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Hydraulic lift: consequences of water efflux from the roots of plants

Abstract Hydraulic lift is the passive movement of water from roots into soil layers with lower water potential, while other parts of the root system in moister soil layers, usually at depth, are absorbing water. Here, we review the brief history of laboratory and field evidence supporting this phenomenon and discuss some of the consequences of this below-ground behavior for the ecology of plants. Hydraulic lift has been shown in a relatively small number of species (27 species of herbs, grasses, shrubs, and trees), but there is no fundamental reason why it should not be more common as long as active root systems are spanning a gradient in soil water potential (Ψ_s) and that the resistance to water loss from roots is low. While the majority of documented cases of hydraulic lift in the field are for semiarid and arid land species inhabiting desert and steppe environments, recent studies indicate that hydraulic lift is not restricted to these species or regions. Large quantities of water, amounting to an appreciable fraction of daily transpiration, are lifted at night. This temporary partial rehydration of upper soil layers provides a source of water, along with soil moisture deeper in the profile, for transpiration the following day and, under conditions of high atmospheric demand, can substantially facilitate water movement through the soil-plant-atmosphere system. Release of water into the upper soil layers has been shown to afford the opportunity for neighboring plants to utilize this source of water. Also, because soils tend to dry from the surface downward and nutrients are usually most plentiful in the upper soil layers, lifted water may provide moisture that facilitates favorable biogeochemical conditions for enhancing mineral nutrient availability, microbial processes, and the acquisition of nutrients by roots. Hydraulic lift may also prolong or enhance fine-root activity by keeping them hydrated. Such indirect benefits of hydraulic lift may have been the primary selective force in the evolution of this process. Alternatively, hydraulic lift may simply be the consequence of roots not possessing true rectifying properties (i.e., roots are leaky to water). Finally, the direction of water movement may also be downward or horizontal if the prevailing Ψ_s gradient so dictates, i.e., inverse, or lateral, hydraulic lift. Such downward movement through the root system may allow growth of roots in otherwise dry soil at depth, permitting the establishment of many phreatophytic species.

Key words Hydraulic lift · Plant water uptake · Water relations and water use · Nutrient acquisition · Plant roots

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Introduction

Hydraulic lift is the process of water movement from relatively moist to dry soil layers using plant root systems as a conduit. Water released from roots during periods when transpiration ceases (usually at night) into the upper soil layers is then absorbed the next day and transpired (Fig. 1). The term "hydraulic lift" was coined to describe this process (Richards and Caldwell 1987) since water is moving in the liquid phase and the direction of movement is usually upward towards the drier and shallower soil layers. Part of the process involves reverse flow, i.e., passive movement of water from roots to soil when reduced transpiration allows xylem water potential to rise above Ψ_s in drier soil layers. This phenomenon has many implications that we discuss following a brief historical account of the phenomenon.

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Fig. 1 Pattern of water flow through the root system during the day and night periods according to the hydraulic lift hypothesis. During the day, water is absorbed from all depths in which soil moisture is available and passes into the transpiration stream. At night when transpiration is reduced and plant water potential rises, the primary pathway of water movement is from moist soil through the root system to drier soil layers. Nighttime water movement is passively down a water potential gradient. If soil at depth is moister, water moves from deeper to more shallow, drier layers (redrawn from Caldwell 1988)
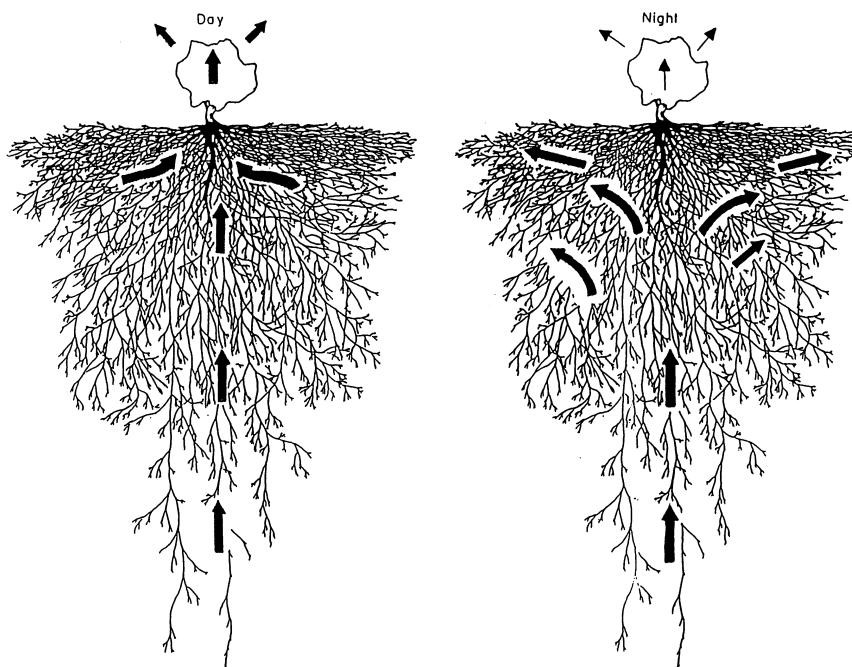
Several questions will be addressed: What are the lines of evidence supporting the concept of hydraulic lift? How general is this phenomenon? Should hydraulic lift be expected in any species if its root system spans a suitable gradient of soil water potential (Ψ_s)? What are the implications of hydraulic lift for rhizosphere processes, species interactions, and water movement in and through plant communities?

