

# Root water uptake and transport: using physiological processes in global predictions

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**Plant water loss, regulated by stomata and driven by atmospheric demand, cannot exceed the maximum steady-state supply through roots. Just as an electric circuit breaks when carrying excess current, the soil–plant continuum breaks if forced to transport water beyond its capacity. Exciting new molecular, biophysical and ecological research suggests that roots are the weakest link along this hydraulic flow path. We attempt here to predict rooting depth and water uptake using the hydraulic properties of plants and the soil, and also to suggest how new physiological tools might contribute to larger-scale studies of hydraulic lift, the water balance and biosphere–atmosphere interactions.**

Plants use water in biochemical reactions, as a solvent and to maintain turgor, but most of the water taken up by plants is transpired to the atmosphere. Globally, plants recycle more than half of the  $\sim 110\,000\text{ km}^3\text{ yr}^{-1}$  of precipitation that falls on land each year<sup>1</sup>. Transpired water moves from soil to plant to atmosphere along a continuum of increasingly negative water potential ( $\psi$ ), flowing ‘downhill’ thermodynamically but ‘uphill’ physically from root to shoot.

Plant water loss is a function of stomatal conductance and atmospheric demand but, to avoid desiccation, it also cannot exceed the maximum supply rate through roots. In theory, maximum steady-state supply rates can be predicted from field data and from transport models that incorporate soil porosity, profiles of soil moisture and root density, and the relationship between whole-plant hydraulic conductance ( $K$ ) and  $\psi$  (Ref. 2). In practice, such supply rates are difficult to estimate because of the challenges of sampling roots and the soil at depth, and of measuring *in situ* root activity. New advances are helping to integrate the above- and below-ground functioning of plants (e.g. determining hydraulic limitations along the entire plant flow path and signals that coordinate hydraulic supply<sup>3</sup>), and to understand biosphere–atmosphere interactions (e.g. feedbacks between vegetation and climate through water uptake, transpiration and latent heat fluxes<sup>4–6</sup>).

This article highlights recent progress in understanding the movement of water in the soil–plant–atmosphere continuum at a range of increasing scales. We emphasize root water uptake and transport as the gateway for plant water supply, complementing traditional emphases on shoot processes and stomatal

controls of water loss. We examine new molecular and physiological tools that should help to predict the quantity and depth of water use at larger scales, present a set of predictions for rooting depth that can be tested at scales from the individual site to the globe, and discuss potential links between plant biology and the physical sciences using new global datasets.

## Applying molecular tools to a global problem

Two recent applications of molecular biology should contribute to a better understanding of rooting depth and water transport: molecular studies of plant aquaporins<sup>7,8</sup> and the use of molecular tools for identifying and studying roots in the field<sup>9–11</sup>. Aquaporins are membrane water-channel proteins that facilitate water movement along a passive gradient in  $\psi$  (Ref. 8). In *Arabidopsis*, >30 genes code for aquaporin homologs and cells generally express several different aquaporins at a time. Although aquaporins are undoubtedly important for cytosolic osmoregulation, inhibition studies *in vivo* and studies with antisense mutants indicate that they are also important for bulk water flow.

*Arabidopsis* plants transformed with an antisense construct of the aquaporin *PIP1b* gene (one of a class of plasma membrane intrinsic proteins) had reduced steady-state levels of PIP1b, water permeability coefficients that were three times lower than in control plants and five times more root biomass than control plants to compensate for reduced aquaporin abundance (shoot biomass and morphology were unchanged)<sup>7</sup>. In studies with *Lotus japonicus*, root hydraulic conductivity varied fivefold during day–night cycles. When mRNAs from the roots were probed

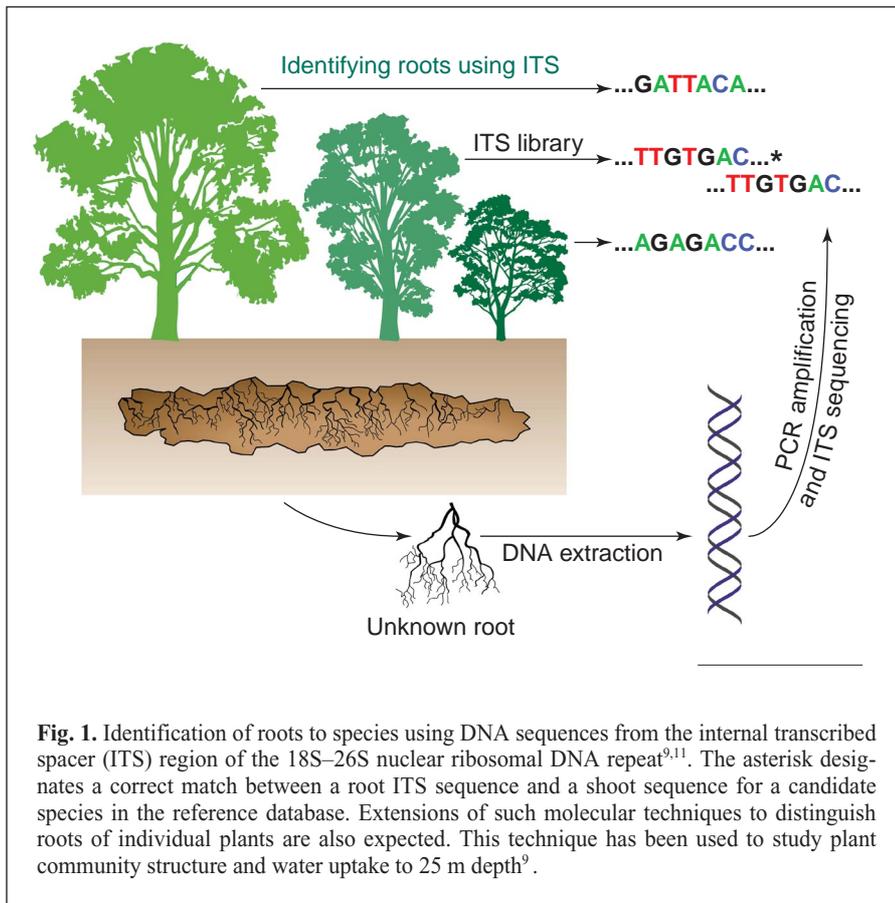
with cDNA from the *Arabidopsis* aquaporin *AthPIP1a* gene, an abundant transcript fluctuated in a pattern that closely resembled the diurnal variation in root hydraulic conductivity<sup>12</sup>. Studies of the importance of aquaporins for whole-plant water transport are needed, especially for woody plants, but it is clear that aquaporins help to orchestrate water movement within the plant and that they might determine the balance between apoplastic and symplastic (cell-to-cell) water movement. Many other potential roles remain untested (e.g. whether they facilitate embolism repair<sup>13</sup>).

