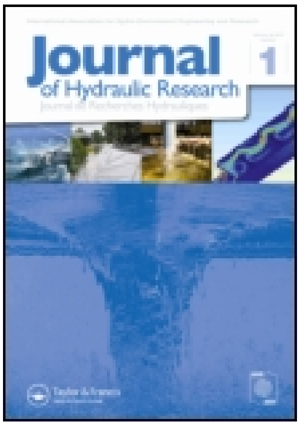

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Hydraulic determinism as a constraint on the evolution of organisms and ecosystems

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Vision paper

Hydraulic determinism as a constraint on the evolution of organisms and ecosystems

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ABSTRACT

The interaction between plant hydraulics and plant structure was documented by Leonardo da Vinci, and its importance as a regulator of vegetation and ecosystem function remains of vital contemporary interest. It is proposed that hydraulics deterministically influence plant structure and function. This vision paper explores some aspects of the role of hydraulics in plant function, with a focus on the regulation of plant stomata and xylem water potentials, the morphology of branching networks in vines and trees, and the spatial organization of vegetation at landscape scales. Outstanding challenges include mechanistic and boundary condition descriptions of specific processes, the need to accommodate multiple spatial and temporal scales that do not lend themselves to statistical treatment and the self-referential nature of Darwinian evolution itself.

Keywords: Biological fluid dynamics; flow–biota interactions; overland flows; shallow flows; vegetation

1 Introduction

Merging observations, theory and experiments to provide engineering solutions and to explain natural phenomena is a defining hallmark of hydraulics. Inspiration from the natural world has generated a long history of hydraulic insights, leading to new fundamental understanding of hydraulic phenomena, as well as shedding new light on issues outside the traditional scope of hydraulics. Poiseuille's law, a fundamental descriptor of viscous laminar flow, was experimentally determined in the context of human physiology, as Jean Léonard Marie Poiseuille attempted to understand capillary circulation (Herrick 1942). A universally known name in hydraulics, Poiseuille, is also familiar to biologists and the medical community. His work on the effects of viscosity (in terms of the flow properties of different liquids in narrow tubes) appears to have been motivated by consideration of how medication might alter blood flow (Sutera and Skalak 1993). The need to quantitatively describe the human circulatory system also motivated Leonard Euler and Daniel Bernoulli's experiments that lead to the derivation of Bernoulli's law for flow energetics (Mikhailov 1999); and inspired the initial study of optimization of flow networks (Murray 1926, Section 2.2). As appreciation of the role of fluid flow in ecology, zoology and plant ecology increases, there are emerging opportunities for fruitful cross-fertilizations between classical hydraulics and its application in the life sciences. This paper aims to illustrate progress and opportunities in this area.

Like Poiseuille, another intellectual leader in hydraulics – Leonardo da Vinci – drew inspiration and insight from observations of the natural world, ranging from the morphology of streams to variations in plant form. In an insightful application of the continuity equation to flow networks, da Vinci stated that: "All the branches of a water [course] at every stage of its course, if they are of equal rapidity, are equal to the body of the main stream". Applying this insight to vegetation, he noted that "branches of a tree at every stage of its height, when put together, are equal in thickness to the trunk below them" (Richter 1970). The da Vinci relationship is one of the first attempts to link aspects of plant structure to the biological functions of the plant, and underpins contemporary pipe-flow models of tree hydraulics.

Understanding the intersection between plant structure and hydraulic function, first outlined by da Vinci, is now a primary aim of the emerging fields of ecohydrology and ecohydraulics, and forms the focus of this paper. Hydrologic and hydraulic drivers can deterministically influence ecological processes related to growth, survival, reproduction and evolutionary adaptation of organisms. Although the coupling between hydraulic processes and evolution is weak in the sense that it may be

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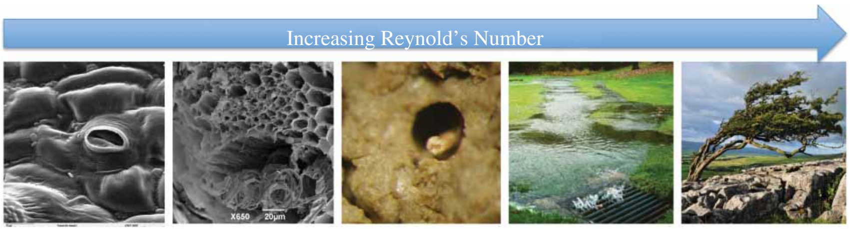
indirect or span a large time-scale separation (Murray 2002); on long time scales, hydraulics places selective pressures on organisms and ecosystems. The biological structures that result from this selective pressure represent nature's "engineering solutions" to hydraulic transport problems, generating hydraulic fingerprints in plant or ecosystem structure, such as coherent patterns in branching or vegetation cover; and determine the role of vegetation in cycling of water and nutrients on scales ranging from individual to global.

Terrestrial plants appear in the fossil record some 500 million years ago, when aquatic algae first migrated to land (Behrensmeyer 1992). As plants adapted to the terrestrial environment, their structure fundamentally changed (Pitterman 2010). Leaves and canopies grew to optimize light interception for photosynthesis. Competition for light generated a race upward, as taller canopies over-shadowed neighbouring trees, and several species now have crowns >100 m above the ground surface (Koch *et al.* 2004). Higher canopies increased dispersal distances of wind-borne pollen and seed, enhancing the spread of genetic information (Thompson and Katul 2008). The reproductive and energetic benefits of tall canopies, however, come at a penalty to plants (Ryan and Yoder 1997). Photosynthesis in the leaves is supplied with carbon dioxide (CO_2) from the atmosphere through leaf pores known as stomata. Stomata allow carbon dioxide into plants, but also release water vapour to the atmosphere through the process of transpiration (Cowan 1977). To prevent photosynthesizing leaves from desiccating, terrestrial plants must replenish them with water from the soil, a process that involves the hydraulic system of the entire plant (van den Honert 1948) and poses a hydraulic challenge that increases with canopy height. Solving this hydraulic problem generates physiological costs for plants, which constrain tree height and the architecture of the roots and the vessels that transport water from the root system to the canopy, the xylem.