A short historical perspective

Indications of water transfer in laboratory experiments

Water transfer by roots between physically separated soil compartments of differing water status has been shown by many workers in glasshouse or laboratory conditions. Some of the earliest experiments were by Breazeale and colleagues (Magistad and Breazeale 1929; Breazeale 1930). For example, Breazeale (1930) demonstrated that roots of wheat seedlings in air-dried soil or soil of moisture content below the "wilting percentage" could be moistened if part of the roots had access either to free water or moist soil (provided that transpiration was inhibited by use of a bell jar). He conducted analogous experiments with maize plants in the field by teasing adventitious prop roots from the soil and inserting them into small jars filled with dry soil. In most cases, these roots survived, proliferated and moistened the soil in the small jar. From these and other studies (Breazeale and Crider 1934), Breazeale spoke of root systems as being "equalizers" of soil moisture (see also de Kroon et al. 1996). Several others subsequently demonstrated water movement between soil compartments by roots in laboratory experiments (Table 1) and

sometimes this represented a substantial quantity of water (e.g., Baker and van Bavel 1988).

Direct measurements of water efflux from individual hypocotyls or roots have also been reported. Schippers et al. (1967) used a modified cylindrical gypsum block conductivity cell surrounding individual hypocotyls of bean plants and reported water efflux, especially under conditions of suppressed transpiration. Dawson (in press) measured water efflux with psychrometers placed next to roots grown in specially designed root boxes in the greenhouse; again, efflux was measured at night when plant transpiration was suppressed. Topp et al. (1996) placed individual maize roots, or groups of roots, adjacent to the center prong of a time-domain reflectometry (TDR) probe and reported increases in the dielectric output (=water content) at night. The authors interpreted this as demonstrating water efflux from the maize roots into dry soil at night. However, TDR data may be subject to problems of interpretation when used to document hydraulic lift; nighttime increase in the dielectric output could be due to changes in water content within the roots without necessarily any efflux into the soil, as recently shown by Dawson and Pate (1996). This would depend on the proximity of the roots to the TDR prongs and the degree to which root tissue water constitutes a sizable component of the TDR field of measurement. Therefore, any probe used to detect hydraulic lift in plants must be placed with care and attention to how much signal may be coming from internal root water rather than from soil moisture.

Another indication of hydraulic lift was provided in laboratory experiments that demonstrated water transfer from roots of one plant to those of another (Hansen and Dickson 1979; Corak et al. 1987). In these experi-

Table 1 Species for which there is laboratory evidence suggesting the potential for hydraulic lift (*NMR* nuclear magnetic resonance)

Species	Reference	Nature of evidence
Triticum vulgare (wheat) and *Zea mays* (maize)	Breazeale 1930	Water transfer between soil compartments
Circidium torreyana (palo verde), *Acacia greggii* (catclaw), *Lycopersicon esculentum* (tomato)	Breazeale and Crider 1934	Water transfer between soil compartments
Phaseolus vulgaris (bean)	Schippers et al. 1967	Water efflux from hypocotyl
Populus species (poplar)	Hansen and Dickson 1979	Water transfer between roots of neighboring seedlings
Cynodon dactylon × *C. transvaalensis* (bermudagrass)	Baker and van Bavel 1986	Water transfer between soil compartments
Medicago sativa (alfalfa)	Corak et al. 1987	Water transfer to maize plants in same pot
Gossypium hirsutum (cotton)	Baker and van Bavel 1988	Water transfer between soil compartments
Prunus persica (peach)	Glenn and Welker 1993	Water transfer between soil compartments
Eucalyptus viminalis	Phillips and Riha 1994	Water transfer between soil compartments
Zea mays (maize)	Topp et al. 1996, Watt et al. in press	Water efflux from individual roots
Acer saccharum (sugar maple)	T.E. Dawson, personal communication	Water transfer between soil compartments, deuterium labeling
Artemisia tridentata (sagebrush)	J.H. Richards, personal communication	Water transfer between soil compartments, proton NMR imaging

ments, roots of both the donor and recipient plants were located in a single dry-soil compartment; another part of the root system of the donor plant had access to an adequate water supply in another soil compartment. Additionally, circumstantial evidence suggesting hydraulic lift can be seen in reports of root growth in very dry soil layers (e.g., Fabiao et al. 1985; Glenn and Welker 1993) and nutrient uptake from dry soil (Nambiar 1976, 1977; Matzner and Richards 1996) when roots deeper in the profile had access to moisture.

Active exudation from roots under certain circumstances has been suggested (Cortes 1992; Schwenke and Wagner 1992) and may contribute to the formation of rhizosheaths in graminoids (Watt et al. 1994; McCully 1995). However, the large quantities of water that can be involved in hydraulic lift, as described later, suggest passive water movement along a gradient from higher root water potential to lower Ψ_s.