A second application is a new ability to identify roots in the field using molecular tools<sup>9–11</sup>. Unlike shoots, which can easily be matched to a specific plant, roots growing in a community are difficult to identify at any taxonomic level, especially fine roots that take up water. A new method (Fig. 1) overcomes this long-standing limitation by using DNA sequence variation of the internal transcribed spacer (ITS), the 18S–26S nuclear ribosomal repeat. The ITS region can be amplified in all plants by using PCR and a set of universal primers<sup>14</sup>. It evolves fairly rapidly and therefore can be used to distinguish genera and, often, species. Such identifications are needed for *in situ* physiological studies and for determining belowground community structure and water uptake at depth<sup>9</sup>. GenBank now has >9000 ITS sequences online and is growing rapidly. Extensions of these techniques are also being made for fingerprinting roots (to distinguish individual plants within a community). Candidates include randomly amplified polymorphic DNA, inter-simple-sequence repeats and amplified fragment-length polymorphisms. Such molecular tools should be useful in determining the zone of water uptake for individual plants and species. They also open new possibilities for *in situ* studies of plant physiological and community processes.

## Hydraulic architecture and water flux in stems and roots

Stomata are the pressure regulators of the plant: they prevent xylem pressure and tissue water status from reaching damaging values by regulating water flow through the soil–plant continuum. For this reason, factors that influence the hydraulic conductance of the continuum (‘hydraulic architecture’) also influence stomatal conductance and transpiration. This is true regardless of the mechanism by which stomata sense water status, a subject of continued investigation involving the hormone abscisic acid (ABA) and other messengers<sup>15</sup>. Recent studies highlight the importance of xylem cavitation, xylem anatomy and the architecture of the root system in influencing leaf water supply and plant water use.

According to the cohesion–tension theory, capillary forces generated by evaporation



**Fig. 1.** Identification of roots to species using DNA sequences from the internal transcribed spacer (ITS) region of the 18S–26S nuclear ribosomal DNA repeat<sup>9,11</sup>. The asterisk designates a correct match between a root ITS sequence and a shoot sequence for a candidate species in the reference database. Extensions of such molecular techniques to distinguish roots of individual plants are also expected. This technique has been used to study plant community structure and water uptake to 25 m depth<sup>9</sup>.

from leaves move water from soil to root to leaf under increasingly negative pressures. However, because xylem water is under tension, conduits can cavitate (fill with air). Recent studies comparing the vulnerability of roots and shoots have shown that roots (especially small roots) are typically more vulnerable to cavitation<sup>16</sup>, suggesting that they might be the weakest link along the hydraulic flow path from soil to atmosphere.

In a study with *Acer grandidentatum*, not only were roots more vulnerable to cavitation at a given  $\psi$  than shoots but the safety margin at which they operated (the difference between minimum  $\psi$  observed in the field and the critical  $\psi$  that induces hydraulic failure via cavitation) was also smaller<sup>17</sup>. Consequently, extensive cavitation in roots during drought limited the gas exchange of shoots. In the same study, a comparison of roots and stems of individual *A. grandidentatum* trees at wet and dry sites showed greater resistance to cavitation in roots from the dry site but no change in vulnerability for stems. That is, roots were more vulnerable to cavitation than shoots and their cavitation responses were more plastic. A growing body of evidence suggests that root transport characteristics might often limit water transport and transpiration (see below).

Differences in anatomy between roots and shoots also affect water transport<sup>18</sup>. Water flow is proportional to the fourth power of the

radius of xylem conduits<sup>19</sup>. Flow is generally more efficient in longer conduits because water passes through fewer pit membranes, which restrict flow. Studies comparing xylem anatomy in roots and shoots have shown that roots typically have longer and larger conduits<sup>20</sup>. Although little is known about the hydraulic properties of deeper roots, recent data indicate that the gradient in anatomy from shoot to shallow roots extends further underground. The roots of *Banksia prionotes* at a depth of 2 m had larger xylem conduits, greater conduit length and higher area-specific  $K$  than shallow roots of the same plants<sup>21</sup>.

Direct measurements of water flow through roots with sap-flow gauges and other techniques open new avenues for understanding water uptake and redistribution at depth<sup>22,23</sup>. Sap-flow measurements of lateral and tap roots near the surface revealed that ~10–30% of spring water use in *B. prionotes* came from the taproot, with the contribution of shallow lateral roots increasing after rainfall<sup>24</sup>. In a different system, water transported from below 7 m contributed 24% of growing-season transpiration in *Juniperus ashei* (W.T. Pockman *et al.*, unpublished) (Fig. 2a). *In situ* measurements of water relations taken along the entire flow path diurnally and seasonally suggest that changes in  $K$  caused by cavitation might have altered water uptake among different portions of the *J. ashei* root system (Fig. 2b,c).

