**Article title:** Modelling plant-water interactions: an ecohydrological overview from the cell to the global scale

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**Abstract**

Vegetation and the water cycle are inherently coupled across a wide range of spatial and temporal scales. Water availability interacts with plant ecophysiology and controls vegetation functioning. Concurrently, vegetation has direct and indirect effects on energy, water, carbon, and nutrients cycles. A better understanding and modelling of plant-water interactions demands for highly interdisciplinary approaches. We present an overview of the main processes and relevant interactions between water and plants across a range of spatial scales, from the cell level of leaves, where stomatal controls occur, to drought stress at the level of a single tree, up to the integrating scales of a watershed, region, and the globe. A review of process representations in models at different scales is presented. More specifically, three main model families are identified: (i) models of plant hydraulics that mechanistically simulate stomatal controls and/or water transport at the tree level; (ii) ecohydrological models that simulate plot- to catchment-scale water, energy and carbon fluxes; and (iii) terrestrial biosphere models that simulate carbon, water, and nutrient dynamics at the regional and global scales and address feedbacks between Earth's vegetation and

the climate system. We identify special features and similarities across the model families. Examples of where plant-water interactions are especially important and how they have led to key scientific findings are highlighted. Finally, we discuss the various data sources that are currently available to force and validate existing models and we present perspectives on the evolution of the field.

## Introduction

Transpiration is the process of water transfer from soil to the atmosphere through plant tissues, during this process water changes its phase and exits from the plant. On average, transpiration amounts to roughly 40 % of the land precipitation[1,2,3] and the correspondent latent heat constitutes about 38 % of the net radiation absorbed by the land surface[4]. Therefore, it is not surprising that vegetation plays a fundamental role in hydrology and climatology[5,6]. Transpiration occurs almost entirely through small openings in the leaves called stomata[7]. This pathway is the same through which plants acquire carbon and thus represents a major nexus between hydrology and the carbon cycle. Plants lose about 100-500 molecules of water to fix one molecule of $CO_2$[8], with water representing a key element determining vegetation function and performance. The coupling of transpiration and photosynthesis creates important feedbacks between water, carbon, and nutrient cycles. Soil biogeochemistry and nutrient dynamics are in fact directly connected to water availability, because soil biota dynamics and rock weathering depend on soil moisture content[9,10], and also indirectly, through the effect that soil water content has on vegetation growth and litter production. Despite the strong connection between vegetation and hydrology, historically, in hydrological applications, vegetation has been represented with constant factors embedded in equations for computing bulk evapotranspiration, as for example in the Penman-Monteith equation[11]. Concurrently, in many ecological applications with detailed characterization of plant processes, hydrology has been represented with a simple bucket approximation[12,13].

Given the central role of water-plant interactions in the climate system, representations of vegetation attributes and especially stomatal functioning were included in early Earth System Models (ESMs)[13,14,15,16]. Since then, in the last two decades, ecohydrology (or hydroecology) has been an emerging scientific field, as testified by the growth of the number of published articles and citation metrics beyond the average increase in scientific productivity (Fig. 1). This has been also the result of the emphasis placed on water-vegetation interactions in a series of seminal works[17,18,19,20]. Ecohydrology has been less recognized as an emerging field in ecology, because many ecologists and ecophysiologists would have regarded themselves as "ecohydrologist" well before this term became popularized by hydrologists[21]. Notwithstanding, the emergence of ecohydrology as a well-distinguished discipline helped a better exchange and an explicit linkage between the two scientific communities. Along with the emergence of ecohydrology, an increasing number of quantitative studies focusing on the carbon, water, and nutrient cycles, at the regional and global scales, have appeared within the realm of "biogeosciences", under the growing pressure to better understand carbon cycle feedbacks to climate change[22,23,24]. There are studies nowadays in which the boundaries between the fields of ecohydrology, ecophysiology, and biogeosciences are very subtle and mostly a

matter of spatiotemporal scales. Beyond affecting water, carbon, and nutrient cycles, vegetation functioning has important implications for addressing other relevant questions, as for example in assessments of land-use change impacts[25], evaluation of ecosystem services[26], soil resources and landscape formation[27], as well as crop productivity[28]. These are all topics where water availability interacts with plant ecophysiology to produce complex dynamics, which are unlikely to be uncovered with narrowly disciplinary approaches that ignore or trivialize either hydrological or vegetation components. Clearly, the perception of significance and integration of vegetation processes into various fields of environmental research has recently undergone a significant transformation.