In many terrestrial climates, it is access to water – rather than to light – that limits the growth and success of individuals (Budyko 1974). If local rainfall over a canopy does not meet the photosynthetic demand of the individual, then plants must expand their root systems laterally to access additional water supplies. Competition for water between individuals can then cause incomplete coverage of the land surface with vegetation canopies (Scanlon *et al.* 2007). Water can move laterally within the root systems of plants, across the land surface as shallow overland flow, or through the soil as porous media flow. In these water-limited ecosystems, a new set of ecological–hydraulic interactions can become important determinants of the spatial distribution of the soil water resources, and thus vegetation biomass (Bromley *et al.* 1997, Galle *et al.* 1999, Dunkerley and Brown 2002). Recent investigations into the ecohydrology of dryland ecosystems highlight the influence of infrequent and short-lived overland flow processes on the structure and function of spatially patchy vegetation in arid environments (Franz *et al.* 2011, Thompson *et al.* 2011).

With this background, it may be conjectured that *hydraulics constrain the function of biological and ecological processes, generating specific structural features on long time scales*. Posing this conjecture begs the provocative question – *can understanding hydraulics in ecological systems permit the interpretation or prediction of structure and function in organisms or ecosystems?* The high-dimensional and nonlinear nature of the problem makes finding a general answer difficult (Strogatz 1994, Katul *et al.* 2007). Water flow through the soil–plant system spans a vast range of length, velocity and time scales, as illustrated by the Reynolds numbers shown in Fig. 1. Covering all aspects of this problem lies beyond the scope of a single study. A more restrictive scope centred on links between photosynthesis and water demand is addressed here, spanning a rich but tractable set of phenomena and their connection to soil–plant hydrodynamics.



Process	Stomatal exchange	Xylem Flow	Soil water flow	Overland flow	Atmospheric flow
R	10^{-6}	<10	<10	<1000	$>10^6$
Other NDs		Capillary number (viscous:capillary forces)	Capillary number (viscous:capillary forces)	Froude number	U/U^*
Timescales	Seconds	Hours - Days	Hours - Days	Minutes - Hours	Seconds-Months

Figure 1 Illustration of the range of Reynolds numbers characterizing the flow behaviour in the plant–soil system. "Time scales" refer to the characteristic time scales of interaction between these flows and the biological processes discussed in the text: for example, overland flow redistributes water on time scales commensurate with individual rainfall events, that is, minutes–hours. Conversely, atmospheric turbulence determines seed trajectories on time scales of seconds. "ND"s refer to other non-dimensional numbers that may usefully characterize these flows

The close dependence of carbon fixation – essential to plant life – on water supply makes the hydraulic connection to plant carbon fixation clear and serves as a logical starting point. To develop the argument, the hydraulic constraints on the processes that deliver carbon into plants (gas exchange at the stomatal level) are first considered. Next, the hydraulic constraints on the fate of this carbon as it forms the structural features of trees is briefly discussed, and finally the spatial organization of carbon on the landscape at the ecosystem scale as dictated by hydraulic and hydrologic constraints completes this paper.

2 Plant hydraulics: stomata, stems and water

Over long time scales, two hypotheses can be made about the linked economies of plant carbon and water. The first is that the physiologically coupled processes of transpiration and photosynthesis must have evolved in a co-ordinated fashion, a conjecture that is supported by physiological and paleoecological evidence (Brodribb and Feild 2000, Katul *et al.* 2003). The second conjecture is that increased efficiency of essential processes confers an evolutionary advantage on plants, so that over long time scales, organisms should "optimize" biological processes. Many plants display features that are consistent with such optimization, at least with respect to water-limited carbon fixation.

2.1 *Gas exchange through stomata*

The finest spatial scale considered here over which carbon and water interact is the stomatal level, as shown in Fig. 2. Undisputed fossil evidence suggests that stomata are over 400 million years old, and that their development closely parallels the development of the broader plant hydraulic apparatus (Pitterman 2010), reflecting the direct coupling between carbon and water fluxes through their aperture. The net transport of carbon and water vapour at a leaf level occurs by Fickian diffusion, or an Ohm's law analogy to it, given by

$$
\begin{aligned}
f_c &= g_s(c_a - c_i) \\
f_e &= a_c\, g_s(e_i - e_a)
\end{aligned}
\tag{1}
$$

where f_c and f_e are the fluxes of CO_2 and water vapour, respectively, per unit area of leaf, c is the CO_2 concentration, e is the concentration of water vapour, subscripts a and i refer to atmospheric and internal (within leaf) concentrations, respectively, and $a_c = 1.6$ accounts for the different molecular diffusivities of water vapour and CO_2. The parameter g_s is the stomatal conductance (for CO_2) that is linked to the diffusivity for CO_2 through a large number of stomata covering the leaf surface. Because stomatal apertures are actively controlled by plants, plants can effectively modulate the values of g_s.