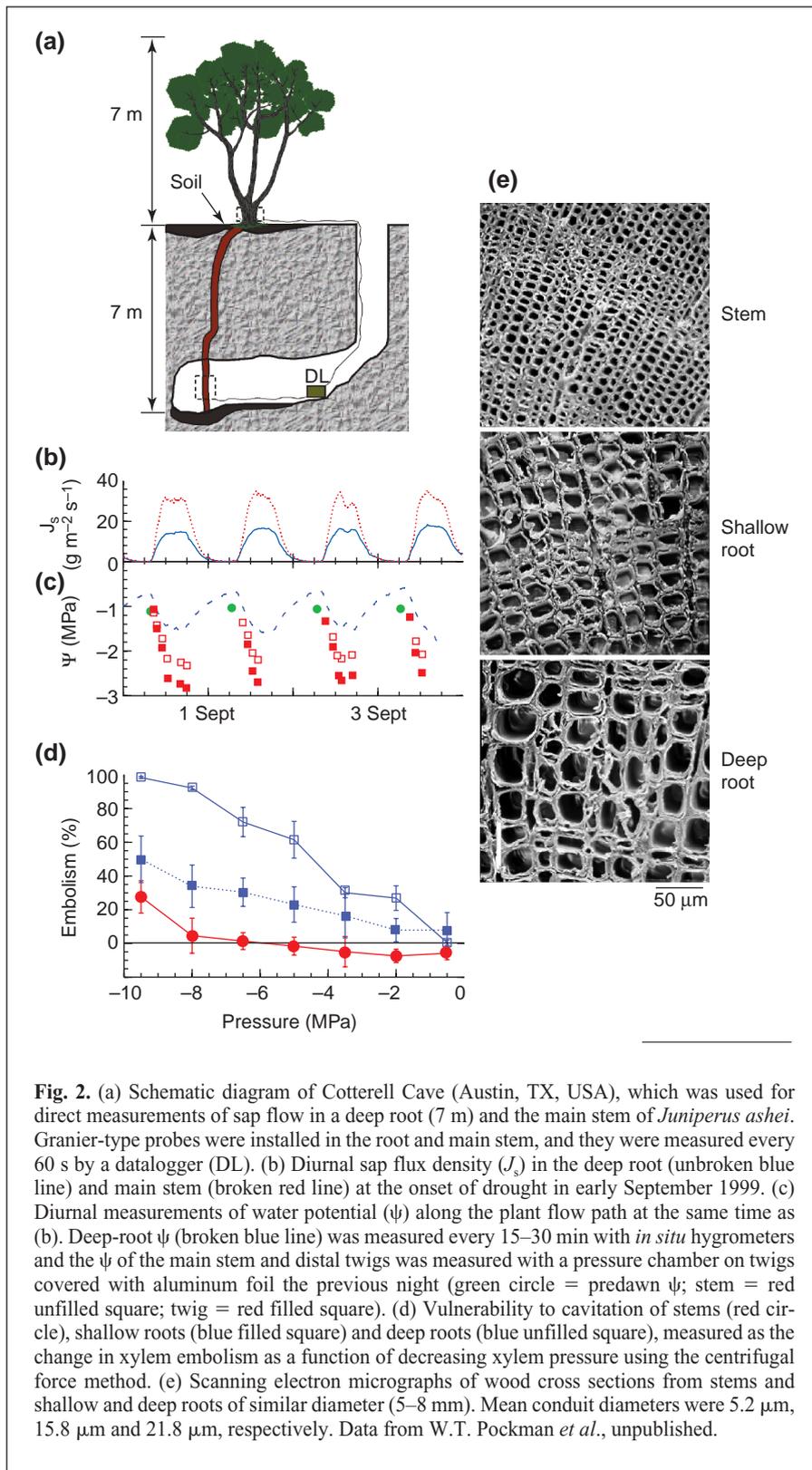
Roots from 7 m depth showed approximately one-third cavitation at  $-2$  MPa, but the same degree of cavitation did not occur until approximately  $-6$  MPa in shallow roots and  $-10$  MPa in shoots (Fig. 2d). Differences in vulnerability to cavitation were accompanied by gradients in xylem tracheid diameters. Mean conduit diameters were more than four times as large in deep roots as in stems of similar size and were intermediate in shallow roots (Fig. 2e). Such studies illustrate the contribution that deep roots can make to whole-plant water use and highlight the need to integrate physiological limits along the entire plant flow path. The results also emphasize the importance of root hydraulic architecture for water uptake at a range of depths.

### Linking plant, soil and climate using transport models

In the same way that the specifications of an electronic device must match those of the incoming current for optimal performance, the hydraulic properties of a plant should be compatible with the soil properties to optimize water use and resource allocation<sup>2,25</sup>. Process models of the soil–plant–atmosphere continuum can integrate plant architectural and hydraulic properties with soil properties to predict these optimal combinations and the actual water use for various plant functional types and soils<sup>4</sup>.

We illustrate this approach here, using a model that is unusual because it incorporates variable  $K$  properties within both plant and soil<sup>25,26</sup>. At each time step, the model determines the gradient in  $\psi$  along the flow path from bulk soil to leaves and  $\psi$ -dependent changes in  $K$ . We apply the model to plant functional types defined by variation in two traits: (1) whole-plant  $K$  for plants that are relatively sensitive, intermediate or insensitive to  $\psi$  (Fig. 3a); and (2) rooting depth from shallow to medium to deep profiles<sup>27</sup> (Fig. 3b). The sensitivity of  $K$  to  $\psi$  is in part determined by cavitation resistance in xylem but might also be affected by changes in non-xylary tissues with drought<sup>28</sup>. This model was also run using progressively drier soil moisture profiles (Fig. 3c), which are represented by  $\psi$  at 50 cm depth (Fig. 3c, broken line, and x axes of Fig. 3d–g).

The model's output includes a steady-state water use 'envelope' (Fig. 3d–g) that reflects the maximum carrying capacity of the soil–leaf continuum. Just as an electric circuit will break when carrying excessive current, the soil–plant continuum will break if forced to transport water beyond its ability. The break occurs when an overly negative  $\psi$  eliminates hydraulic conductance in the flow path. The plant's stomata must regulate water loss to stay within this limiting envelope or water loss will exceed supply and foliage will desiccate.



**Fig. 2.** (a) Schematic diagram of Cotterell Cave (Austin, TX, USA), which was used for direct measurements of sap flow in a deep root (7 m) and the main stem of *Juniperus ashei*. Granier-type probes were installed in the root and main stem, and they were measured every 60 s by a datalogger (DL). (b) Diurnal sap flux density ( $J_s$ ) in the deep root (unbroken blue line) and main stem (broken red line) at the onset of drought in early September 1999. (c) Diurnal measurements of water potential ( $\psi$ ) along the plant flow path at the same time as (b). Deep-root  $\psi$  (broken blue line) was measured every 15–30 min with *in situ* hygrometers and the  $\psi$  of the main stem and distal twigs was measured with a pressure chamber on twigs covered with aluminum foil the previous night (green circle = predawn  $\psi$ ; stem = red unfilled square; twig = red filled square). (d) Vulnerability to cavitation of stems (red circle), shallow roots (blue filled square) and deep roots (blue unfilled square), measured as the change in xylem embolism as a function of decreasing xylem pressure using the centrifugal force method. (e) Scanning electron micrographs of wood cross sections from stems and shallow and deep roots of similar diameter (5–8 mm). Mean conduit diameters were 5.2  $\mu\text{m}$ , 15.8  $\mu\text{m}$  and 21.8  $\mu\text{m}$ , respectively. Data from W.T. Pockman *et al.*, unpublished.

relatively coarse soils should have more sensitive plant conductance curves regardless of soil moisture regime, and plants of finer soils and drier habitats should have relatively insensitive conductance curves. Both trends have been observed<sup>2</sup>.

The interaction of rooting depth and soil texture on maximum water use (Fig. 3f,g) leads to additional predictions. Deeper root systems increase the water-extraction capability regardless of soil type (analogous to the ‘deeper bucket’ of land-surface models). The effect is more pronounced in coarse soils (Fig. 3f,g) because the drying surface layers of a coarse soil yield their water at higher (less negative)  $\psi$  and roots must go deeper to find water during drought. This result suggests that, for habitats with prominent drying of the surface soil, plants growing in coarser soils should have deeper rooting profiles than similar plants growing in finer soils. This difference might be enhanced if plants in fine-textured soils also have relatively insensitive plant conductance curves, as predicted, because such curves duplicate some of the benefits of deep roots for water extraction (e.g. compare Fig. 3e with g).

