. Isotopically labeled water was used to follow the path of water as it moved from a lower water source to the upper soil layers[15].

Ecological implications of hydraulic lift

Hydraulically lifted water could be beneficial to the plant that transports it as long as a significant amount of HLW is not lost via evaporation[16] or water uptake from neighboring plants[7]. Richards and Caldwell[7] suggested that hydraulic lift in *A. tridentata* increases the efficiency of deep roots. Without HLW stored in the upper surface, where the majority of the plant's fine roots are located[4], the deep roots may be unable to provide enough water to meet the peak transpirational needs of the plant. However, with HLW stored in the surface soil at night, the plant has two reservoirs of water to draw from the next day. Hydraulic lift was essentially eliminated in plants that were dimly illuminated at night, and thus maintained low rates of transpiration. As a result, transpiration rates in these plants were reduced by 25–50% the following day[8]. Emerman and Dawson[10] showed that a mature *A. saccharum* could hydraulically lift 50–150 L of water each night, which could be up to 30% of the water transpired the next day. Plants that used hydraulically lifted water were able to maintain higher transpiration rates and experienced less water stress than plants that did not[17]. One prediction stemming from these results is that the improvements in plant water status should translate into increases in plant competitive ability and ecosystem net primary productivity.

Table 1. A summary of the potential effects of hydraulically lifted water at different spatial scales

| Individual	Community	Ecosystem
Altered soil water distribution	Increased competitive ability of the hydraulic lifter	Increased net primary productivity due to greater individual carbon gain
Reduced stomatal closure and/or increased transpiration	Increased competitive ability for non-lifting neighbors able to utilize HLW	Altered ecosystem water balance (greater evapotranspiration)
Increased carbon gain due to greater transpiration	Altered community composition and distribution patterns	Altered nutrient cycling due to enhanced rhizosphere processes

Box 1. Glossary

Field capacity: The amount of water remaining in a soil following saturation once gravity drainage has ceased.
Water potential (Ψ): A measure of the difference between free energy of a water sample relative to that of pure water. An indicator of water availability in soils and water stress in plants.
δD: $[(D/H_{sample}/D/H_{standard})-1] * 1000$ (where D is deuterium and H is hydrogen). Ratio of the isotopic composition of a sample relative to some standard, in this case V-SMOW (Vienna standard mean ocean water).
**Stomatal conductance:** A measure of the water loss from plant leaves controlled by stomatal aperture and driven by the gradient between internal and external water vapor pressures.
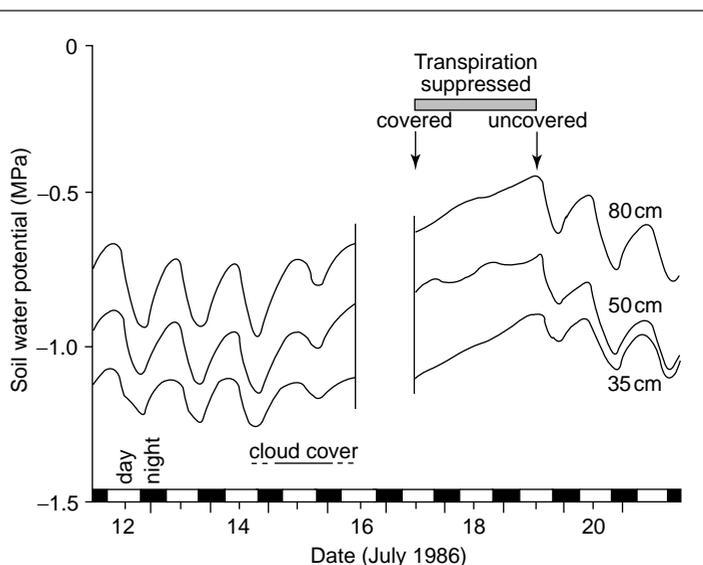
Fig. 1. Time course of soil water potential (Ψ_s) at three soil depths under sagebrush (*Artemisia tridentata*) shrubs during a drying cycle and a transpiration-suppression experiment in July 1986. Periods of cloud cover and transpiration suppression are indicated. Missing data on 16–17 July are the result of power failure. *Reproduced, with permission, from Ref. 7.*

Dawson[15] reported that *A. saccharum* seedlings that performed hydraulic lift were able to achieve higher daily integrated carbon gain than plants in which hydraulic lift was experimentally suppressed. Hydraulically lifting seedlings did not have higher maximum photosynthetic rates but were able to maintain high rates longer, resulting in assimilation of up to 2.3 times more carbon than those seedlings that did not perform hydraulic lift (Fig. 2). This higher daily carbon gain translated into 24–30% greater rates of root growth and 8–14% greater rates of shoot growth.