Any upscaling of g_s from leaf level to the canopy depends on the spatial arrangement, density and behaviour of stomata on individual leaves, the spatial arrangement of veins supplying water to those stomata, the leaf area and the ambient conditions experienced across the canopy (Mott and Buckley 2000). The flux relationships in Eq. (1) must therefore be viewed as a macroscopic representation, where much of the network complexity in delivering water and removing carbon within the leaf is surrogated to g_s (and c_i). Leaves close their stomata (reducing g_s) to prevent gaseous exchange when conditions are unfavourable for photosynthesis or when water potentials Ψ_p in the plant become sufficiently low to induce embolism or cavitation, that is, the obstruction of xylem by air bubbles (see Section 2.2). Water needed to sustain the f_e flux is delivered to the leaves from a soil reservoir by the plant hydraulic system, consisting of roots, xylem and leaf veins. These structures require carbon for growth and maintenance respiration (i.e. energy used to maintain baseline cellular activity of the plant). In this way, loss of water from leaves imposes a carbon penalty on the plant. If each leaf maximizes its carbon gain for a given water loss by autonomously regulating g_s, then the whole plant system effectively maximizes its carbon gain at a given water loss. This assumption is a variant on Pontryagin's maximum principle, which implies that with known initial conditions (e.g. the quantity of carbon in the whole plant system), globally optimal carbon gain at the plant scale (a linear sum of that at the leaf scale) is guaranteed if the "local" maximum is always selected at the stomatal level for the set of environmental conditions. This leaf optimality condition can be used to predict g_s from the carbon economy of the leaf via the condition:

$$
\begin{aligned}
f'(g_s) &= 0 \quad \text{where} \\
f(g_s) &= f_c - \lambda f_e
\end{aligned}
\tag{2}
$$

Here, λ represents the carbon cost of water (in carbon units) and is called the marginal water-use efficiency. Equation (2) is solved by expressing f_c in terms of the photosynthetic carbon demand

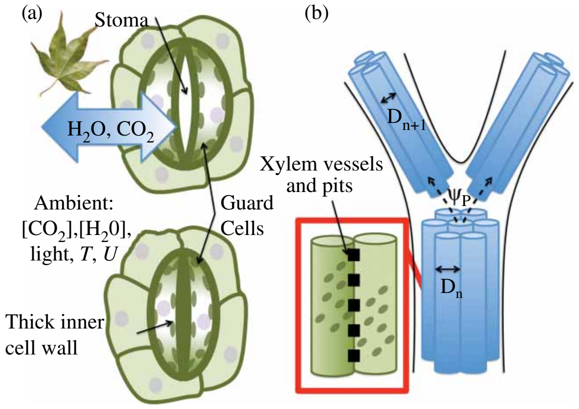


Figure 2 (a) Stomata are pores on the leaf surface that are opened or shut by guard cells. When open, water and carbon dioxide diffuse through the stomata. Stomatal opening responds to multiple environmental stimuli including concentrations of carbon dioxide and water vapour, light, temperature and the plant water potential (Ψ_P). (b) A network of xylem supply water to the leaves. Xylem are formed of dead, lignified and hollow cells with diameter $D \sim \mu$m. Xylem are connected to each other by pitted walls, with pores of diameter $\sim$ nm

(Farquhar *et al.* 1980):

$$f_c = \frac{a_1(c_i - c_p)}{a_2 + c_i} \tag{3}$$

where a_1 and a_2 are biochemical parameters (selected based on environmental conditions and varying with photosynthetically active radiation or temperature) and c_p is the minimum CO_2 concentration needed to sustain photosynthesis. To solve Eq. (2), Eq. (1) is combined with Eq. (3) to express f_e and f_c in terms of g_s, allowing the optimal conductance that maximizes carbon gain for a given water loss to be determined. To illustrate the canonical features of this solution, a simplified solution based on a linearized version of Eq. (3) that preserves the key stomatal dynamics gives g_s as follows (Katul *et al.* 2010):

$$g_s = \left(\frac{a_1}{a_2 + s\,c_a}\right)\left(-1 + \left(\frac{c_a}{a_c \lambda D}\right)^{1/2}\right) \tag{4}$$

where s represents a long-term mean of c_i/c_a (and can be independently measured from stable isotope techniques) and D is the vapour pressure deficit approximating $e_i - e_a$. This "optimality theory" has been used successfully to predict the dynamics of plant–atmosphere exchange in chamber experiments (Manzoni *et al.* 2011) and forested ecosystems (Launiainen *et al.* 2011). There is broad consistency between this theory and the response of stomatal conductance to varying D and CO_2 concentrations, suggesting that optimal stomatal regulation in plants is a plausible zero-order model on rapid time scales (Katul *et al.* 2009, 2010). On longer time scales, adjustment of stomatal conductance to maintain optimal carbon–water economies has also been proposed as a plausible mechanism allowing plants to acclimate to climate change (de Boer *et al.* 2011). More complex (two-dimensional spatial) models have also been proposed dealing with vein network development in leaves as influenced by environmental conditions (Roth-Nebelsick *et al.* 2001, Blonder *et al.* 2011, Haworth *et al.* 2011). Because of the tight coupling between water transport and photosynthetic demand, these networks impact whole plant photosynthesis and the mechanical properties of leaves, and thus vary between species that have evolved or have been bred under different conditions. Venation theory applied to water delivery is another example of hydraulic determinism, but is not covered further here. Developing scaling relationships that can span the properties of gas exchange from stomata to leaves to entire canopies remains an ongoing area of research.