It is important to underline that ecohydrology should not be regarded as the analysis of how vegetation properties and organization affect streamflow. It is a broader discipline that examines the two-way interactions between the entire hydrological cycle and plant functioning. When the main interest is on relatively short-term (≈ decade) analyses of streamflow and water availability or in hydrological engineering design, classic hydrological tools such as the Penman-Monteith equation can often suffice the purpose of representing vegetation and approaches that involve multiple processes and feedbacks such as carbon cycle or plant physiology are unlikely to improve considerably predictive capabilities or specific design criteria. However, when the focus shifts toward land-surface climate feedbacks, carbon and nutrients cycles or the aim is to elucidate ecological mechanisms through which water availability affects vegetation functioning, then the necessity of explicitly accounting for vegetation physiology and anatomy and/or soil biogeochemistry becomes extremely relevant. Furthermore, feedbacks between vegetation and water cycle cannot be captured, if these are not explicitly represented in models, and hypothesis testing can be severely impaired by simplified model structures. An illustrative example is provided by potential effects that model complexity and explicit consideration of elevated $CO_2$ feedbacks can have in evaluating drought trends[29,30] or aridity projections in a changing climate[31,32]. Too simple representation of vegetation has been shown to provide quite misleading assessments. Another example is represented by the study of the effects of land cover change (e.g., deforestation, grassland management) on evapotranspiration and streamflow. Detailed numerical analyses[25,33] and actual observations[34,35,36] suggest that the impact of land cover change on the hydrological cycle, may be typically less pronounced in comparison to results obtained with model simulations using simplified approaches (e.g.,[37]), or from small scale manipulation experiments[38]. However, if the effects of disturbances or long-term analyses (≈ multiple decades) are sought, water cycle is more tightly connected to the vegetation cover (e.g.,[39,40]). For instance, shifts in forest composition due to species-specific mortality have been shown to produce hydrological relevant consequences[41]. The latter is the result of processes typically unaccounted for in classic ecohydrology such as soil-biogeochemistry, forest demography, and disturbances, which therefore may represent fundamental "ecohydrological" components. Another example of ecohydrological links among vegetation, energy, and water cycle is vegetation-snow interaction. Plant canopy that intercepts snow typically favors sublimation, thereby reducing the amount of snowpack at the ground. Vegetation also alters the radiation balance, shading ground snowpack from direct radiation, yet typically increasing the longwave radiation reaching the ground during snow melting periods[42,43,44].

3

Additionally, the presence of vegetation affects the turbulent exchanges modifying the wind profile[45,46]. All of these processes are highly non-linear and can contribute to the increase or decrease of total snow-melt below vegetation, when compared to cleared areas[47].

In this overview, we provide an essential description of the main processes and relevant interactions between water and plants across a range of spatial scales, from the cell level of leaves, where stomatal controls occur, to drought stress at the level of a single tree; up to the integrating scales of a watershed, region, and the globe (Fig. 1). We treat only terrestrial ecosystems and leave aside aquatic plants in water bodies and oceans[48]. Water controls are also regarded from the plant perspective and therefore issues related with vegetation as mechanical roughness element and its effect on modulating river and overland flows[49,50,51] are not addressed. In combination with the description of the physical and ecological processes, we also refer to models available in literature that simulate specific processes at the different scales. We only focus on those models that simulate the temporal and, eventually, spatial dynamics of key vegetation states (e.g., Leaf Area Index, LAI). With the above constrain, we do not explicitly discuss steady-state models and analytical derivations (e.g.,[52,53,54,55,56,57]), which have led to considerable advances in the understanding of plant water interactions but are less amenable to address real case studies. Models developed in forestry research for simulating long-term (≈century) forest succession and management[58,59] are also excluded because of the rather minimalistic representation of hydrological processes. Finally, we favour models with a certain degree of generality that can be applied beyond the specific conditions for which they were derived.

Examples where plant-water interactions are especially important and have already led to key scientific findings are presented. We also focus on which data are currently available to force and validate the existing models, concluding with perspectives on the evolution of the field.