The prediction that there are deeper root profiles in coarse than in fine soils was tested using a global root database<sup>27,30</sup> for water-limited systems. The depth that captured 95% of root biomass in deserts and arid shrublands was 1.06  $\pm$  0.15 m on clay and loam soils and 1.90  $\pm$  0.53 m on sandy soils ( $n = 17$  and 12, respectively;  $p = 0.08$ ). For dry tropical savannas, the average 95% rooting depth was 1.05  $\pm$  0.19 m on clay and loam soils and 1.67  $\pm$  0.19 m on sandy soils ( $n = 11$  and 12, respectively;  $p = 0.035$ ; H.J. Schenk and R.B. Jackson, unpublished).

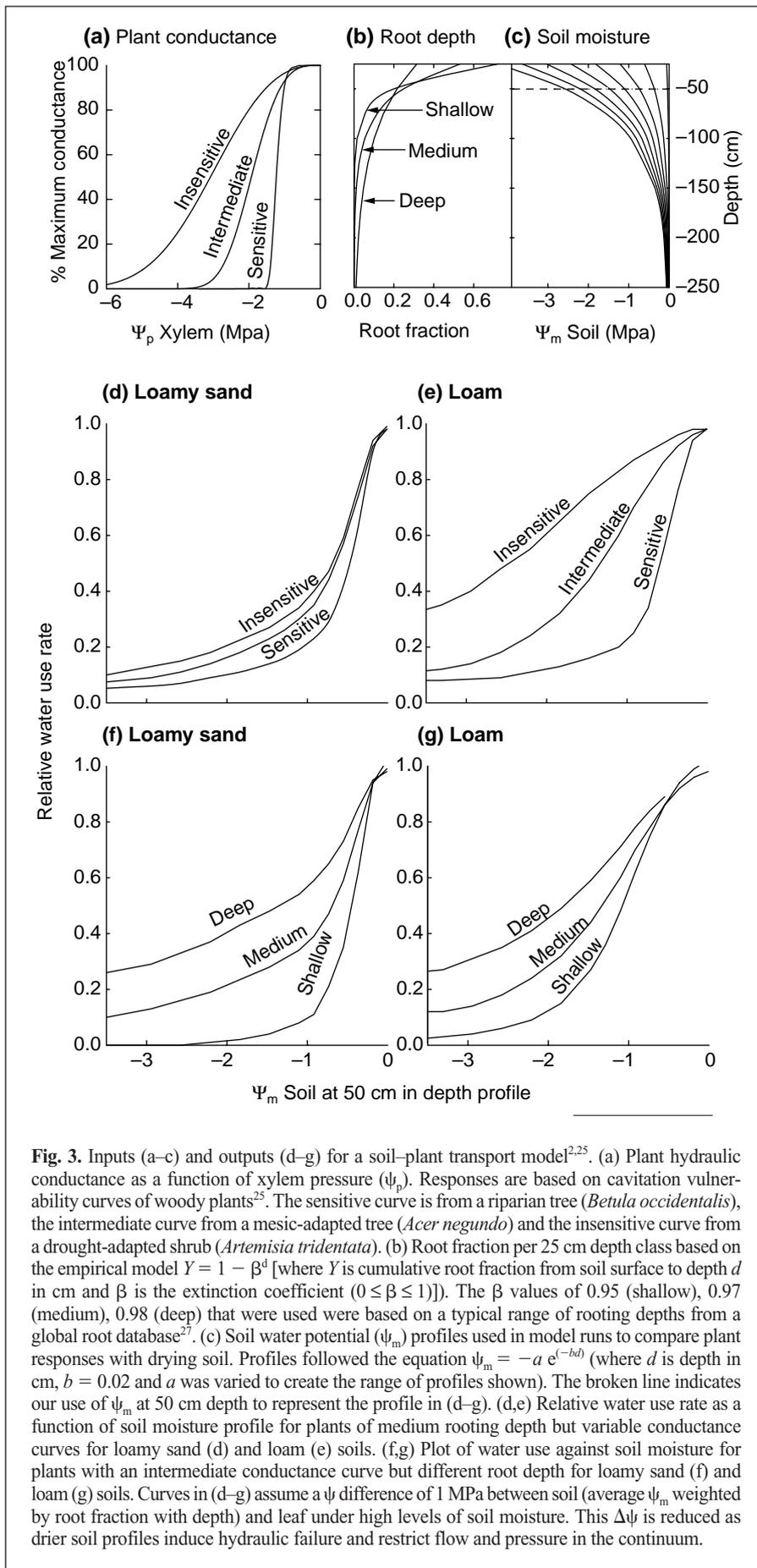
For simplicity, the influence of plant allocation in Figure 3 is not shown. If there are too few roots relative to leaves then this causes critically steep rhizosphere gradients in  $\psi$ , causing hydraulic failure and reducing water uptake capacity<sup>25</sup>. A threshold ratio of root area to leaf area shifts hydraulic failure from the rhizosphere to the plant and maximizes water extraction from a drying soil<sup>25,26</sup>. This threshold is greater in a coarse than in a fine soil, suggesting a corresponding gradient in root area to leaf area ratio across soil textures, as has been shown for *Pinus taeda*<sup>2</sup>.

The fact that root xylem can be much more vulnerable to cavitation at a given  $\psi$  than stem xylem means that roots might be the point of failure during drought. Smaller roots might operate as a ‘hydraulic fuse’, localizing failure to relatively cheap and replaceable units compared with tap roots, stems and branches<sup>31</sup>. Localized failure in small, shallow roots would direct water uptake to deeper layers during drought without disrupting major arteries of axial transport. Once drought ends, conductance in undamaged roots could be

The water-use envelope provides a mechanistic definition of the permanent wilting point and available soil water as determined by plant and soil properties.