2.2 *Transport in the xylem*

Stomatal regulation determines the movement of water within the xylem system. Xylem are lignified cells connected to each other by a porous section of cell wall known as the xylem pit membrane (see Fig. 2). Xylem diameters range from 5 to 500 μm (Hacke and Sperry 2001), but the radii of pores in the pit membrane are usually much smaller, ranging from 10 to 224 nm (Jansen *et al.* 2009). The bulk flow of water in these vessels is laminar (Re $<$ 10). Given the small length scales involved, formal analysis of xylem flow requires some consideration of microfluidic effects. Microfluidic flows are affected by surface tension and capillarity, elastic interactions with polymers and even discrete molecular effects, all of which become more nonlinear and important as the length scales decline (Squires and Quake 2005). Surface and interfacial effects are particularly important due to the high surface-area-to-volume ratios. For instance, plants appear to regulate flow across xylem pit membranes by lining these membranes with hydrogels that shrink or swell in response to the ionic strength of the solution (Zwieniecki *et al.* 2001). A complete description of xylem flow accounting for microfluidic processes over the full xylem system remains an open problem, which is not covered here.

Continuum arguments have been usefully employed to represent xylem flow as being analogous to porous media flow described by Darcy's law (Bohrer *et al.* 2005) or multiple pipes flowing in parallel (each described by Poiseiulle's law) (Tyree and Ewers 1991), and these arguments form the basis for most operational models. Complications arising from the network structure and flow processes in these models are surrogated to nonlinearities in the xylem hydraulic conductivity or resistance (Tyree 2003). The key nonlinearities lie in a sigmoidal relationship between the loss of xylem conductivity with increasing tension (the so-called vulnerability curve, analogous to a hydraulic conductivity function in unsaturated soils) due to formation of air bubbles in the xylem, a process known as cavitation (Tyree and Ewers 1991). Widespread cavitation in a plant results in a catastrophic failure of the hydraulic system (Sperry 2000). Cavitation is a pervasive threat because xylem sap is held under tension – that is, at less than atmospheric potential – meaning that the water column is unstable to the growth of an air bubble. From the Young–Laplace equation for the pressure difference across a fluid interface, stability requires that a force balance prevails where $\Delta P = 2\tau/r$. Here ΔP is the pressure difference between the fluid and atmospheric pressure, τ is the surface tension of the xylem sap, comparable to water ($\tau = 0.072\,\mathrm{Nm}^{-1}$) and r is the radius of the bubble, constrained by the vessel radii (Sperry and Tyree 1988). Given typical xylem radii, air bubbles exert a pressure difference of 10–100 kPa, and bubbles in pit membrane pores have ΔP on the order of 1–10 MPa. Typical xylem sap pressures are ~ -0.1–0.5 MPa. Thus, xylem sap is *unstable* to bubble formation. Air bubbles can form readily in individual xylem, but the small radii of the xylem pits limits the spread of cavitation into other vessels (Sperry and Tyree 1988).

Despite the appeal of this physical description, linking xylem structure to cavitation probability remains a challenge (Sperry *et al.* 2003). Additional mechanisms, such as the role of solutes as air bubble condensation nuclei (Wheeler and Stroock 2008), the potential for pit membrane deformation prior to cavitation spreading (Hacke *et al.* 2001) or even the possible role of mechanical failure of cell walls in spreading cavitation (Hacke *et al.*

2001), are likely to be responsible for the difficulty of predicting cavitation using the Young–Laplace theory.

Regulating xylem sap pressure to avoid cavitation is essential for plants, and is mostly achieved by the stomata. The geometric arrangement of xylem throughout the branching template of a tree crown offers a second set of physical constraints on xylem transport, and presumably underlies da Vinci's original observation about network branching. An optimization hypothesis can again be invoked, this time based on minimizing the energy expended for xylem flow and the bio-energetics needed to construct and sustain the xylem conduits. Two energetic costs are considered: the power inputs associated with sustaining water movement (P_q), and the metabolic inputs needed to construct and sustain respiration in the stems (P_m). The optimality hypothesis for this system can then be posed, specifically that *minimizing energy inputs per unit length of the stem needed to sustain xylem flow rate q with least amount of construction and maintenance respiration confers a selective advantage*. Such a work-minimization hypothesis was first proposed for the human circulatory system (Murray 1926). Applied to plants, and assuming a continuum description of the xylem flow, the optimal network law will minimize $L_T = P_q + P_m$. In fluid movement, $P_q = q\Delta P$, where ΔP is the pressure difference driving the flow within the xylem and can be derived as a function of q and the stem radius R depending on the Reynolds number. Hence, the work $q\Delta P$ can be expressed as $K_q q^2 R^{-\epsilon}$, where the units of K_q vary with ϵ, and ϵ is determined by the nature of the flow within R. The metabolic energy can be expressed as $P_m = K_m R^n$, where K_m is a metabolic rate (i.e. consumption of energy due to cellular respiration, growth, etc.) per unit length, with units that depend on whether the metabolic consumption depends on the stem length ($n = 0$), surface area ($n = 1$) or volume ($n = 2$). The L_T is minimized with respect to R (i.e. $\partial L_T/\partial R = 0$) when:

$$q = \sqrt{\frac{K_m}{K_q}\frac{n}{\epsilon}} R^{(\epsilon+n)/2} \tag{5}$$

If q is described by Poiseuille's formula (pipe model), then $q = (\pi/(8\mu))(\Delta P/Lp)R^4$, which leads to a ΔP scaling as qR^{-4}, and a P_q scaling as q^2R^{-4}, where μ is the dynamic viscosity and Lp is the length of the conduit. With this pipe-flow model, $\epsilon = 4$ and $K_q = 8\mu Lp/\pi$. Assuming that the volume of the stem is primarily responsible for metabolic consumption, $n = 2$, yielding the prediction that in optimal conduits, $q \sim R^3$. Because q is conserved in a branching network due to fluid continuity, this suggests that $\sum R_i^3$ must also be conserved at each branching level (compared to da Vinci's conjecture that $\sum R_i^2$ or the sum of areas was conserved). If the velocity profile inside the branch is independent of R (as originally assumed by da Vinci), then $\epsilon = 2$ and minimization of L_T with respect to R results in the R^2 da Vinci conservation rule. The R^3 conservation rule is commonly called Murray's law. Corrections to K_m originating from Kleiber's law (i.e. $K_m \sim M^{(1/4)}$, where M is the mass) can also be accommodated in this framework, and result in $q \sim R^{(11/3)}$ instead of $q \sim R^3$. Applicability of Murray's law to plant hydrodynamics appears to be supported in non-structural components of plants (e.g. vines or compound leaves) (McCulloh *et al.* 2003) although it can be confounded when stems have non-hydraulic functions, such as providing mechanical support to trees. Recent investigations of tree growth patterns that result when all limbs bear an equal probability of fracture (induced, for instance, by wind stress) reproduce the R^2 da Vinci conservation pattern (Eloy 2011). Potentially, the structural steady state and the hydraulic optimum place limits on the scaling exponents, which in many real plants lie between 2 (structural) and 3 (hydraulic).

2.3 *Hydraulic constraints on whole plant structure*

The complex nature of cause-and-effect between plant structure and function can obscure the effects of hydraulics. Conversely, it may also illuminate unexpected effects of hydraulic constraints that arise in plant functions that are only indirectly associated with water. For instance, there is a direct trade-off between mechanical strength (favoured by increased lignification of vessels) and hydraulic conductance (Sperry *et al.* 2003). Similarly, the minimum bound on xylem water pressures due to cavitation limits the ability of trees to grow to great heights (since the vertical distance from roots to leaves imposes a constant energy gradient that must be overcome) (Sperry 2000). Alternative applications of carbon–water optimization allow the estimation of the optimal allocation of carbon to roots versus leaves (Givnish 1986), although the difficulty of incorporating stem biomass into this optimization limits its application. In general, there is a need to link the mechanical, energetic and hydraulic functions of plant organs to arrive at a complete understanding of the determinants of whole plant form (Sperry *et al.* 2003).

3 Ecosystem engineering: hydraulic drivers of carbon distribution in ecosystems

The previous section considered hydraulic determinism operating on the scale of individual organisms with a focus on a tight coupling between carbon fixation and water. The need for plants to obtain water also allows hydraulics to influence assemblages of individuals, that is, ecosystems. To illustrate this control, consider the prototypical ecosystem shown in Fig. 3. If this ecosystem is strongly water-limited, then carbon fixation is coupled to water availability via (HilleRisLambers *et al.* 2001, Rietkerk *et al.* 2002, Kefi *et al.* 2008):

$$\begin{aligned}
\frac{\partial B(x,y,t)}{\partial t} &= f_c(V_W)\mathrm{LAI} - (K_m + m)B + Q_{Bx} + Q_{By} \\
\frac{\partial V_W(x,y,t)}{\partial t} &= I - \alpha f_c(V_W)\mathrm{LAI} - E(V_W) + Q_{V_Wx} + Q_{V_Wy} \\
\frac{\partial h(x,y,t)}{\partial t} &= P - I + Q_{hx} + Q_{hy}
\end{aligned} \tag{6}$$

In this mass balance, B represents the plant biomass density, V_W the volume of water stored in the soil per unit area and h represents the depth of ponded water following a rainfall event with depth P. The biomass growth represents a balance of carbon fixation (given by the product of the leaf-level carbon flux f_c and the leaf area index LAI), and respiration, assumed to occur at a rate of K_m per unit biomass (compared to per unit length as in Eq. 5). The LAI is the surface area of plant leaves per unit area of the ground. Here, it is assumed that LAI is a known function of the biomass density (Kefi *et al.* 2008), that light is not limiting and that all leaf area contributes equally to photosynthesis. Biomass density declines due to mortality and/or herbivory at a rate m. Biomass can spread in two lateral dimensions (x and y) through seed dispersal or vegetative reproduction, as represented by lateral fluxes Q_B. The stored soil water increases due to infiltration I, declines due to plant uptake (proportional to carbon assimilation with an assumed constant water use efficiency of $1/\alpha$) and soil evaporation E, and may also move laterally (Q_{V_W}). Ponded water depths increase due to P, decrease due to I and again may flow laterally (Q_h). A reasonable prescription of water availability, and thus potential plant growth in this ecosystem, requires understanding the hydraulics governing the lateral redistribution of water. The following sections outline the processes described in Eqs. 6 in more detail.