## Cell to plant scale

Plants developed a vascular system consisting of non-living and living cells, in which water, carbohydrates, and nutrients can move without an active "pump" such as a heart, designed to control and coordinate such movements[60]. Vascular plants need to solve the problem of water and nutrient transport from soil to different plant organs, especially leaves, which are exposed to continued dehydration because of partial contact with the sub-saturated atmosphere through stomatal apertures. Concurrently, plants have to transport the products of photosynthesis, such as sugars, from the leaves to the other living organs. To overcome the lack of a central pump, plants exploit physical gradients in water potential (the energy state of water[61]) and concentrations of osmotic substances[62]. The mechanisms for water entering the roots and leaving the leaves are described in Section "Stomatal Controls" and "Root controls", while in Section "Plant Vascular Transport" we provide the key elements of water transport mechanisms within plants. Fluxes of water or mass are expressed using a "flux-gradient" relation, where the flux is proportional to a gradient in the "concentration" of the driving quantity, times a conductance term. Throughout the

4

text, we reference existing models with different degrees of approximation of the current process understanding. We refer the reader to more specific reviews and books for a complete treatment of plant physiology and plant vascular transport[8,63,64,65,66,67] .

**Stomatal controls**

Leaves are the sites where water transported from the xylem, i.e., the non-living vascular conduits of plants used for water transport from roots to leaves, is evaporated (commonly referred to as "transpired") to the atmosphere. At the same time, carbon from the atmosphere is assimilated through the photosynthetic reaction, which takes place in the chloroplasts, mostly located in the mesophyll cells[68,69,70][Box 1]. Water is transported to the terminal part of the xylem network in the leaf veins, while carbon is loaded and exported in the opposite direction in the phloem (the vascular conduits that transport sugars produced by photosynthesis to other tissues in the plant, Fig. 2). Stomatal size and density and leaf venation have been recognized to be important for plant functioning and evolution[71,72,73]. At the same time the bulk of the resistance to water transport in the leaf is occurring outside the venation network[74,75,76]. Transpiration to the external atmosphere takes place through stomatal apertures of few micrometers in size (2-40 μm), mostly located in the lower side of the leaf[7,77]. Stomatal apertures are the common pathways for water and carbon fluxes and therefore represent one of the most essential linkages between ecological and hydrological dynamics. There is a large amount of literature on environmental factors influencing stomatal aperture, such as light, temperature, $CO_2$, vapour pressure deficit[78,79,80,81] but despite the critical role that stomata play, the details of their regulation are still not fully understood[82]. Ultimately, stomata are largely biologically regulated and it is through these tiny apertures (or lack of thereof, if leaves are shed) that vegetation imprints a unique signature on the water cycle.

Each stoma is surrounded by a pair of guard cells that are, in turn, in contact with multiple epidermal cells (Fig. 2). Stomata tend to open when guard cells increase their turgor (the sum of water potential and osmotic pressure, see equation (4)), while an increase in epidermal cell turgor plays in the opposite direction, exerting a hydromechanical negative feedback[83,84,85] (Fig. 2b). Since the guard cell turgor is the sum of osmotic pressure and water potential, stomatal aperture is controlled by both hydraulic and chemical factors[86] (Fig. 2c). Stomata close when water potential in the leaf drops, because of a large transpiration flux or low water potential in the upstream xylem conduits[87,88,89]. The hydraulic control acts directly in the reduction of guard cell turgor, while chemical signals are less well quantified[90]. However, it is well established that chemical factors are essential for stomata opening in response to light[91,92,93]. Furthermore, chemicals compounds, such as Abscisic Acid (ABA), are typically released in response to water stress from the leaves and roots[94,95,96] and contribute to a reduction in the stomatal aperture[97]. Release of ABA is an important evolutionary trait since in early plants such as lycophyte and ferns, stomata closure is purely hydraulically controlled[98]. A differential sensitivity of stomata aperture to chemical compounds is a likely explanation why certain plants close stomata considerably in response to dehydratation, keeping a fairly constant leaf water potential (commonly referred to as "isohydric behaviour"), while others tend to keep stomata open

5

to favour carbon assimilation, experiencing larger fluctuations and lower values of the leaf water potential ("anisohydric behaviour").