Examining the interaction of plant conductance and soil texture (Fig. 3d,e) shows that, in finer soils, there is a large benefit for

water availability of less sensitive (‘insensitive’) plant conductance as the soil dries (Fig. 3e). Interestingly, this advantage diminishes in coarser soils (Fig. 3d) because the loss of soil conductivity with drying is more severe – soil rather than plant  $K$  limits water uptake<sup>29</sup>. We predict that plants growing on



**Fig. 3.** Inputs (a–c) and outputs (d–g) for a soil–plant transport model<sup>2,25</sup>. (a) Plant hydraulic conductance as a function of xylem pressure ( $\Psi_p$ ). Responses are based on cavitation vulnerability curves of woody plants<sup>25</sup>. The sensitive curve is from a riparian tree (*Betula occidentalis*), the intermediate curve from a mesic-adapted tree (*Acer negundo*) and the insensitive curve from a drought-adapted shrub (*Artemisia tridentata*). (b) Root fraction per 25 cm depth class based on the empirical model  $Y = 1 - \beta^d$  [where  $Y$  is cumulative root fraction from soil surface to depth  $d$  in cm and  $\beta$  is the extinction coefficient ( $0 \leq \beta \leq 1$ )]. The  $\beta$  values of 0.95 (shallow), 0.97 (medium), 0.98 (deep) that were used were based on a typical range of rooting depths from a global root database<sup>27</sup>. (c) Soil water potential ( $\Psi_m$ ) profiles used in model runs to compare plant responses with drying soil. Profiles followed the equation  $\Psi_m = -a e^{(-bd)}$  (where  $d$  is depth in cm,  $b = 0.02$  and  $a$  was varied to create the range of profiles shown). The broken line indicates our use of  $\Psi_m$  at 50 cm depth to represent the profile in (d–g). (d,e) Relative water use rate as a function of soil moisture profile for plants of medium rooting depth but variable conductance curves for loamy sand (d) and loam (e) soils. (f,g) Plot of water use against soil moisture for plants with an intermediate conductance curve but different root depth for loamy sand (f) and loam (g) soils. Curves in (d–g) assume a  $\Psi$  difference of 1 MPa between soil (average  $\Psi_m$  weighted by root fraction with depth) and leaf under high levels of soil moisture. This  $\Delta\Psi$  is reduced as drier soil profiles induce hydraulic failure and restrict flow and pressure in the continuum.

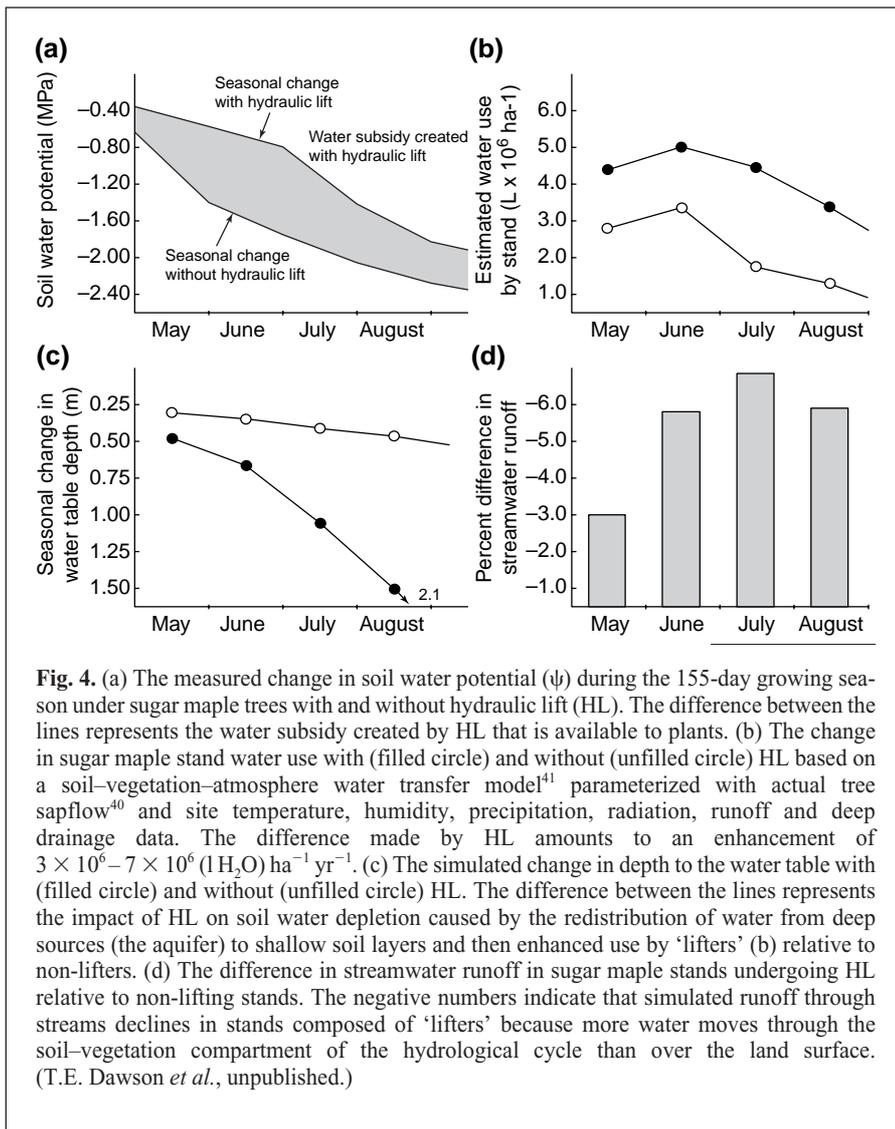
restored by cavitation reversal<sup>32</sup>, with aquaporins playing a potential role. New small roots could also be readily regrown. An analogous situation has been identified for shoots, in which leaf xylem is more vulnerable to cavitation than stem xylem<sup>33</sup>.

By integrating the influences of  $K$ , rooting depth and allocation, a process-modeling approach provides a set of testable hypotheses for how much root properties affect plant water use across gradients in soil texture and  $\Psi$ . Under a similar soil  $\Psi$  regime, a shift to deeper and denser root systems is likely in coarser soils because these soils amplify the effects of water stress. Conversely, increased rooting depth and density should be less important in finer-textured soils. Wetter soil profiles during the growing season would tend to reduce differences between soil types, as indicated by the convergence of water use curves at high soil  $\Psi$  (Fig. 3). Hydraulic lift (HL) might have similar consequences by mitigating surface soil drying, shifting plants higher on their water use curves and improving gas exchange. Scaling this type of model to analyse competitive interactions among plants and linking it to larger-scale meteorological and hydrological models might also help to close the water cycle<sup>4</sup>. Such models can be important tools for predicting plant water use with changing vegetation and land use.

#### Hydraulic lift and the consequences of soil water redistribution

Plants with dimorphic root distributions (e.g. shallow lateral and deep tap roots) influence soil water distributions in novel ways. One current research focus is the importance of HL (Ref. 34), which is the passive movement of water through roots from wetter, deeper soil layers into drier, shallower layers along a gradient in  $\Psi$  (Refs 34,35). HL redistributes water to shallow soil layers with higher root densities, where it can then be taken up again, enhancing transpiration by both the ‘lifter’ and its neighbors<sup>36</sup>. Recently, reverse HL has also been shown to occur. This is the downward flux of soil water through roots when upper layers have a higher  $\Psi$  and is sometimes called ‘hydraulic redistribution’<sup>23,37</sup>. HL has now been demonstrated in nearly 50 plant species, with more than 20 new reports in the past few years. Most of these new examples are from species in Mediterranean climates but they also come from arid and cool temperate regions, and from seasonally dry tropical and subtropical habitats.