Evidence of hydraulic lift in the field

Seasonal water transfer from lower to upper soil layers by *Prosopis tamarugo* in the Atacama Desert was advanced by Mooney et al. (1980) to explain comparatively moist soil and an anomalous mat of dense roots in the upper soil layers. Precipitation is essentially nonexistent in this extreme desert, yet soils were moist; the authors conjectured that this water might come from the root system itself. Some soil-plant-atmosphere water flux models could produce indications of hydraulic lift on a diel time scale if no provisions were included in the models to diminish hydraulic conductivity between the roots and soil when Ψ_s was more negative than root water potential (e.g., Landsberg and Fowkes 1978; Kirkham 1983; Campbell 1985). However, the predicted release of water to dry soil in the field awaited experimental verification.

The first strong evidence that hydraulic lift occurs in the field was observation of diel fluctuations in Ψ_s associated with the shrub, *Artemisia tridentata* (Richards and Caldwell 1987). The diel fluctuations of Ψ_s were clearly associated with day-night cycles; Ψ_s increased at night and decreased during the day (Fig. 2). When the shrubs were covered with opaque plastic bags to prevent transpiration, Ψ_s rose continuously for more than 2 days until the shrubs were again exposed to daylight. Conversely, if the shrubs were illuminated at night, the increase of Ψ_s was suppressed (Caldwell and Richards 1989). Hydraulic lift was further indicated with a labeling experiment in which deep roots of this shrub were given highly enriched deuterated water: the deuterium signal was subsequently seen in the xylem water of neighboring grass plants (Caldwell and Richards 1989). The interpretation of these results is that water released into the upper soil layers by the shrub was obtained by the neighboring grasses whose roots intermingled with those of the shrub in the upper, drier soil layers. Wan et al. (1993) grew the suffrutescent *Gutierrezia sarothrae* in buried pots in the field, but allowed roots to extend below the pot into the ambient soil. They reported increases in soil water content in the pots and also at the same shallow depths in the ambient soil where other *Gutierrezia* were growing. They also observed increases in soil moisture during the day if they covered the plants to stop transpiration over a 3-h period.

Dawson (1993) reported hydraulic lift around mature, isolated maple trees (*Acer saccharum*) during a summer drought in upstate New York, based on diel fluctuations in Ψ_s and the natural abundance of deuterium in xylem water of the trees and neighboring vegetation. Deuterium signatures of the maple xylem water indicated it was using primarily groundwater and not the remnants of summer precipitation. Neighboring species, which were less deeply rooted than the maple and did not themselves tap groundwater, acquired some
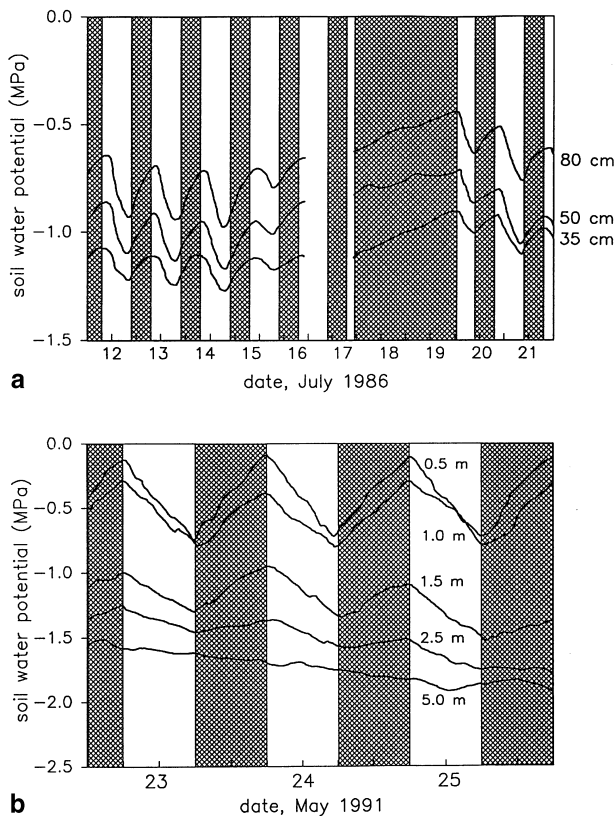
Fig. 2 a Diel fluctuations of Ψ_s at three depths under a stand of *Artemisia tridentata* shrubs during a period of drying. The *shaded zones* indicate nighttime. Missing data on 16–17 July are the result of a power failure. Beginning in the morning of the 17th, the shrubs were covered with opaque plastic bags to create an artificial "night" lasting 2 days. The covering totally suppressed transpiration, leading to a continuing increase of Ψ_s during that period. With return of the normal night-day cycles, after the plants were uncovered midday on the 19th, the diel Ψ_s cycling returned (redrawn from Richards and Caldwell 1987). **b** Diel fluctuations in Ψ_s at the same depths (lines are an average of 20 and 35 cm depths) but at progressively greater distances (0.5–5 m) from the trunk of a large *Acer saccharum* tree conducting hydraulic lift (redrawn from Dawson 1993)

proportion of their moisture from the hydraulically lifted water of the maple. The degree to which neighboring species acquire the lifted water by other plants is addressed in more detail below.

