



Biological constraints on water transport in the soil–plant–atmosphere system

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ABSTRACT

An effective description of water transport in the soil–plant–atmosphere continuum (SPAC) is needed for wide-ranging applications in hydrology and climate–vegetation interactions. In this contribution, the theory of water movement within the SPAC is reviewed with emphasis on the eco-physiological and evolutionary constraints to water transport. The description of the SPAC can be framed at two widely separated time scales: (i) sub-hourly to growing season scales, relevant for hydro-climatic effects on ecosystem fluxes (given a set of plant hydraulic traits), and (ii) inter-annual to centennial scales during which either hydraulic traits may change, as individuals grow and acclimate, or species composition may change. At the shorter time scales, water transport can be described by water balance equations where fluxes depend on the hydraulic features of the different compartments, encoded in the form of conductances that nonlinearly depend on water availability. Over longer time scales, ontogeny, acclimation, and shifts in species composition in response to environmental changes can impose constraints on these equations in the form of tradeoffs and coordinated changes in the hydraulic (and biochemical) parameters. Quantification of this evolutionary coordination and the related tradeoffs offers novel theoretical tactics to constrain hydrologic and biogeochemical models.

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1. Introduction

Water transport through soil, vegetation, and the atmosphere typically constitutes the largest hydrologic output in most terrestrial systems. On the one hand, soil properties and plant activity influence the partitioning of rainfall into evapotranspiration, runoff, and deep percolation, thus impacting the regional-scale water balance. On the other hand, transpiration is tightly coupled to the carbon cycle through simultaneous exchanges of CO₂ and water via the stomatal pathway, thus ultimately controlling C uptake by vegetation and affecting long-term C storage in ecosystems. Because of these fundamental roles, water movement through the soil–plant–atmosphere continuum (SPAC) remains a subject of active research in hydrology and plant and agricultural sciences, and a key topic in any assessment of elemental cycling in natural and agro-ecosystems, under current and future climate scenarios. Moreover, because terrestrial plants are first users of precipitated water, they directly affect the recharge of water systems: as such, their impact on water resources cannot be ignored.

Quantifying water movement through the SPAC requires understanding water dynamics in three main compartments (soil, plant

tissues, and atmosphere) and through the interfaces and connections among them (soil–root interface and leaf surface). The driving force for water movement is provided by the gradient in total water potential between the soil and the atmosphere [1,2], which causes liquid water to move from the soil into the plant and then to evaporate and diffuse from the mesophyll and epidermal cells through the stomata (also directly through the cuticle) and into the atmosphere [3]. By means of guard cell movements, which alter the size of the stomatal aperture, plants are able to regulate water losses through transpiration at the most effective location, i.e., where the steeper water potential gradient develops between the nearly saturated stomatal cavity and the atmosphere [4]. The flux of liquid water through the soil and plant tissues takes place under high tension, and is generally framed within the context of cohesion–tension theory [5–9].

Quantitatively describing this water flux is complicated by incomplete knowledge of microscopic-scale processes, the large spatial heterogeneity of the transporting medium (e.g., root and branch architecture), and the temporal variability of the external drivers [10,11]. Because of these intrinsic complexities, simplified models that capture the macroscopic dynamics through mass balance equations are a viable alternative to a detailed representation of the micro-scale processes. Following this simplified approach and in the context of cohesion–tension theory, the flux of liquid water is often described by an electrical analogy, where water encounters a series of resistances (or conductances) from the soil

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to the leaves together with decreased gravitational potential with elevation [2,4,6,12–14]. A price to pay for such simplified macroscopic view of the dynamics within the SPAC is a high degree of nonlinearity in conductances with respect to water potential. In fact, conductances in both the soil and the plant tissues are known to be nonlinearly related to water potential (or water saturation; see Fig. 1): such nonlinearities are caused by air entry and reduction of liquid water films in soils [12,15,16] and the occurrence of cavitation in the xylem [9,17]. Similarly, stomatal conductance declines nonlinearly as water potential decreases, besides changing as a function of other environmental and biochemical factors [18–21].