Models have been presented to describe mechanistically stomatal behaviour and reproduce the hydraulic dynamics in the leaf[84,99,100,101,102,103,104,105,106] or simply to reproduce functional relations in agreement with observations[78,107,108]. Representing in models the exact mechanisms through which stomata respond to the external environment and chemical signals[109,110,111] still represents an open research frontier. Mechanistic models have been mostly applied in plant physiological studies, while ecohydrological models and ESMs adopted empirical/conceptual solutions, where different environmental factors are treated independently[78], or the stomatal conductance ($g_s$) is assumed to be proportional to carbon assimilation ($A_n$) and inversely related to leaf interior $CO_2$ concentration ($c_i$) and Vapour Pressure Deficit (VPD). These are for instance the structures of the Ball-Berry[112] and Leuning equations[113,114]:

$$g_s = g_0 + a \frac{A_n}{C_i - \Gamma} f(VPD) \qquad (1)$$

where $g_0$ is the residual (or "leakage") stomatal conductance, when $A_n$ is equal to zero, $a$ is an empirical parameter and $\Gamma$ is the $CO_2$ compensation point, i.e., the concentration of $CO_2$ at which the rate of carbon dioxide uptake is exactly balanced by the rate of carbon dioxide release in respiration. The Leuning equation (Eq. 1) is widely used and typically requires an estimate of net assimilation $A_n$, which is carried out using biochemical models of photosynthesis, such as the Farquhar model or its subsequent refinements[115,116,117,118,119].

An alternative approach to characterizing stomatal regulation is to assume that stomatal aperture is regulated to maximize carbon gain, while minimizing water loss[120,121]. These approaches, known as "optimality arguments" are appealing from theoretical standpoint because they are based on ecological evolutionary principles and seem to be corroborated by observed stomatal behaviour[121]. However, they require specific assumptions for the optimality function and temporal and spatial scales of integration, which all have been questioned[82]. Specific formulations of the optimality principle lead to different analytical expressions for leaf-scale conductance[122,123,124] and the approach starts to be also adopted in ESMs[125]. Note that most of the models referenced above do not directly account for effects induced by plant water stress beyond VPD, which needs to be introduced empirically, by either directly modifying $g_s$, or the parameters of the biochemical photosynthesis model[126,127], or some of the terms in the analytical form of optimal stomatal conductance[128].

**Root controls**

Roots represent an interface between plants and soil, providing entrance and initially distributed pathways for fluxes of water and nutrients from the external environment to the plant. The soil environment surrounding the root is called "rhizosphere" and can present strong gradients of water potentials and nutrient concentrations[129,130,131,132]. Roots with diameters smaller than 2 mm are

6

generally defined as "fine roots", while roots of larger diameter are named "coarse roots". Fine roots are mostly composed of living tissues and are essential for the uptake of water and nutrients, while coarse roots serve as aggregated conduits for transport and structural stability of the plant[133,134]. Water flows into the roots because the water potential is typically larger in the soil than inside the plants[135]. Situations of reverse flow from roots to soil may also occur and are typically referred to as "hydraulic redistribution"[136,137]. There is still a debate as to whether the phenomenon is a part of typical plant life process or confined to specific conditions, however it is generally believed that it is of considerably smaller magnitude than water uptake[138]. Water moves from the soil to the inner part of fine roots overcoming a barrier called Casparian strip mostly composed of suberin for isolating the plant interior, preventing for instance the entrance of pathogens. Afterwards, water movement continues across cell cytoplasm (sympalstic pathway) or through cell walls (apoplastic pathway) and reach the xylem and therefore the vascular network, where it can flow to the main stem[139,140,141]. Given a certain plant demand, water uptake is a function of the rhizosphere water potential distribution, axial and radial root conductivities, and the three-dimensional architecture of the root system[142,143,144]. The axial and especially the radial conductivities to water flow are not constant, but vary with water potential and can be partially chemically controlled by the plant through aquaporins[145,146], even though the exact mechanisms underlying this control are still uncertain. Nutrient uptake can be passive and follows water uptake or can be enhanced through osmotic gradients at the root interface or by the synthesis of various specialized transporters that are dynamically integrated into the cell membrane[147,148, 149].