Is hydraulic lift widespread?

The finding that hydraulic lift can occur in a mesic forest species indicates that the phenomenon of hydraulic lift is not restricted to arid and semiarid environments. Dry periods, even if rather short, are a feature of most biomes and the necessary Ψ_s gradients for hydraulic lift may exist sporadically or regularly in many soils during the growing season. The diversity of species represented in Tables 1 and 2 does not suggest that hydraulic lift is necessarily limited to particular plant groups, but the sample is quite small. Including both laboratory and field investigations, hydraulic lift has now been reported

in 19 woody taxa (trees and shrubs) and in 8 different species of herbs or grasses. Ongoing investigations with a variety of trees and shrubs in temperate (e.g., maple-oak forests, T.E. Dawson, personal communication; oak woodlands, J.H. Richards, personal communication) and tropical environments (forests in southeast Asia, P. Becker, personal communication) are also showing hydraulic lift.

Evidence that hydraulic lift does not occur is also limited. Are there species or situations in which active roots in drier soil layers do not experience nocturnal water efflux if other parts of their root system have access to moisture? If Ψ_s measurements do not reveal diel fluctuations, this is not necessarily convincing evidence that hydraulic lift does not occur in a particular species. Soil psychrometers effectively sense only a very small volume of soil, only a few cubic centimeters, and sufficient sampling by many psychrometer sensors would be needed to rule out hydraulic lift. Measures of soil moisture content, such as by TDR or neutron probe, may not be sufficiently sensitive to detect the diel fluctuations of Ψ_s. Also, as mentioned before, care must be taken that the sensing probe is not simply responding to internal root water content. There may be times during the year when reverse flow cannot occur, even though Ψ_s would be conducive for it, because of developmental changes in roots that reduce hydraulic conductivity, active root surface area, or root-soil contact (e.g., during quiescent periods of the normal root growth cycle when most of the surficial roots are older, more lignified or suberized, when root hairs and fine laterals have been shed, or when the entire root cortex has deteriorated). Thus, hydraulic lift may only be observed for a portion of a growing season as the root system progresses from a state that would allow hydraulic lift to one preventing such water movement despite appropriate water potential gradients. Measurements through extended time periods would be required to be assured of observing such temporary periods of hydraulic lift or to document that hydraulic lift did not occur.

There are a few reports, e.g., from alfalfa (Dirksen and Raats 1985) and cotton (Molz and Peterson 1976), that roots of some species largely prevent reverse flow. But these reports are not in agreement with other reports for the same species (Table 1). In these apparently conflicting studies, there is usually a large discrepancy in the severity and duration of water stress to which the roots were exposed before reverse flow determinations were made. Thus, at this point, it is difficult to label some species as inherently and distinctly incapable of reverse flow and hydraulic lift.

Root characteristics that may inhibit reverse flow

Reverse flow is the primary component of hydraulic lift. If roots are active in water absorption, is there any fundamental reason why they should not also passively allow water to move into soil if Ψ_s is more negative than

Table 2 Species exhibiting hydraulic lift in the field

Species	Reference	Nature of evidence
Artemisia tridentata (sagebrush)	Richards and Caldwell 1987, Caldwell and Richards 1989	Ψ_s fluctuations, daytime bagging experiment, deuterium labeling, nighttime lighting experiments
Agropyron desertorum (crested wheatgrass)	Caldwell 1990	Ψ_s fluctuations, nighttime lighting experiments
Gutierrezia sarothrae (broom snakeweed)	Wan et al. 1993	Water accumulation in upper root zone, soil water content fluctuations
Acer saccharum (sugar maple)	Dawson 1993, 1996	Ψ_s fluctuations, natural abundance of deuterium
Dipterocarps (three species)	P. Becker, personal communication	Natural abundance of stable isotopes
Quercus douglasii (blue oak)	C. Millikin and C. Bledsoe, personal communication	Ψ_s fluctuations
Sarcobatus vermiculatus (greasewood), *Quercus douglasii* (blue oak), *Artemisia filifolia* (sand sagebrush)	J.H. Richards, personal communication	Ψ_s fluctuations
Yucca schidigera (Mojave yucca), *Larrea tridentata* (creosote bush), *Ephedra nevadensis* (Nevada joint-fir), *Ambrosia dumosa* (white bur sage) *Lycium pallidum* (pale thornbush)	C. Yoder and R. Nowak, personal communication	Ψ_s fluctuations, nighttime lighting and daytime bagging experiments