Studies are under way to measure the effects of HL on the water balance. The effects of HL by sugar maple (*Acer saccharum*) on stand and regional water use by northeastern deciduous forests in the USA are being studied using measurements of whole-tree water use<sup>38,39</sup> and a soil–vegetation–atmosphere water



**Fig. 4.** (a) The measured change in soil water potential ( $\psi$ ) during the 155-day growing season under sugar maple trees with and without hydraulic lift (HL). The difference between the lines represents the water subsidy created by HL that is available to plants. (b) The change in sugar maple stand water use with (filled circle) and without (unfilled circle) HL based on a soil–vegetation–atmosphere water transfer model<sup>41</sup> parameterized with actual tree sapflow<sup>40</sup> and site temperature, humidity, precipitation, radiation, runoff and deep drainage data. The difference made by HL amounts to an enhancement of  $3 \times 10^6 - 7 \times 10^6$  (l H<sub>2</sub>O) ha<sup>-1</sup> yr<sup>-1</sup>. (c) The simulated change in depth to the water table with (filled circle) and without (unfilled circle) HL. The difference between the lines represents the impact of HL on soil water depletion caused by the redistribution of water from deep sources (the aquifer) to shallow soil layers and then enhanced use by ‘lifters’ (b) relative to non-lifters. (d) The difference in streamwater runoff in sugar maple stands undergoing HL relative to non-lifting stands. The negative numbers indicate that simulated runoff through streams declines in stands composed of ‘lifters’ because more water moves through the soil–vegetation compartment of the hydrological cycle than over the land surface. (T.E. Dawson *et al.*, unpublished.)

transfer model<sup>40</sup>. The soil compartment of the model is modified to refill the upper soil horizon from deeper water (in this case, ground water) on a daily basis (see Ref. 41 for a similar approach applied at a larger scale). The magnitude of refilling is estimated from field measurements of soil  $\psi$ , soil properties and the size distribution of trees. In many northeastern forests, >60% of all the trees in the stand are sugar maple. Furthermore, large trees transpire 350–600 l day<sup>-1</sup> and can ‘lift’ 100 l of water into the rhizosphere each night throughout much of the growing season<sup>38</sup>. Small trees lack access to deeper ground water and do not redistribute much water.

Simulations indicate that HL has the potential to influence the rate and magnitude of water use by plants and might change the hydrological cycle of the forest (Fig. 4). Annual water use by sugar maple forests is 19–40% greater than that of forests without lifters, in which soil  $\psi$  declines steadily (Fig. 4a) and water stress ensues. This is an annual enhancement of  $3 \times 10^6 - 7 \times 10^6$  l ha<sup>-1</sup>

(Fig. 4b). Because the lifted water in this simulation comes from an aquifer, the water table declines an estimated 16–33% (Fig. 4c). In addition, because more water moves through the vegetation, the model predicts that 3–6% less water per month is available to streams, particularly when forest water use and leaf area peak (e.g. July; Fig. 4d).

These simulations show how the water subsidy created by HL, a root-level phenomenon, can influence the hydrology of the stand or region. Model outputs also suggest that, as sugar maple has grown more abundant in the northeastern USA (with the abandonment of agriculture and the onset of chestnut blight), the region’s hydrological cycle might also have changed through greater transpiration. The difference in forest hydrology is largely driven by the pattern and unique functioning of sugar maple roots and suggests that plant rooting strategies might influence hydrology directly.

HL has also been modeled using gradients in soil  $\psi$ , the vertical distribution of active roots and the root–soil conductance for water

(R.J. Ryel and M.M. Caldwell, unpublished). These simulations for a shrub–grassland steppe suggest that most vertical soil water movement during the growing season occurs through roots, not through soil capillary flow. This vertical redistribution extends the period of water use by plants in the system.

Such simulations highlight the potential importance of HL for ecosystems and for the water balance, but they need confirmation in the field. Future research will examine how hydraulic properties of the soil–plant system interact with HL. For example, transport models such as those outlined in the previous section could be combined with landscape models that explicitly incorporate HL to predict where on the water-use curve a ‘lifter’ operates and what role species differences play across the landscape. Moreover, locally derived information of rooting patterns and root functioning could be combined more fully with global databases for scaling plant physiology to catchment, landscape and regional levels.

**Think globally, act locally: opportunities for scaling the physiology of water uptake**

Models provide a useful tool for linking root water uptake and transport with larger-scale processes<sup>4,42</sup>. In the recent Project for Intercomparison of Land Surface Parameterization Schemes (PILPS), rooting depth and vertical soil characteristics were the most important factors explaining scatter for simulated transpiration in 14 land-surface models<sup>43</sup>. Three approaches for calculating root water uptake are typically used in such models<sup>42,43</sup>: (1) the minimum of a demand and a soil water supply function; (2) a derivative of an Ohm’s law model that calculates soil moisture effects on canopy resistance; or (3) a direct function of soil moisture availability. Models that do not calculate transpiration rates often use rooting depth to set an upper limit on the amount of soil water available for total evapotranspiration. Such models vary in the degree of ‘physiology’ they include.

New gridded, spatially explicit root and soil databases (Table 1, Fig. 5) should be useful in examining controls on plant water uptake at regional and global scales and for testing predictions such as those made above. Two such databases (Table 1) include >20 000 soil profiles [the US Dept of Agriculture (USDA)] and selected physical and chemical data for >4350 soil profiles [International Soil Reference and Information Centre (ISRIC)]. The three other databases in Table 1 translate soil maps and soil classification data into physical and hydrological properties, including global estimates of water holding capacity: the International Geosphere Biosphere Programme’s global soil database, the HYPRES dataset for European

**Table 1. Database names, number of soil profiles, and contact and website information for five global soil databases**

Database/institution	No. of profiles	Contact	Website
Amazonia, Embrapa (Brasil)	1153	D. Nepstad dnepstad@whrc.org	www.whrc.org/science/tropfor/LBA/WHRCsoilpr01.htm
HYPRES, European Community	1100	A. Lilly a.lilly@mluri.sari.ac.uk	www.mluri.sari.ac.uk/hypres.htm
IGBP Data and Information Services	Variable	R. Olson rjo@ornl.gov	www.daac.ornl.gov
NSCD, US Dept of Agriculture	>21 000	E. Benham ellis.benham@nssc.nrcs.usda.gov	www.statlab.iastate.edu/soils/ssl/natch_data.html
WISE, ISRIC	>4350	N.H. Batjes batjes@isric.nl	www.isric.nl/WISE.htm

Abbreviations: HYPRES, Hydraulic Properties of European Soils; IGBP, International Geosphere Biosphere Programme; ISRIC, International Soil Reference and Information Centre; NSCD, National Soil Characterization Database; WISE, World Inventory of Soil Emission potentials.

soils and the Amazonia database for mapping plant-available water and rooting depth. Additional work is also under way to create gridded, spatially explicit root datasets<sup>27,30</sup> (Fig. 5). When matched to the scale of the soil databases (e.g.  $0.5 \times 0.5^\circ$  grid squares), the combined datasets can be used in general circulation models to test climatic, edaphic and plant controls on water fluxes<sup>4,41,42</sup>, and to predict some of the consequences of vegetation and land-use change<sup>5,42</sup>.