3.1 *Vegetation–infiltration feedbacks*

Under certain circumstances, lateral redistribution of overland flow Q_h can be linked to the spatial structure of ecosystems. Overland flow arises in arid ecosystems when infiltration rates are low and rainfall intensity is high. Typically, overland flow occurs in response to gradients in topography, but it may also occur on topographically flat surfaces if the infiltration rate I varies in space (Thompson *et al.* 2011). Such variability in infiltration capacity (the rate at which water moves into saturated soil under the action of gravity) often differs between vegetated and bare areas in patchy arid ecosystems. Plant canopies and litter layers protect the soil surface from the physical impact of rain drops, which cause soil surface sealing (Assouline and Mualem 2000). They shade soil surfaces, preventing organisms from forming biological soil crusts (Philip 1998, Belnap 2006). They also concentrate soil organisms and root density, increasing macropore formation and permeability (Greene 1992, Vanes 1993, Hallett *et al.* 2004). Infiltration capacity thus tends to increase with local biomass, approximately as a sub-linear power law (Thompson *et al.* 2010a). Where biomass is unknown, the more easily observed LAI can be used as a surrogate, allowing the infiltration capacity to be expressed as

$$I(t) \propto (1 + b_1 \mathrm{LAI}^{b_2}) \tag{7}$$

where b_1 and b_2 are empirical parameters. This coupling means that water infiltrates more rapidly beneath plant canopies, leading to a free-surface gradient in ponded water between bare and vegetated sites. On flat terrain, such free-surface gradients can drive lateral flow (Khanna and Malano 2006, Biscarini *et al.* 2010). Thus, infiltration contrasts create conditions under which water can flow from bare to vegetated sites. To quantify Q_h on these surfaces, however, the surface resistances must be specified. This can be challenging on natural land surfaces, which exhibit soil roughness, microtopographic variations and patchily-distributed vegetation, and on which flow depths h rarely exceed mm to cm. Characterizing the energetic losses in these regimes is non-trivial. Roche *et al.* (2007) concluded that “although local Reynolds number values do not clearly indicate that the flow is turbulent …head losses …are dominated by inertia” (p. 10). Classical laminar flow assumptions, such as the Hagen–Poiseuille equation, generates a Darcy–Weisbach friction factor of $f = 64/\mathsf{R}$, which also describes rough shallow flows poorly (Abrahams *et al.* 1986, Lawrence 2000). In what follows, the turbulent intensity of the shallow flows is assumed to be high, despite the low Reynolds numbers. However, the precise nature of energetic losses in these shallow flows remains unresolved.

The turbulent surface resistance f is a nonlinear function of flow depth h. Given a surface for which the momentum roughness height $z_o \ll h$, f is computed from the 1/7 power law (Blasius 1913, Brutsaert and Yeh 1970, Chen 1991, Katul *et al.* 2002), as

$$\sqrt{\frac{f}{8}} \approx 0.18 \left(\frac{z_o}{h}\right)^{1/7} \tag{8}$$

As $z_o \to h$, this formulation becomes invalid, and the drag imposed by rough surface elements or vegetated canopies must be addressed. Progress requires fundamental understanding of how vegetation elements interact with shallow flows, a problem which is now receiving significant attention (Nepf 2012). Katul *et al.* (2002) proposed a mixing layer analogy that prescribed the shape of the velocity profile across the roughness layer as a hyperbolic-tangent. Poggi *et al.* (2009) showed that estimates of bulk velocity and shear velocity could be recovered from first-order closure models parameterized with the vegetation geometry and boundary conditions. Analytical expressions for f for flows through vegetated canopies can be obtained by depth-averaging the mean momentum balance, thereby explicitly accounting for the drag force on vegetated elements (Katul *et al.* 2011).

3.2 *Lateral water flows induced by infiltration contrasts*

Given a roughness parameterization and the large differences in infiltration capacity between bare and vegetated sites (10-fold contrasts are reported at some sites (Dunkerley 2002)), how significant is Q_h for vegetation? To address this question, the 1D Saint Venant equations are coupled to lateral inputs and losses

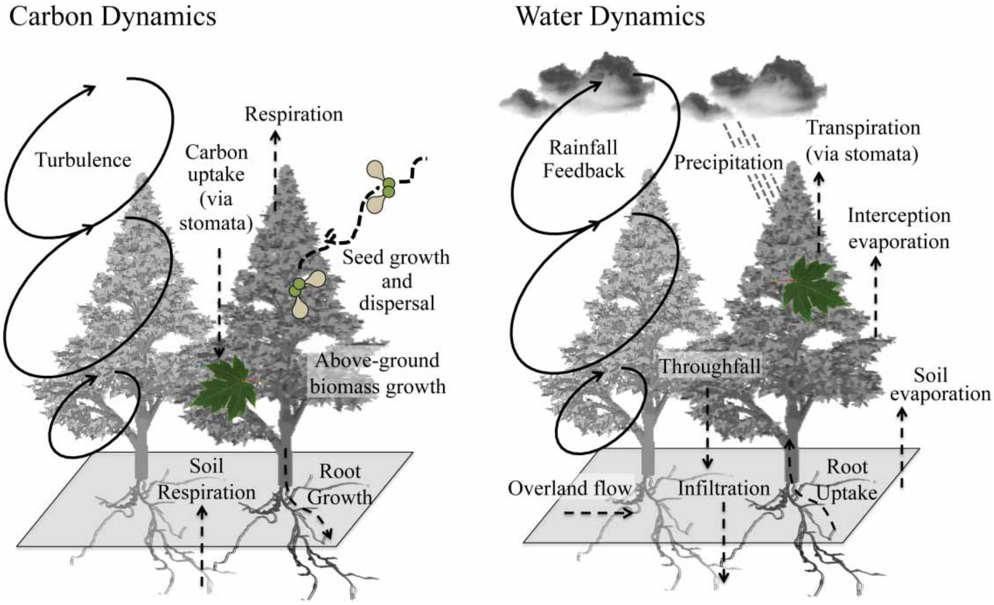


Figure 3 Ecosystem-level carbon and water dynamics are distributed between atmospheric, soil surface, subsurface and within-plant environments. Carbon uptake in the leaves allows biomass growth and respiration, and the production of seeds to propagate plant populations. Carbon uptake is dependent upon sufficient water supply to the roots, which is dictated by the quantity of water infiltrating into the root zone and the processes other than plant uptake that deplete the water store

of water from rainfall and infiltration:

$$\frac{\partial h}{\partial t} + \frac{\partial q_x}{\partial x} = P(t) - I(t) \tag{9}$$

$$\frac{\partial q_x}{\partial t} + \frac{\partial}{\partial x}\left(\frac{q_x^2}{h} + \frac{gh^2}{2}\right) + gh(S_f - S_0) = 0 \tag{10}$$