The variability in soil water potential, axial and radial conductivities, and three-dimensional root architecture (Fig. 3) is preserved in a number of plant-scale models that generally have a specific emphasis on root processes[150,151,152,153,154,155,156,157]. The most common approach in ecohydrological models and ESMs is to consider only root depth (zero-dimensional model), in combination with some empirical function of water content or water potential limiting water uptake or transpiration in conditions considered to be "water stress"[157,158,159]. Several models started considering also the vertical distribution of root biomass (one-dimension[160,161]), and others include a bulk soil-to-root conductance[162,163], which is a function of the amount of roots expressed through some index such as root-length-index or root-area-index[164]. A hybrid approach has been recently developed that preserves three-dimensional information and hydraulic conductivities in a simplified form[143], and may represent an important way forward in representing hydraulic relations (and constraints) in describing the process of plant water uptake. However, an important limitation in studies of root functioning and uptake capacity is in extreme challenge of instrumenting and monitoring roots in field conditions, which has likely prevented the development of a larger number of models or conceptualization of intermediate complexity.

**Plant vascular transport**

It is currently accepted by the scientific community that water movement in the xylem is governed by the cohesion-tension theory[60,165,166], while the flow of water in the phloem follows the Münch

7

hypothesis[167,168,169]. According to the cohesion-tension theory, water molecules are transported in the plant in a metastable state generated by surface tension at the air–water interfaces in the leaves, the tension is transmitted throughout the entire water column in the plants and molecules remains cohesive among themselves and adherent to the walls because of the small size of conduits and cells. Under extreme negative potentials or external perturbations, water transport can be interrupted by formation of air bubbles (the process of cavitation) and thus the plant vascular transport becomes impaired[166].

The water flow in the xylem in the vertical, upward direction ($J_{xyl}$) in a conduit of length ($\Delta L$) can be expressed through a "flux-gradient" relation as the product of the xylem conductivity ($K_{xyl}$) and the gradient of water potential ($\Delta\Psi_{xyl}$) minus the gravitational potential ($\rho g\Delta z$):

$$J_{xyl} = K_{xyl}\left(T, \Psi_{xyl}\right)\frac{\Delta\Psi_{xyl} - \rho g\Delta Z}{\Delta L} \tag{2}$$

where the xylem conductivity $K_{xyl}$ is a plant/tissue specific parameter, which varies with temperature (T), because temperature affects the water viscosity, and water potential itself. The dependence of $K_{xyl}$ on the water potential is typically described with a sigmoidal shape and it is particularly important because it defines the resistance to cavitation, i.e., the formation of air bubbles (embolism) in the xylem. Cavitation implies a reduction of the conductive capacity of the xylem conduits[170,171,172,173], typically indicated as Percentage Loss of Conductivity (PLC) (Fig. 4). The xylem vulnerability curve (PLC versus $\Psi_{xy}$) can be described by the knowledge of the water potential at 50 % loss of conductivity ($\Psi_{xyl,50}$) and of another characteristic value (e.g., $\Psi_{xyl,12}$), typically correlated to $\Psi_{xyl,50}$[174,175]. The term $J_{xyl}$ is referred to as sapflow and can be measured directly in the plants with various methods[176].

Similarly, following the Münch hypothesis of a turgor-pressure driven flow, the water flux in phloem in the vertical downward direction ($J_{phl}$) in a conduit of length ($\Delta L$) is driven by the gradient of turgor ($\Delta P_{phl}$) plus the gravitational potential ($\rho g\Delta z$) times the phloem conductivity ($K_{phl}$), which depends on temperature and on the concentration of osmotic solutes in the phloem ($C_{phl}$) because sucrose concentration affects the fluid viscosity[177] (Fig. 4):

$$J_{phl} = K_{phl}\left(T, C_{phl}\right)\frac{\Delta P_{phl} + \rho g\Delta Z}{\Delta L} \tag{3}$$

The turgor (P) is defined as the sum of osmotic pressure ($\Pi$), directly related to the concentration of osmotic solutes through the van't Hoff relation or other empirical functions[178,179] and water potential[180,181]:

$$P = \Pi + \Psi \tag{4}$$

Conversely to sapflow, phloem flow is particularly challenging to measure due to the size of the phloem tissue and to the disturbances induced by the measurement itself. It has been only

8

measured in laboratory experiments[65,182], although promising techniques for field measurements are emerging[183].