Soil moisture and root water uptake influence water and energy fluxes, including the parti-

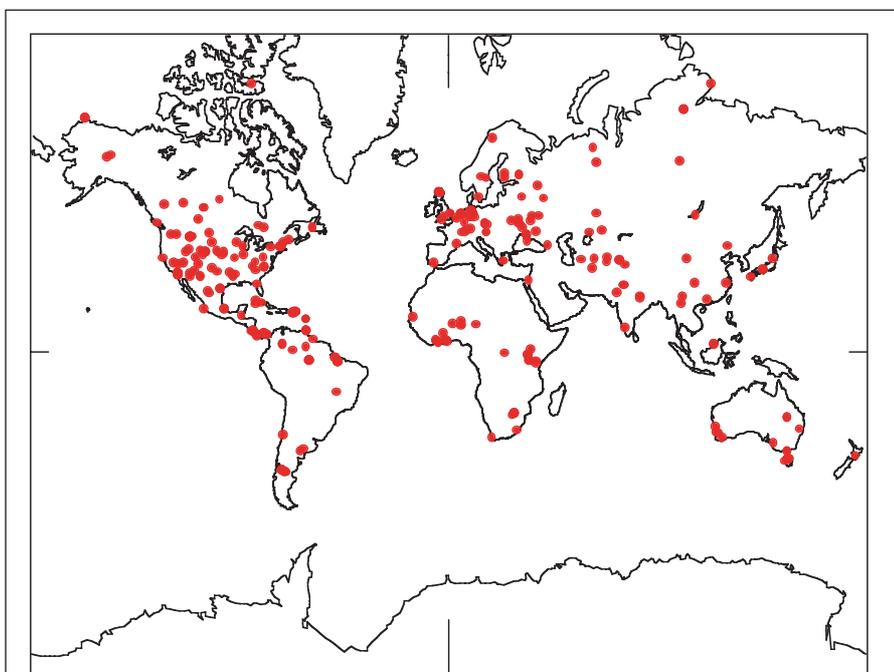
tioning of evaporation and runoff, and sensible and latent heat fluxes. Large-scale field studies increasingly demonstrate such interactions. In eastern Amazonia, water from 2–8 m soil depths contributed more than three-quarters of the transpiration of evergreen forest in the dry season and helped to maintain an evergreen canopy on  $>1\,000\,000\text{ km}^2$  of tropical forest<sup>44</sup>. Sap-flux and eddy-flux techniques have been combined with stable-isotope analyses to estimate the quantity and source of water evaporated from plants and the soil (e.g. using  $^{18}\text{O}$  or  $^2\text{H}$  signatures)<sup>45</sup>. Field- and satellite-

derived data can be used to scale photosynthesis and transpiration regionally and globally<sup>46</sup>. Direct measurements of root water uptake and transport supplement such approaches with information about the controls of water uptake, the consequences of underground plant competition and the depth from which water uptake occurs.

Our focus here on root water uptake and transport as the starting point of the plant water supply complements traditional studies of shoot physiology and stomatal controls on water loss. As tools for laboratory and *in situ* studies of root physiology improve, the ability to integrate all portions of the plant flow path should yield important physiological insights and improved mechanistic understanding of plant–water relations. Studying key genes for whole-plant water transport (e.g. those involved in aquaporin function or root development) will be an important step, especially for woody plants. At larger scales, determining the ecosystem consequences of whole-plant processes such as HL will also be important. Physiological information can be more broadly applied in predictions of ecosystem processes, the water balance and biosphere–atmosphere interactions. Further progress in understanding water movement along the soil–plant–atmosphere continuum should be accomplished by integrating new approaches at scales from molecules to the globe.

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**Fig. 5.** The location of 512 root profiles from 279 geographic locations in a global root database<sup>27,30</sup>. Where available, information on soil properties such as the texture and depth of the humus layer is included, as are data on vegetation type. (H.J. Schenk and R.B. Jackson, unpublished.)