the water potential of the root? Some reports suggest (and many basic plant biology textbooks 'factually' state) that roots may have "rectifier" properties, i.e., that water should more readily flow into than out of roots (e.g., Molz and Peterson 1976; Nobel and Sanderson 1984; Dirksen and Raats 1985; Shone and Clarkson 1988; North and Nobel 1991, 1992; Nobel and Huang 1992). However, upon closer inspection of the data and the species, one sees that the time scale and degree of rectification vary. In a strict sense, rectification is the immediate property of a barrier to allow flow in one direction and not in the other. A limited degree of rectification has been shown to be a normal property of the hypodermis and the development of the Casparian bands and suberin lamellae which prevent water efflux along symplastic and apoplastic pathways (Peterson et al. 1992). However, even if water efflux is prevented along the apoplastic pathway, this barrier is not always sufficient to totally prevent efflux from roots (Shone and Clarkson 1988) because radial water transport in roots may involve several pathways (e.g., the composite transport model: Steudle 1994; Steudle and Frensch 1996; and see below). Roots may greatly decrease in radial conductivity when exposed to water stress in drying soils over a period of weeks or longer, but this usually involves developmental changes in the roots. With desert succulents, Nobel and colleagues have reported several cases of substantially reduced water permeability of roots after they were exposed to severe drying in air or soil (e.g., Nobel and Sanderson 1984; Nobel and Huang 1992). The loss of radial conductivity was due to structural changes in the roots, such as the development of intercellular lacunae in the root cortex and abscission of lateral roots (Nobel and Huang 1992; North and Nobel 1995). With rewetting, permeability gradually increased and new root growth contributed to an increased capacity for water uptake. These longer-

term changes would not operate on a 24-h cycle for active roots under less extreme conditions; thus, it is not rectification in a strict sense that is relevant to prevention of reverse flow.

Apart from the root itself, curtailment of water loss from roots might also take place if an air gap forms between the root and the soil as the root and/or soil shrink with water stress (Nobel and Huang 1992; Nobel and Cui 1992a–c; Nobel 1994). Root shrinkage has been observed in several species with drought and theory predicts an air gap can substantially increase resistance to water movement (Huck et al. 1970; Nobel and Cui 1992b; Nobel 1994). Again, the issue of time scale is germane if root shrinkage is to prevent hydraulic lift. On a diel time scale, some root shrinkage has been observed in a cotton root (Huck et al. 1970). This could contribute to short-term reduction of root-soil water transfer; however, it would probably not contribute to prevention of reverse flow at night since most of the shrinkage occurred during the afternoon and root diameter recovered at night. In addition, even with root shrinkage, root characteristics in many species (e.g., persistent root hairs, mucilage and other root exudates) contribute to maintenance of root-soil contact.

For desert succulents, with much of the root system in the very shallow layers (e.g., upper 10 cm) and where Ψ_s may drop to -10 MPa (Young and Nobel 1986), the combination of loss of root hydraulic conductivity and air gaps would be very beneficial. However, in the desert succulent, *Yucca schidigera*, which has some deeper roots, C. Yoder and R. Nowak (personal communication) found Ψ_s cycling indicating hydraulic lift (Table 2). This CAM species exhibited diel Ψ_s cycling in a pattern inverse to that of other species, i.e., nighttime declines and daytime increases of Ψ_s. This indicates that the Ψ_s fluctuations symptomatic of hydraulic lift are the result of diel patterns of stomatal opening and closing, as in C_3

plants: CAM plants open stomates at night and close them during the day. Thus, at night for this CAM plant, the prevailing water potential gradient is from the deeper roots into the atmosphere, whereas during the day, with stomates closed, water flows along the water potential gradient from deeper to shallower soil.

On a diel or shorter time scale, we are not aware of any proposed mechanism conferring a true rectification sufficient to prevent reverse flow. Over longer time periods, root hydraulic conductivity may decline with aging roots (see next section) and lowering Ψ_s. However, hydraulic lift may persist even when soils become rather dry if part of the root system has access to some moisture and fine roots remain alive and active in dry soil. For example, the telltale Ψ_s fluctuations indicated that hydraulic lift often continued in very dry soil (−5.0 MPa) for *A. tridentata* (Williams et al. 1993). Hydraulic lift may tend to mitigate some of the loss of root conductivity.

Localization of water loss from roots

In the few species studied, much of the uptake and efflux of water may occur in young roots (Watt et al., in press). Roots may also possess apoplastic gaps through which water can be transported and passed into the transpiration stream or lost in the process of hydraulic lift or in exudation driven by internal root pressure (Henzler and Steudle 1995; McCully 1995; Steudle and Henzler 1995). The direction of flow in these cases is apparently determined by the water potential gradient. Work with graminoids (Watt et al. 1996) and trees [*A. saccharum* (Dawson 1993, 1996) and *Eucalyptus viminalis* (Phillips and Riha 1994)] shows that the cyclic exudation of water into the soil is localized in the younger portions of the root system where the Casparian bands and suberin lamellae of the hypodermis are not fully formed. Water loss can also occur at junctions within the highly branched fine-root system where roots are less than 2.5 mm in diameter (Dawson, in press).

Selective water channels, called aquaporins (Chrispeels and Maurel 1994; Steudle and Henzler 1995) may provide a high-conductivity symplastic pathway for flow out of the roots, even when apoplastic pathways are blocked by mature exodermis and endodermis (Tyerman and Steudle 1982; Henzler and Steudle 1995; Steudle and Henzler 1995). Our current understanding of these channels is that they are not selective in any flow direction and would not, therefore, serve as rectifiers in preventing reverse flow (E. Steudle, personal communication).

How much water is lifted overnight?