In order for the water transport to occur, there should be a difference larger than the gravitational potential in the water potential between roots and leaves, which is typically the case during daytime in the growing season. Water is not only exchanged vertically in the phloem and xylem but it can move also radially between phloem and xylem and between storage reserves (mostly composed by living parenchyma cells residing near xylem conduits) and the xylem. These exchanges make xylem and phloem hydraulically coupled[184,185] and confer to the plant a given capacitance in absorbing fluctuations between the water demand of the leaves (transpiration) and the water uptake from the roots[186,187,188,189,190]. Capacitance is typically more significant in stems of larger trees[191] and it is due to a combination of elastic shrinkage and swelling of phloem, living bark and xylem tissue, and due to the release of water from "stiff" storage in the parenchyma cells near the xylem. Elastic shrinkage and swelling of the tree is the main mechanism to release stored water in young trees, but it becomes marginal in older trees where larger "stiff volumes" of stored water are the main contributors to tree capacitance[192,193]. In both young and old trees, the elastic behaviour of xylem and phloem is large enough to be clearly measured with high-resolution dendrometers[183,194,195], that can therefore provide important information on plant hydraulic behaviour[196,197,198]. Time-scales through which capacitance can buffer the difference between root water uptake and transpiration demand are confined to less than an hour for small young trees and in the order of several hours, or even days during droughts, for large old trees[190,199].

Only few models have been currently presented to describe plant vascular transport in detail, since the prevalent option has been to lump the entire plant system in a single conductance or resistance term[200] or to ignore plant hydraulics completely, and use the root zone soil water potential to directly simulate the controls at the leaf level (the case of ecohydrological models and ESMs, but see[125]). Important exceptions are the Sperry model[140] and the TREES model[201,202], which use a series of resistances from the soil to the leaves and xylem vulnerability curves to describe plant hydraulic behaviour; the FETCH model[203], the XWF model[204,205,206], and the model presented by Chuang et al. 2006[207], which described water flow through the plants with a porous media analogy using the one-dimensional Richards equation for the water potential along the hydraulic path. Attempts to include numerical descriptions of phloem transport, tissue growth, and diameter variations have been even more rare, although important examples are available with different degrees of complexity[177,208,209,210,211,212,213,214], as follow up of first pioneering attempts[215].

## Plant physiology during a progressive drought

When the soil water potential near the roots decreases (or VPD substantially increases), a plant may be unable to fully satisfy the transpiration demand and thus progressively enters into a phase of water stress. This is characterized by a drop of water potential throughout the various plant compartments, accompanied by a reduction of turgor in living tissues, since the plant is only partially able to compensate for lower water potentials through osmotic adjustments[216,217,218]. The first

9

process to be affected by the low water potentials is growth (Fig. 5). Cell growth is mostly the result of cell division, enlargement, and cell wall synthesis[219,220]. Cell enlargement is a function of turgor pressure[181,221,222,223]. A small reduction of water potential can decrease significantly or stop the growth well before photosynthesis or stomatal conductance are affected[224,225,226]. As the growth stops, respiration associated with the growth also ceases[227,228]. Growth impairment has been often neglected by ecohydrological literature and models but, in fact, it represents the first consequence of water stress onset.

If water potential continues dropping, plants need to preserve sufficiently high water potentials to avoid catastrophic levels of cavitation and thus start reducing the stomatal conductance (see Section "Stomatal Controls"). A reduction of stomatal conductance typically leads to a decrease in gas exchanges, e.g., photosynthesis and transpiration. These are the controls, which have been typically placed at the foundation of ecohydrology[18] and embedded in ESMs[16]. The decrease in turgor and photosynthesis further modifies the plant metabolism and carbon allocation strategies[229,230]. The decrease in transpiration alters the leaf energy budget, with lower latent heat and higher sensible heat fluxes and eventually higher emitted longwave radiation because, given constant forcing, leaf temperature tends to increase with lower stomatal conductance. A similar response in the energy budget is observed also at canopy or larger spatial scales[231].