In these equations, t is time, $q_x = Vh$ is the flow rate in the longitudinal (x) direction, V is the depth-averaged velocity, g is gravitational acceleration, S_0 is the ground slope and S_f is the friction slope, and other variables are as defined above. Parameterizations of the friction slope in the momentum equation (10) are obtained from the Darcy–Weisbach equation assuming locally uniform flow, giving

$$S_f \approx \frac{f}{8g}\frac{q_x^2}{h^3} \tag{11}$$

with the friction factor defined separately over bare soil and vegetated sites. Canopy LAI links the roughness effects to the appropriate infiltration contrast through Eq. (7). Solving Eqs. (7)–(11) for a range of storm intensities and durations allows the cumulative infiltration in vegetated sites to be estimated as a function of the rainfall input. Thompson *et al.* (2011) showed that lateral fluxes could cause an increase in water availability of approximately 100% of the rainfall volume when vegetation grew in small isolated clusters with large "catchment" areas between them. Linear bands of vegetation increased access to water by ~40% of the precipitation. This flux is sensitive to small variations on the soil surface, however, as microtopographic variation can significantly reduce Q_h fluxes. The storage of rainfall in microtopographic depressions, and the elevation of the effective sorptivity of the soil surface by the microtopographic variations can increase infiltration by 200%, greatly decreasing runoff (Thompson *et al.* 2010b). Despite the significance of shallow sheet flows for the spatial structure, function and resilience of ecosystems, a complete theory to describe such flow and its interaction with vegetative or microtopographic roughness elements remains lacking, and requires further investigation (Nepf 2012).

3.3 *Spatial organization of ecosystems*

If the Q_h fluxes are significant, the relationship between biomass and infiltration in arid ecosystems enhances soil moisture storage near vegetation, promoting further vegetation growth. Ultimately, however, competition for water limits the growth of vegetated patches. The combination of positive and negative feedbacks destabilizes homogeneous vegetation cover, and can lead to spatial organization or patterning (Borgogno *et al.* 2009). Coherent vegetation patterns with distinct wavelengths and directions are found on the margins of deserts worldwide (Deblauwe *et al.* 2008).

The plurality of time scales that describe carbon–water coupling in patterned ecosystems makes the simulation of the system's evolution challenging. Dryland vegetation tends to grow slowly, often on decadal time scales. Redistribution of rainwater, however, occurs during a single storm (minute–hourly time scales). One way to overcome this scale separation is to treat biomass as stationary while surface water redistribution occurs, and then to treat surface water as a steady-state (zero value) process over the time scales on which vegetation depletes soil moisture and grows (Murray 2002). By using such a "two-timing" approach, Konings *et al.* (2011) reproduced the spatiotemporal dynamics of vegetation patterns while resolving both within-storm redistribution of surface water and the feedbacks between vegetation transpiration and rainfall. Biomass dynamics, however, are not always decoupled from rapid processes. Seed dispersal, for instance, is integral to the spatial self-organization of vegetation, but is significantly influenced by (fast) turbulent processes and variation in mean wind speed. To upscale this variability to long time scales, combined distribution approaches or "superstatistics" (Beck and Cohen 2003) can be used to link stochastic processes over multiple scales. Thompson and Katul (2008) demonstrated that such an interaction between time scales greatly increased the distances over which wind-borne seeds disperse. In patchy arid ecosystems, overland flow, particularly on sloping sites, may also transport seeds. Such movement may increase the stability of banded vegetation patterns by slowing upslope migration (Thompson and Katul 2009), but few detailed studies have been made of seed dispersal in overland flow. Despite the process complexity and multiple time scales involved, global coherent vegetation patterning provides a dramatic landscape-scale signature of hydraulic influence on ecosystem structure.

4 Discussion and vision

The case for hydraulic determinism lies in the hydraulic regulation of plant stomatal function, the optimization of the physical structure of branching tree canopies to reduce hydraulic losses per conduit length and the spatial organization of water-limited systems as driven by overland hydraulic redistribution of rainfall. Nonetheless, a complete theory of the relationship between structure and hydraulic function of organisms or ecosystems remains an outstanding challenge.

In some cases, this is due to the fact that the process descriptions for flow and the boundary conditions remain incomplete. For example, the description of flow in xylem remains largely confined to continuum representations, despite experiments that have successfully created "synthetic trees" by drawing on microfluidic effects (Wheeler and Stroock 2008). A similar gap in hydraulic theory relates to the energetics and behaviour of shallow overland flows. Flow visualization techniques that can be used to observe mean streamlines and estimate velocities in shallow flows are sorely needed to address this problem (Savat 2006).