Hydraulically lifted water might also moisten shallow soil layers sufficiently to allow roots to take up nutrients that
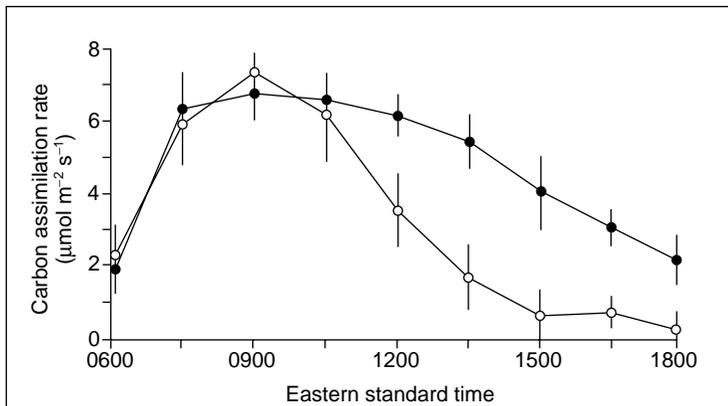
Fig. 2. Daily course of carbon assimilation for sugar maple (*Acer saccharum*) seedlings that were either performing hydraulic lift (closed circles) or not (open circles). Each data point is the mean of five replicates. Vertical bars denote ± one standard deviation of the mean. *Reproduced, with permission, from Ref. 15.*

Box 2. The effect of hydraulic lift on ecosystem water balance estimates

The effect of hydraulically lifted water (HLW) on ecosystem water-balance estimates will depend on the methods employed in estimating water balance. Methods, like those used by Joffre and Rambal[24], that rely on direct measurements of soil water content as an input into water balance equations are most likely to be affected, for example:

$$dS/dt = Pr - E - R - D$$

where E is total system evapotranspiration, Pr is precipitation, dS/dt is change in soil water storage over time, R is surface runoff, and D is deep drainage.

In this method, the sampling design of soil water content measurements is extremely important. If significant hydraulic lift occurs each night, then the timing of soil water measurements becomes a factor. If sampling is done at predawn, before the plants start transpiring, the soil water content will be high (possibly higher than expected) which could lead to low values of dS/dt, resulting in over-estimates of system evapotranspiration. However, if the soil water measurements are made later in the day, after the HLW pool is depleted, then soil water content would be low which could lead to high values of dS/dt, resulting in an underestimate of system evapotranspiration. If hydraulic lift occurs and transports a significant amount of water, measurements of soil water content will need to be made so that the diurnal pattern of soil water content is known, and an average value of soil water content can be used to determine dS/dt in the water balance equation.

The popular micrometeorological methods for estimating water balance employ direct measures of water vapor fluxes from canopies (or energy fluxes as a proxy for water vapor). These methods would include HLW contributions to evapotranspiration in their total water balance estimates. However, using these techniques alone would not allow one to determine the contribution of HLW to total evapotranspiration. One area where hydraulic lift might affect energy-balance approaches to ecosystem water balance is the omega factor[26] (the degree of stomatal control of transpiration). In isolated or open canopies that are well mixed, stomata are tightly coupled with the atmosphere, whereas in a closed, continuous, smooth canopy, stomatal control of transpiration is less important and stomata are decoupled from the environment[26,27]. Significant contributions of HLW might cause plants to transpire more, significantly altering microclimatic conditions in the canopy boundary layer and causing a greater degree of stomatal decoupling relative to canopies of non-lifting species.

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might otherwise be unavailable[4,12,15–17]. However, pearl millet (*Pennisetum americanum*), grown in a split-root experiment, failed to improve nutrient uptake in the upper soil layer once soils were dry. Nevertheless, HLW might still have prolonged conditions of favorable uptake as the soil dried[14]. Hydraulic lift might not only extend the length of time in which soil nutrients are available but may also increase plant fine-root longevity[4]. Because root growth and maintenance can use a substantial fraction of the net carbon assimilated by plants[3,18], hydraulic lift will also increase plant growth and ecosystem net primary productivity by reducing the carbon costs associated with soil resource acquisition[4].