If the drought persists further, plant vascular transport is also affected because the leaf and xylem conductivities decrease at water potentials low enough to allow the formation of emboli and thus cavitation in the xylem conduits (Section "Plant Vascular Transport", Fig. 5). At relatively low water potentials, leaves lose turgor and the photosynthetic machine starts to be structurally damaged[218,232,233]. At this stage, roots can also become completely disconnected from soil, a process typically unaccounted for in models (but see[202]). Maintenance respiration has also been found to decrease as the drought progresses[228,234]. This is probably due to a slow-down of metabolic activities, although specific mechanisms are yet not fully understood. It is indeed not rare that plants start to shed leaves when exposed to a long-lasting severe drought[235,236]. For some plants, such as drought-tolerant deciduous trees, this is actually a routinely adopted strategy[237,238,239].

The decrease or even cessation of photosynthesis poses a challenge for the plant that is called to rely only on non-structural carbohydrate reserves (NSC) for its maintenance. Permanent hydraulic failure of vascular transport and carbon starvation due to exhaustion or impossibility to access NSC, or a combination of these mechanisms have been hypothesized as reasons for plant mortality[240,241]. Recent evidence supports an earlier occurrence of hydraulic failure and a consequent blockage of NSC transport[234,242]. Regardless of the exact mechanisms, a severe and extended drought unavoidably leads to plant mortality, a phenomenon occurring in many ecosystems worldwide, even in those that are not typically associated with droughts[243,244,245]. This is particularly relevant since drought stress conditions can be potentially exacerbated by higher temperatures and VPD in the future[246,247,248]. Given the fact that the exact mechanisms that lead to plant mortality are still unknown, its modelling is a daunting task[249,250] and represents an important challenge for improving

10

models of water-vegetation interactions. Widespread plant mortality can in fact lead to a considerable shift in species composition and/or vegetation cover fraction, with potentially long-lasting consequences for surface energy exchanges and the water cycle, even though recent observations suggest that observed changes may be smaller than expectations in several ecosystems[35,36,251].

## Plot to catchment scale

Historically, vegetation was included in land-surface and hydrological models because it affects transpiration through surface roughness, albedo, and canopy resistance $r_c = r_s/LAI$, where $r_s = 1/g_s$ is the reciprocal of stomatal conductance. Through $r_c$ vegetation modifies water and energy exchanges at the land-surface because it may offer a larger resistance between soil and atmosphere with respect to bare ground in well-water conditions, and a lower-resistance in dry conditions accessing through roots relatively deep water storages. The well-known Penman-Monteith equation[11,252] accounts for these vegetation properties and it has been widely used in hydrological models. In its basic form it provides a static representation of vegetation functioning in space and time, which has been recognized to be a severe limitation in numerous contexts (e.g.[160,253]) but still provides a reasonable approximation for many other studies[254]. Consequently, models that solve explicitly and simultaneously hydrological and vegetation dynamics (Box 2) have been presented in the last fifteen years (Table 1). In literature, the definition of "ecohydrological model" has been used in very different contexts, and in this article we refer to ecohydrological models as those models that evolve in time and eventually in space some of the key vegetation states and concurrently solve the water budget. In the simplest case, they only dynamically simulate canopy resistance or LAI, while in the most complex case, a series of carbon pools and vegetation attributes (e.g., plant height, or root density) are prognostically simulated. Note that with the above definition we do not include steady-state models and analytical derivations (e.g., [52,57]). Rather than describing each ecohydrological model separately, a non-exhaustive list of models is presented in Table 1. In the following, we summarize processes that these models represent. Ecohydrological models typically solve water, energy, carbon, and, quite rarely, nutrient cycles at the land surface (Fig. 6).

## Water budget

In terms of water budget, models use precipitation as input that can be partitioned to rainfall and snowfall. Liquid precipitation can fall directly on the ground or be intercepted by the canopy, where it can subsequently evaporate or drip. Depending on the intensity of water flux reaching the ground and on soil water content (or, more appropriately, water potential) near the surface, water can either infiltrate into the soil, or run off from the surface. Solid precipitation can fall directly to the ground or become intercepted by vegetation where it can sublimate or subsequently fall to the ground. Snow accumulates on the ground in the form of snowpack, where it melts or sublimates. Water in the soil undergoes vertical and horizontal redistribution following gravitational and capillarity gradients, typically modelled with the Richards equation[255,256,257]. Depending on the