Although the potential for reverse flow has been acknowledged for some time as indicated in the brief historical account above, it was not thought to result in large quantities of water efflux (e.g., Landsberg and Fowkes 1978). The measurements of Ψ_s fluctuations for a broad range of plant taxa (Tables 1, 2), however, suggest that a considerable amount of water is lifted each night (Fig. 2). The quantity is perhaps most meaningfully related to the daily evapotranspiration (ET). Estimates of hydraulically lifted water range from 14% of daily ET for the suffrutescent shrub *G. sarothrae* (Wan et al. 1993) to roughly 1/3 of ET (1 l m^{-2} ground surface area per night) for the shrub, *A. tridentata* (Richards and Caldwell 1987). These estimates are usually made by converting Ψ_s to soil water content (if soil water content was not measured directly as in Wan et al. 1993) and extrapolating over the depth and/or lateral extent of the root system. For example, Emerman and Dawson (1996) recently combined measurements of the diel variation in Ψ_s with an empirically determined relationship between Ψ_s and soil water content. From this information, as well as information on the soil hydraulic conductivity and the extent of the tree root system, they estimated that a mature (ca. 20 m tall) maple tree lifted 102 ± 54 l of water per night over the course of a 5-day period. This same tree transpired between 400–475 l the following day during the same period. Hydraulic lift, therefore, temporarily recharged the upper soil layers to nearly 25% of the total daily water use of the tree. Of course some of this water is lost to evaporation and neighboring plants (Dawson 1993, 1996), but the data demonstrate the potential for hydraulic lift to augment the available soil water in upper soil layers for plant use; mature maple trees which conduct hydraulic lift do transpire more than small trees which do not, suggesting that maple trees accrue a benefit from the hydraulic lift process (Dawson 1996). There are necessarily some uncertainties in these extrapolations, but at least it is apparent that significant quantities of water can be involved. These field estimates are in agreement with laboratory measurements of the amount of water that can be moved by hydraulic lift; van Bavel and Baker (1985) and Baker and van Bavel (1988) reported that averages of 42% and 31% of daily transpiration were supplied by water lost from roots overnight into dry soil compartments for bermudagrass and cotton, respectively. An indirect estimate of the magnitude of hydraulically lifted water also comes from experiments showing the facilitation of ET by hydraulic lift (next section).

Hydraulic lift can facilitate water movement in the soil-plant-atmosphere system

In most plant communities, root length density decreases exponentially with depth (Jackson et al. 1996) as portrayed in Fig. 1. This root distribution combined with some direct evaporation from the soil surface results in drying of the soil profile from the surface downward. For long drying cycles, moisture is available only at depth. Even if plants have roots reaching mois-

ture at depth, the root length density is generally very small, which limits the rate of water uptake. Hydraulic lift provides a mechanism for the temporary storage each night of water external to the plant in the upper soil layers. The internal water capacitance of most plants is limited, thus, the external storage allows the deep roots to continue water absorption overnight when transpiration is reduced (Caldwell and Richards 1989). This temporarily stored water is rapidly extracted during the following morning since it has been deposited in a region of high root length density. This was demonstrated in the field by experiments with *A. tridentata* shrubs enclosed in whole-plant cuvettes in which the temperature, humidity, CO_2, and light were controlled. The nights were cool, and the days, hot and dry in the cuvettes. After several normal night-day cycles, the plants were given nighttime illumination to circumvent hydraulic lift by forcing stomatal opening, which was verified by suppressed nocturnal Ψ_s increases. Following a night of illumination, whole-plant transpiration the following day was reduced by 25–50% of that expected under the normal controlled daytime conditions. If the shrubs were subsequently allowed a normal night to reestablish hydraulic lift, transpiration the following day recovered to expected levels. With the circumvention of hydraulic lift by nighttime illumination, the plant was deprived of the lifted water for transpiration the next day. Thus, the reduction in transpiration is an indirect measure of the quantity of hydraulically lifted water. This indirect measure corresponds with the general magnitude of hydraulically lifted water for these shrubs based on extrapolation of Ψ_s fluctuations discussed above.

At the landscape level, hydraulic lift may contribute significantly to ET by providing the daily pool of stored water in the upper soil layers for both the deep-rooted plants that conduct the hydraulic lift and also for associated, more shallow-rooted species that utilize the lifted water but do not participate in the lifting. The importance of deep roots in the water balance of ecosystems is receiving increased interest (e.g., Canadell et al. 1996). However, the contribution of hydraulic lift to water flux in the soil-plant-atmosphere continuum when deep roots tap moist soil at depth has received much less attention (but see Caldwell and Richards 1989; Dawson 1996). The degree to which hydraulic lift directly contributes to ET when upper soil layers are dry depends on several factors, such as the vertical soil moisture and root length density distributions. For the lifting plant species, if the deep root system has sufficient soil-root conductive capacity to be able to absorb and transport water to the shoot during the day at a rate matching the rate of transpiration, then hydraulic lift should not be necessary to facilitate their transpiration rates. For example, under conditions of low evaporative demand, deep root acquisition of water may well be able to keep pace with transpiration; but, under strong evaporative demand, the nighttime acquisition and lifting of water might be necessary to support the 24-h transpiration demand. For plants not lifting, but utilizing the lifted water, hydraulic lift obviously greatly facilitates transpiration if residual soil moisture from precipitation is limited. In this way, the water use of many community members is promoted by hydraulic lift (Dawson 1993; and next section).