Much work on the soil–plant system has focused on describing water fluxes when a given set of plant characteristics are known, and where the time scales are those imposed by soil drying, stomatal control, and cavitation development (sub-hourly to the growing season). However, the various components of the SPAC respond to environmental changes also over longer time scales, at which individuals acclimate and grow, and species composition changes [22,23]. Thus, especially in the face of climatic changes, it is becoming necessary to assess how these hydraulic features are altered at longer time scales in both individuals and at the ecosystem level. In this contribution, such two time scales are explored exploiting their large time scale separation. First, a simplified framework for a short-term description of water flow is presented, assuming static plant traits. Spatially explicit representations are simplified to provide lumped ‘macroscopic’ equations primarily intended to illustrate the role of mechanisms and plant characteristics. These lumped equations are applicable and testable using quantities

commonly measured at the macro-scale (e.g., soil cores, leaves, and stem segments, up to field-scale flux measurements), which are becoming readily available through published global databases (e.g., TRY, [24], FLUXNET, [25]). Next, coordinated changes of plant hydraulic characteristics in response to environmental variations during ontogeny or succession are explored. From a practical perspective, such coordination between traits necessarily implies a set of constraints that can be formulated as linkages between the various elements of the soil–plant hydraulic apparatus, and between the hydraulic and photosynthetic machinery of the plant itself. From the point of view of plant function, coordination among plant conductances improves the hydraulic efficiency along the SPAC [26–30], and the scaling of water supply with leaf photosynthetic capacity optimizes resource use [31–35]. Plant form also results from evolutionary tradeoffs between structural and functional constraints [36], leading to optimal branching networks and xylem vessel size [34,37,38]. After discussing how these optimality criteria are used to relate the key hydraulic characteristics of plants to each other, the review concludes with future research priorities necessary for implementing such biological constraints on the dynamics of water in the SPAC.

2. Governing equation for water transport through the SPAC

As a starting point, horizontal homogeneity is assumed so that the focus is only on vertical transport of water from the soil to the atmosphere. To describe water transport within a common framework, total water potential is employed as a natural unit to

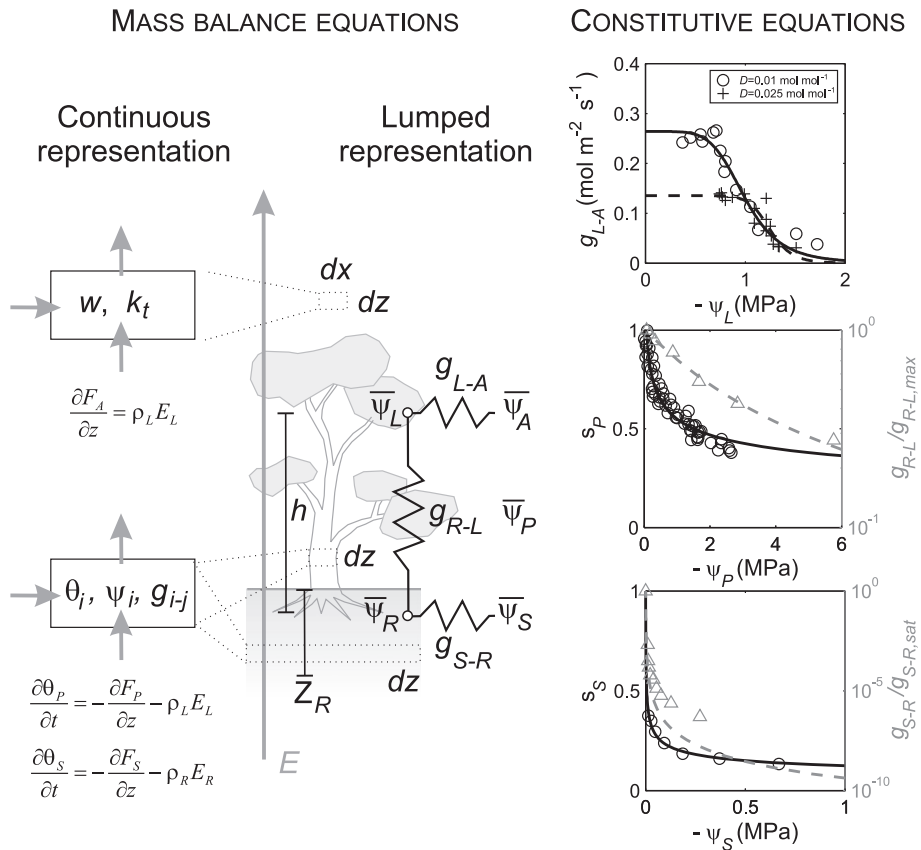


Fig. 1. General scheme of the soil–plant–atmosphere continuum (SPAC): illustration of the mass balance in the continuous and lumped representations and constitutive equations for water flow through soil (subscript S), plant xylem (subscript P), and atmosphere (subscript A). Top, stomatal conductance (g_{L-A} for well ventilated conditions) as a function of leaf water potential at two contrasting vapor pressure deficits (D) in *Nerium oleander* [178]; middle, water retention curve (black) and vulnerability to cavitation (gray) of *Tapiria guianensis* branches [63]; bottom, water retention and hydraulic conductivity data and curves (Eqs. (5) and (9)) for a sandy loam soil (black and gray, respectively) [46].

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