In other instances, even if the hydraulics of the problem could be described, the biological response to the flow conditions may be unknown. This is exemplified by the lack of a physiological theory to predict likelihood cavitation curves. The biological implications of how multiple constraints on tree structure and mechanical, energetic, water, nutrient and other functions interact to render particular morphologies more or less optimal for individuals remain unclear; as does the interaction of multiple constraints, including (but not limited to) water availability (particularly outside water-limited ecosystems), in determining ecosystem structure. At the level of individual plants, understanding constraints on maximum possible canopy heights might be a logical starting point. A comprehensive response to this challenge calls for interdisciplinary investigations spanning tree physiology, structural engineering, hydraulics and biochemistry.

The need to link different processes over wide-ranging time scales presents an ongoing challenge to research in this area. This paper outlined three different approaches: employing ecological hypotheses, such as optimization, as "closure" principles that predict the nature of a long-term solution, and avoid the need to simulate transient processes; two-timing or scale separation (Murray 2002); and nonlinear averaging based on super-statistics (requiring a detailed understanding of the stochastic processes occurring on different time scales). While these approaches are all broadly suitable, their application is often non-trivial and involves problem-specific development.

Beyond the engineering challenges, however, lie the theoretical complexities associated with understanding the history of evolutionary processes. Evolution is a self-referential process, meaning that the nature of the governing equations is dependent on the solution to those equations (Goldenfeld and Woese 2011). Perhaps the closest analogy to these hydraulic, self-referential systems arises in the study of fluvial geomorphology, in which the state of fluid flow controls erosive and depositional processes, which in turn alter the boundary conditions on the flow and its subsequent behaviour. Once biological evolution is considered, however, not only the boundary conditions but the governing equations themselves may become dependent on the systems' history. Self-referential phenomena are thus theoretically problematic. Discerning the role of hydraulics in such phenomena is confounded by the weakness of the coupling between the fast hydraulic and slow evolutionary success. Together, the weakly coupled and self-referential nature of plant–water interactions means that understanding how hydraulics shaped the evolution of individuals, let alone entire terrestrial ecosystems, remains a largely aspirational goal. The analogy to fluvial geomorphology provides consolation, however: while complex, self-referential systems regularly generate multiple solution states, self-organization, criticality, threshold behaviours and other nonlinear behaviour. A theory of plant hydraulics over evolutionary time scales may remain elusive, but ongoing investigation of hydraulic determinism should continue to reveal phenomena that are similarly rich and fascinating.

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Notation

α = water transpired per mass carbon fixed ($\mathrm{mm\,kg^{-1}\,m^{-2}}$)

a_1 = biochemical parameter ($\mathrm{mmol\,m^{-2}\,s^{-1}}$)

a_2 = biochemical parameter ($\mathrm{mmol\,m^{-3}}$)

a_c = ratio of molecular diffusivity of water vapour and CO_2 (–)

b_1 = empirical parameter relating LAI to infiltration (–)

b_2 = empirical parameter relating LAI to infiltration (–)

c_a = CO_2 concentrations in air ($\mathrm{mmol\,m^{-3}}$)

c_i = CO_2 concentrations within leaves ($\mathrm{mmol\,m^{-3}}$)

c_p = minimum CO_2 concentration allowing photosynthesis ($\mathrm{mmol\,m^{-3}}$)

D = vapour pressure deficit ($\mathrm{mmol\,m^{-3}}$)

e_a = water vapour concentration in air ($\mathrm{mmol\,m^{-3}}$)

e_i = water vapour concentration within leaves ($\mathrm{mmol\,m^{-3}}$)

ϵ = exponent in flow–energy relation (–)

E = soil evaporation rate ($\mathrm{mm\,s^{-1}}$)

f = Darcy–Weisbach friction factor (–)

f_c = CO_2 flux per unit leaf area ($\mathrm{mmol\,m^{-2}\,s^{-1}}$)

f_e = water vapour flux per unit leaf area ($\mathrm{mmol\,m^{-2}\,s^{-1}}$)

h = depth of overland flow (m)

I = infiltration rate ($\mathrm{mm\,s^{-1}}$)

K_m = metabolic rate per unit length area (variable)

K_q = proportionality constant (variable)

λ = marginal water use efficiency ($\mathrm{mmol\,mmol^{-1}}$)

LAI = leaf area index ($\mathrm{m\,m^{-1}}$)

Lp = conduit length (m)

L_T = total energy expenditure by xylem network (J)

μ = dynamic viscosity (Pa s)

M = mass (kg)

P = rainfall rate ($\mathrm{mm\,s^{-1}}$)

ΔP = pressure drop (kPa)

P_q = energy requirement to sustain flow (J)

P_m = energy requirement to sustain respiration (J)

Ψ_p = plant water potential (kPa)

q = flow rate in the xylem ($\mathrm{m^3\,s^{-1}}$)

q_x = flow rate in x direction ($\mathrm{m^3\,m^{-1}\,s^{-1}}$)

Q_B = biomass lateral flux ($\mathrm{kg\,m^{-2}\,s^{-1}}$)

Q_h = water lateral flux ($\mathrm{mm\,m^{-2}\,s^{-1}}$)

r = radius (of bubble or xylem) (m)

R = Reynolds number (–)

R = radius (of plant stem) (m)

s = long-term mean of c_i/c_a (–)

S_0 = ground slope (–)

S_f = friction slope (–)

τ = surface tension ($\mathrm{Nm^{-1}}$)

t = time co-ordinate (s)

V = depth-averaged velocity ($\mathrm{m^3\,s^{-1}}$)

x = longitudinal spatial dimension (m)

y = lateral spatial dimension (m)

z_o = momentum roughness height (m)

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