Water utilization by neighbors

Early laboratory experiments (Table 1) had shown that water could be transferred from one plant to another and the deuterated-water labeling field experiment (Caldwell and Richards 1989) mentioned above also indicated the potential for utilization of hydraulically lifted water by neighboring plants. However, the magnitude of water utilization by neighbors was first demonstrated in the field by Dawson (1993) using the natural abundance of deuterium in xylem water as mentioned earlier. Using the known isotope ratios (signatures) of xylem, soil, and ground water and a mixing model, he determined the proportion of hydraulically lifted water used by neighboring plants. This proportion ranged from 3 to 60% even though many of these species were in close proximity to one another. Subsequent work has shown that the roots of some understory species are in much closer association with the water moving into the soil from the roots of the tree than are those of other species (T. Dawson, personal communication). The water utilized by some of the neighboring plants had a positive influence on their water use patterns and growth (Dawson 1993). This adds support to an emerging view that not all plant-plant interactions are necessarily negative and that facilitation is an important process in plant communities (see Callaway 1995; Hacker and Bertness 1995; Callaway et al. 1996).

In the study just discussed (Dawson 1993), the root systems of the plants receiving the water subsidy from hydraulic lift were separated in depth from the deeper roots of the maple tree by a distinct fragipan. Another study (Caldwell 1990) did not find that a significant quantity of water was used by *Agropyron desertorum* tussock grass neighbors of *A. tridentata* shrubs. This investigation was conducted by measuring whole-plant gas exchange of the grasses growing next to the shrubs. Hydraulic lift of the shrubs was circumvented using nighttime illumination while the grasses experienced a normal dark period. Although a decreased transpiration rate of the grasses in the day after this nighttime treatment of the shrubs was expected, this did not occur. In the course of this study, it became apparent that the tussock grasses had sufficiently deep roots to tap moister soil and were themselves conducting hydraulic lift. Thus, the dependence of the grasses on water subsidy from the shrubs was small.

The buffered behavior of hydraulic lift

As evaporative demand varies, the amount of water extracted daily from the upper soil layers should also

vary. An indication of this is seen in Fig. 2a: on a cloudy day (15 July) the decrease of Ψ_s was less pronounced than on the other days which were sunny. Based on the continued increase of Ψ_s in the upper soil layers during total transpiration suppression (17–19 July in Fig. 2a), one might expect that during periods of reduced evaporative demand, hydraulic lift would lead to a net accumulation of soil moisture in the dry soil layers until the return of sunny weather. However, this is not the case, at least in the *A. tridentata* study system. Nocturnal resupply of moisture to the shallower layers appears to be self-limiting and nocturnal increases in Ψ_s are a surprisingly consistent proportion of daily Ψ_s decreases (Williams et al. 1993). Over the course of much of the dry summer season from mid-June (when Ψ_s averaged −0.5 MPa in the upper soil layers) to early September (average Ψ_s of −4.2 MPa in the upper soil layers), the nocturnal increase was 80% of the daily Ψ_s decline. This behavior of hydraulic lift was attributed to several factors, but both experimental data and the modeling results indicate that principal among them is that soil moisture depletion during the day is largely responsible for creating the water potential gradients that drive the nocturnal recharge the next night. Thus, unlike the effect of totally suppressing transpiration (Fig. 2a), shading and lowered ET caused by normal cloud cover during the day should not be expected to lead to accumulation of soil moisture over a period of days. This behavior could theoretically be different during rainy weather, but separating the effect of reduced ET from water addition to the soil by rain is not straightforward and needs further exploration.

Hydraulic lift and rhizosphere processes in dry soil

The persistence of hydraulic lift over appreciable periods in otherwise dry upper soil layers has several implications for rhizosphere processes and plant nutrient acquisition (Richards and Caldwell 1987). These include prolonging the activity (e.g., growth and solute uptake) and life span of fine roots, root hairs and associated microorganisms such as mycorrhizae, improving nutrient ion mobility, and potentially smoothing spatial heterogeneity of nutrients. Nutrients are usually most plentiful in the upper layers of most soils. As these layers dry, ion mobility rapidly decreases and, thus, water supplied by hydraulic lift can facilitate ion diffusion to roots. Otherwise, plant nutrient supply would be restricted to deeper, moister soil layers where nutrients are much less plentiful. Emerman (1996) has developed a model which calculates ion uptake enhancement by the water provided from hydraulic lift in otherwise dry soil. His model shows that despite a possible decrease in ion concentration in the soil solution during hydraulic lift, relative to nonlifting species, there is still an overall benefit of acquiring soil nutrients by hydraulically lifted water whenever the root ion uptake rate is a strong function of the ion concentration in the soil solution.

Biogeochemical nutrient cycling processes of decomposition, mineralization, and nitrification are also most active in upper soil layers and are all very moisture dependent (Schlesinger 1991). Thus, there are several important possible effects of increased moisture in upper soil layers resulting from hydraulic lift, but experiments designed to test these implications, especially in the field, are only beginning. An attempt was made to determine if hydraulic lift contributes to reducing spatial heterogeneity of nutrients in dry upper soil layers (Caldwell and Manwaring 1995); however, this field experiment failed to show reduced spatial heterogeneity relative to soils where hydraulic lift was suppressed by nighttime lighting.