In addition, hydraulic lift can have implications for neighboring plants. Caldwell and Richards[8] showed the potential for uptake of HLW by neighboring plants by exposing excavated deep-root tips of *A. tridentata* to deuterated water. Within 24 hours, deuterated water showed up in the xylem water of neighboring, more shallow-rooted tussock grass (*Agropyron desertorum*). Uptake of HLW by neighboring plants may be at least part of the explanation accounting for clumped patterns of desert vegetation (which have formerly been attributed to such factors as a more favorable microclimate, increased soil organic matter, and greater nutrient availability associated with shrubs[4]). However, subsequent studies have failed to find evidence of substantial use of HLW by *A. desertorum*[19]. This species has roots up to 1.7 m deep and might perform hydraulic lift itself. In a split-root culture experiment with deep-rooted alfalfa (*Medicago sativa*) and shallow-rooted corn (*Zea mays*), water hydraulically lifted by the alfalfa allowed the corn to survive a lethal drought period but did not provide enough water to stimulate growth[13]. However, in a field study in a mesic forest, water hydraulically lifted by sugar maple supplied up to 60% of the water used by neighboring shallow-rooted species. Both leaf water potential and stomatal conductance of these shallow-rooted species decreased with increasing distance from the hydraulically lifting tree[5]. In this environment, the ability to use hydraulically lifted water might confer a competitive advantage that translates into greater growth when soil water content is low[10].

If hydraulic lift is an extensive phenomenon, it could have important influences on ecosystem nutrient cycling. For example, hydraulic lift might delay soil dry-down, allowing mycorrhizae and other soil microorganisms to remain active for longer[7]. This might increase nutrient mineralization[20], and could lead to greater nutrient availability and uptake by plants[5,8,15]. However, HLW might also cause lower nutrient concentration in the soil solution, thus decreasing the concentration gradient from the soil to the root, and possibly lowering nutrient uptake. Emerman[21] has developed a model that predicts, for systems where nutrient uptake is strongly related to ion concentration, an overall benefit of acquiring soil nutrients with hydraulically lifted water relative to non-lifting species, despite possible decreases in the ion concentration of the soil solution. Dawson[15] found that NH_4^+ and dissolved organic nitrogen, but not NO_3^-, concentrations were higher around *A. saccharum* roots conducting hydraulic lift than around the roots of plants in which hydraulic lift was prevented. In another study, Matzner and Richards[22] found that *A. tridentata* (a known hydraulic lifter) was able to maintain nutrient uptake even at very low (–5.0 MPa) soil water potentials. Although hydraulic lift was not specifically tested in this study, it seems likely that hydraulic lift helps this species maintain nutrient uptake in dry soils.

Hydraulic lift may also act to homogenize nutrient availability[23]. Nutrients generally become depleted around roots as they assimilate nutrients. Hydraulically lifted water may moisten soil allowing not only greater mineralization, but also greater rates of nutrient diffusion through the soil[23]. However, a study on *A. tridentata* in a semi-arid shrubland did not show differences in nutrient heterogeneity due to hydraulic lift, suggesting that, at least in this system, the overall low daily Ψ_s could have counteracted any benefit of nocturnal hydraulic lift on nutrient homogeneity[23].

Hydraulic lift might also have implications for ecosystem water balances (Box 2). Species that perform hydraulic lift can transpire up to twice as much daily water as similar sized species that do not[17]. If an ecosystem consists of plants

that conduct substantial hydraulic lift, the stand might lose more water than expected, because many of the plants, both deep- and shallow-rooted species, could be using both soil and ground water[17]. Joffre and Rambal[24] found that, in a mixed oak–grassland ecosystem in Spain, trees transpired 25 to 50% more water than predicted from a water balance equation. The authors suggested two reasons for the discrepancy; they had failed to account either for roots that were extracting water from below the zone of their soil water measurements or for roots that were involved in water uptake that extended beyond the canopy crown. Dawson[25] suggested that the discrepancy could result from hydraulic lift. Greater transpirational water loss caused by the use of HLW could ameliorate adverse microclimate conditions in a tree or forest canopy, causing the canopy to be decoupled from the atmosphere. This would result in less stomatal and more environmental control of transpiration in ecosystems with plants performing hydraulic lift[17]. Hydraulic lift, if it occurs in significant amounts, will have to be included in water balance equations to accurately model water flux through ecosystems.

Conclusions and prospects

There is a growing body of evidence supporting the phenomenon of hydraulic lift in arid, semi-arid and mesic ecosystems. Hydraulic lift can have substantial benefits to the plant lifting the water, such as greater daily carbon gain, increased growth and increased nutrient uptake, but may benefit neighboring plants as well. While substantial evidence has been presented by Dawson[15] on the benefits of hydraulic lift to *A. saccharum* seedlings, more work needs to be done in other systems to investigate the role of hydraulic lift for promoting growth and nutrient uptake, not only for lifters, but also for non-lifters able to use HLW. Investigations that combine measurements of diurnal soil-water-content patterns, stable-isotope analysis (to determine water uptake source), and micrometeorological energy balance techniques may shed light on the magnitude of hydraulic lift and its contribution to ecosystem water flux. The degree and extent to which hydraulic lift occurs in natural ecosystems needs to be described before a clear understanding of ecosystem function can be achieved[10,12].

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