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## References

- 1 Chahine, M.T. (1992) The hydrological cycle and its influence on climate. *Nature* 359, 373–380
- 2 Hacke, U.G. *et al.* (2000) Influence of soil porosity on water use in *Pinus taeda*. *Oecologia* 124, 495–505
- 3 McDonald, A.J.S. and Davies, W.J. (1996) Keeping in touch: responses of the whole plant to deficits in water and nitrogen supply. *Adv. Bot. Res.* 22, 229–300
- 4 de Rosnay, P. and Polcher, J. (1998) Modelling root water uptake in a complex land surface scheme coupled to a GCM. *Hydrol. Earth Syst. Sci.* 2, 239–255
- 5 Foley, J.A. *et al.* (1998) Coupling dynamic models of climate and vegetation. *Global Change Biol.* 4, 561–579
- 6 Hoffmann, W.A. and Jackson, R.B. (2000) Vegetation–climate feedbacks in the conversion of tropical savanna to grassland. *J. Clim.* 13, 1593–1602
- 7 Kaldenhoff, R. *et al.* (1998) Significance of plasmalemma aquaporins for water transport in *Arabidopsis thaliana*. *Plant J.* 14, 121–128
- 8 Kjellbom, P. *et al.* (1999) Aquaporins and water homeostasis in plants. *Trends Plant Sci.* 4, 308–314
- 9 Jackson, R.B. *et al.* (1999) Ecosystem rooting depth determined with caves and DNA. *Proc. Natl. Acad. Sci. U. S. A.* 96, 11387–11392
- 10 Bobowski, B.R. *et al.* (1999) Identification of roots of woody species using polymerase chain reaction (PCR) and restriction fragment length polymorphism (RFLP) analysis. *Mol. Ecol.* 8, 485–491
- 11 Linder, C.R. *et al.* A universal molecular method for identifying underground plant parts to species. *Mol. Ecol.* (in press)
- 12 Henzler, T. *et al.* (1999) Diurnal variations in hydraulic conductivity and root pressure can be correlated with the expression of putative aquaporins in the roots of *Lotus japonicus*. *Planta* 210, 50–60
- 13 Netting, A.G. (2000) pH, abscisic acid and the integration of metabolism in plants under stressed and non-stressed conditions: cellular responses to stress and their implication for plant water relations. *J. Exp. Bot.* 51, 147–158
- 14 Baldwin, B.G. *et al.* (1995) The ITS region of nuclear ribosomal DNA: a valuable source of evidence on angiosperm phylogeny. *Ann. MO Bot. Gard.* 82, 247–277
- 15 McDonald, A.J.S. and Davies W.J. (1996) Keeping in touch: responses of the whole plant to deficits in water and nitrogen supply. *Adv. Bot. Res.* 22, 229–300
- 16 Hacke, U. and Sauter, J.J. (1996) Drought-induced xylem dysfunction in petioles, branches and roots of *Populus balsamifera* and *Alnus glutinosa* (L.) Gaertn. *Plant Physiol.* 111, 413–417
- 17 Alder, N.N. *et al.* (1996) Root and stem xylem embolism, stomatal conductance and leaf turgor in *Acer grandidentatum* populations along a soil moisture gradient. *Oecologia* 105, 293–301
- 18 Steudle, E. and Peterson, C.A. (1998) How does water get through roots? *J. Exp. Bot.* 49, 775–788
- 19 Tyree, M.T. and Ewers, F.W. (1991) Tansley Review No. 34. The hydraulic architecture of trees and other woody plants. *New Phytol.* 119, 345–360
- 20 Ewers, F.W. *et al.* (1997) Vessel diameters in roots versus stems of tropical lianas and other growth forms. *Int. Assoc. Wood Anatomists J.* 18, 261–279
- 21 Pate, J.S. *et al.* (1995) Hydraulic architecture and xylem structure of the dimorphic root systems of southwest Australian species of the Proteaceae. *J. Exp. Bot.* 46, 907–915
- 22 Lott, J.E. *et al.* (1996) Sap flow measurements of lateral tree roots in agroforestry systems. *Tree Physiol.* 16, 995–1001
- 23 Burgess, S.S.O. *et al.* (1998) The redistribution of soil water by tree root systems. *Oecologia* 115, 306–311
- 24 Burgess, S.S.O. *et al.* (2000) Seasonal water acquisition and redistribution in the Australian woody phreatophyte, *Banksia prionotes*. *Ann. Bot.* 85, 215–224
- 25 Sperry, J.S. *et al.* (1998) Limitation of plant water use by rhizosphere and xylem conductance: results from a model. *Plant Cell Environ.* 21, 347–359
- 26 Ewers, B.E. *et al.* Influence of nutrient *versus* water supply on hydraulic architecture and water balance in *Pinus taeda*. *Plant Cell Environ.* (in press)
- 27 Jackson, R.B. *et al.* (1996) A global analysis of root distributions for terrestrial biomes. *Oecologia* 108, 389–411
- 28 Nobel, P.S. and North, G.B. (1993) Rectifier-like behaviour of root-soil systems: new insights from desert succulents. In *Water Deficits* (Smith, J.A.C. and Griffiths, H., eds), pp. 163–176, Bios, Oxford, UK
- 29 Bristow, K.L. *et al.* (1984) The effects of texture on the resistance to water movement within the rhizosphere. *Soil Sci. Soc. Am. J.* 48, 266–270
- 30 Jackson, R.B. *et al.* (1997) A global budget for fine root biomass, surface area and nutrient contents. *Proc. Natl. Acad. Sci. U. S. A.* 94, 7362–7366
- 31 Zimmerman, M.H. (1983) *Xylem Structure and the Ascent of Sap*, Springer-Verlag
- 32 Zwieniecki, M.A. and Holbrook, N.M. (2000) Bordered pit structure and vessel wall surface properties: implications for embolism repair. *Plant Physiol.* 123, 1015–1020
- 33 Tyree, M.T. *et al.* (1993) Drought induced leaf shedding in walnut: evidence for vulnerability segmentation. *Plant Cell Environ.* 16, 879–882
- 34 Caldwell, M.M. *et al.* (1998) Hydraulic lift: consequences of water efflux from the roots of plants. *Oecologia* 113, 151–161
- 35 Horton, J.L. and Hart, S.C. (1998) Hydraulic lift: a potentially important ecosystem process. *Trends Ecol. Evol.* 13, 232–235
- 36 Dawson, T.E. (1993) Hydraulic lift and water use by plants: implications for water balance, performance and plant–plant interactions. *Oecologia* 95, 565–574
- 37 Schulze, E-D. *et al.* (1998) Downward flux of water through roots (i.e. inverse hydraulic lift) in dry Kalahari sands. *Oecologia* 115, 460–462
- 38 Emerman, S.H. and Dawson, T.E. (1996) Hydraulic lift and its influence on the water content of the rhizosphere: an example from sugar maple, *Acer saccharum*. *Oecologia* 108, 273–278
- 39 Dawson, T.E. (1996) Determining water use by trees and forests from isotopic, energy balance and transpiration analyses: the role of tree size and hydraulic lift. *Tree Physiol.* 16, 263–272
- 40 Vertessy, R.A. *et al.* (1993) Predicting water yield from a mountain ash forest using a terrain-based catchment model. *J. Hydrol.* 150, 665–700
- 41 Kleidon, A. and Heimann, M. (1998) A method of determining rooting depth from a terrestrial biosphere model and its impacts on the global water and carbon cycles. *Global Change Biol.* 4, 275–286
- 42 Jackson, R.B. *et al.* (2000) Belowground consequences of vegetation change and their treatment in models. *Ecol. Applic.* 10, 470–483
- 43 Mahfouf, J-F. *et al.* (1996) Analysis of transpiration results from the RICE and PILPS workshop. *Glob. Planet. Change* 13, 73–88
- 44 Nepstad, D.C. *et al.* (1994) The role of deep roots in the hydrological and carbon cycles of Amazonian forests and pastures. *Nature* 372, 666–669
- 45 Ehleringer, J.R. *et al.* (2000) Assessing ecosystem-level water relations through stable isotope ratio analyses. In *Methods in Ecosystem Science* (Sala, O.E. *et al.*, eds), pp. 181–198, Springer
- 46 Myneni, R.B. *et al.* (1996) Satellite-based identification of linked vegetation index and sea surface temperature anomaly areas from 1982–1990 for Africa, Australia and South America. *Geophys. Res. Lett.* 23, 729–732

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