In pot experiments, there is some evidence that plants can acquire nutrients in very dry soil, if another portion of the root system has access to moisture (Nambiar 1976, 1977). Recently, Matzner and Richards (1996) showed that *A. tridentata* roots maintain nutrient uptake capacity even under considerable water stress and this may be coupled with hydraulic lift, although the role of hydraulic lift was not explicitly tested in these experiments. Dawson (in press) has documented enhanced daily carbon fixation and root and shoot growth in sugar maple seedlings undergoing hydraulic lift in special root boxes compared with control plants in which hydraulic lift was circumvented by continuous illumination. The enhanced performance was further correlated with higher concentrations of NH_4^+, (but not NO_3^-), dissolved organic nitrogen, and K^+ in the soil solution surrounding leaky roots (Dawson, in press).

Growing roots in dry soil: inverse hydraulic lift

Some of the deepest roots have been reported in arid areas (Canadell et al. 1996). Growing tens of meters deep into the soil can pay dividends if roots eventually reach sources of moisture. But before this, roots must presumably grow in very dry soil or sand below the depth to which the annual precipitation penetrates. Such growth might be facilitated if there was water transfer from the moist surface soil following precipitation to the roots growing at depth in dry conditions. Although hydraulic lift has been described primarily as water transfer from lower, moist soil layers to shallower, drier layers, there should be no reason why this should not operate in the opposite direction if the Ψ_s gradient so dictates (inverse hydraulic lift). Breazeale and Crider (1934) mused over the problem of root persistence and growth in dry soils and conducted some field observations and laboratory experiments. They found roots of desert plants could persist over several months and penetrate very dry soil. In the laboratory, they conducted several experiments with different desert plant seedlings. One with catclaw (*Acacia greggii*) reported the ability of seedling roots to grow from a shallow layer of moist soil through an air gap isolated with a double barrier of paraffin and beeswax and into very dry soil

below. They also observed that this dry lower soil layer eventually increased in moisture content after the roots had become established.

In the Kalahari Desert, well drillers must bore to great depths in very dry sand to reach water and observant drillers reported some of the deepest roots thus far recorded in the world at 68 m (Canadell et al. 1996). Even in sand, the annual precipitation of this desert area does not penetrate very deeply. Recently, a field experiment involving the application of deuterated water to shallow sand and roots of some Kalahari Desert species showed the deuterium label appearing in the deeper roots and also in the sand immediately adjacent to these deeper roots. These deeper roots were located at least half a meter below the wetting front associated with the deuterium labeling (E.-D. Schulze et al., personal communication). This experiment clearly indicates the potential for inverse hydraulic lift. Under other circumstances, lateral movement of water through roots should also occur if the appropriate Ψ_s exists.

The possible origins of hydraulic lift: why give up your water?

The origins of hydraulic lift in plants remain an open question and have been the topic of some speculation. In previous work, we have pondered the possible costs and benefits of hydraulic lift and the selective forces which may underlie its evolution and existence in apparently many, though not necessarily all, species (Richards and Caldwell 1987; Caldwell and Richards 1989; Dawson 1993, in press). Optimality theory (Givnish 1986) would suggest that if a plant is to pay a cost in terms of giving up water to the surrounding soils, and ultimately to evaporation and to neighboring plants, then there should be some benefit for this behavior. As discussed earlier in this review, hydraulic lift can facilitate transpiration by supplying water overnight to upper soil layers where it can be utilized the following day. Nutrient acquisition, root longevity and biogeochemical processes can all likely benefit from water lifted into upper, otherwise dry soil layers as discussed above. Alternatively, hydraulic lift may be largely an inevitable consequence of root membranes that do not have true rectification properties which have not yet evolved; this is analogous to stomates that cannot selectively admit CO_2 while preventing water vapor transfer.

Conclusions

An increasing number of studies are showing that hydraulic lift may be a general root system phenomenon, widespread both in different taxa and ecosystems. If active root systems span a suitable gradient in Ψ_s, hydraulic lift might be expected and considerable evidence now supports this. Mechanisms that provide true rectification (root barriers preventing reverse flow but at the same time allowing water uptake) have yet to be found. There are many implications of hydraulic lift, including facilitation of neighboring plants, nutrient acquisition, biogeochemical nutrient cycling processes, and root growth and persistence in otherwise dry soils. These indirect consequences of hydraulic lift are likely to be the most ecologically meaningful and may underlie its evolution in plants.

Progress is needed in understanding root properties that may regulate or inhibit reverse flow and when reverse flow should be expected in different taxa. The extent and magnitude of hydraulic lift in perennial and annual crop systems is not known, but if hydraulic lift is present it would have implications for irrigation, fertilization practices, and intercropping. Though challenging to design and conduct, field experimentation to probe the contribution of hydraulic lift in community- and ecosystem-level phenomena such as plant population dynamics (e.g., establishment), facilitation of neighboring species, ET, nutrient acquisition, and biogeochemical processes is needed.

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