11

vertical profile of soil water potential and plant demand, water is evaporated from the surface as ground evaporation, or taken up by plants and transpired. Since water storage in the plants is typically ignored, root uptake and transpiration are exactly the same flux in most of the models. Water that percolates to deeper layers or into fractured bedrocks remains mostly inaccessible for plants (but see[258]) and typically contributes to aquifer recharge first, and streamflow at a later stage. In models that do not have an explicit representation of the spatial dimension, this water is subtracted from the water budget as "deep leakage" or "recharge". In models with an explicit spatial representation, after reaching the stream network as surface or sub-surface flow, water is routed through channel network downstream to a specified outlet.

**Energy budget**

Latent heat flux is the energy equivalent of the sum of all water vapour fluxes (transpiration and evaporation), therefore it makes the water and energy cycles tightly coupled. Models that solve explicitly the energy budget compute the latent heat flux and its partition into the different components (evaporation and transpiration) concurrently with the water budget (e.g.,[160,161,259,260,261,262]). Latent heat flux ($\lambda E$) is typically solved assuming conservation of energy in a given domain:

$$R_n - H - \lambda E - G - \lambda_p A_n - A_H = \frac{dS}{dt} \tag{5}$$

where $R_n$ is the net radiation, $H$ is the sensible heat flux, $G$ is the ground heat flux, $\lambda_p$ is the specific energy consumed in the process of photosynthesis ($A_n$), $A_H$ is the advected energy to the domain either from lateral or vertical fluxes and $dS/dt$ is the change in the energy stored into the system. Most of the models assume negligible storage capacity of energy, i.e., $dS/dt=0$, and also neglect the last two terms of the left hand side of eq. (5). Even with this assumption, the problem remains difficult to solve because all of the energy fluxes depend on one or, generally, more prognostic surface temperatures (e.g., soil, and sunlit and shaded canopy temperatures). Models that do solve the energy budget face the problem of solving one or a system of non-linear equations embedded in eq. (5), to derive the unknown surface temperature(s). This operation is typically quite computationally demanding. Therefore, several ecohydrological models still use simplified solutions of the energy budget such as the Penman-Monteith or Priestly-Taylor equations (e.g.,[263,264,265,266]).

**Carbon budget**

The carbon cycle is linked to the water and energy cycles, because carbon assimilated through photosynthesis uses the same pathway between outer atmosphere and leaf interior as transpired water (see Section "Stomatal controls") and because changes in vegetation properties (e.g., plant height and LAI) modify boundary conditions for energy and water exchanges (Fig. 6). For instance, change in LAI modifies interception capacity, energy absorption and emission, as well as roughness; a change in photosynthetic rate, $A_n$ (Eq. 1) may change stomatal conductance and therefore

transpiration. The computation of carbon assimilation can be carried out with various degrees of complexity. Some models use a biochemical model of photosynthesis, in which $A_n$ and leaf internal $CO_2$ concentration ($c_i$) are computed as prognostic variables in a non-linear equation (e.g.,[160,161, 259,261,267]), others have simpler approaches exploiting the Water Use Efficiency (WUE; i.e., the ratio between net carbon assimilation and transpiration[268]) or Light Use Efficiency (LUE; i.e., the efficiency through which radiation absorbed by vegetation is converted into carbon[269]) concepts that link empirically carbon assimilation to the transpired water or intercepted light (e.g.,[262, 266, 270, 271, 272]). In some ecohydrological models, vegetation dynamics are essentially reduced to the simulation of carbon assimilation only (e.g.,[267,273]). In others, the assimilated carbon is used to grow plants and to evolve a given number of carbon pools. Carbon pools are the way models accounts for the size and dynamics of different plant compartments[274]. The number of carbon pools varies from model to model but a typical set is composed at least of a foliage pool, a fine-root pool, a sapwood or stem pool, and, more recently, a carbon reserve pool (e.g.,[161,265]). Carbon reserves have been ignored in early ecohydrological and ESMs with rare exceptions (e.g.,[275]) but it is currently recognized that plant dynamics cannot be simulated meaningfully without accounting for carbon reserves[276,277,278]. Models that use carbon pools can also simulate the dynamics of the biophysical structure of vegetation, e.g., LAI, vegetation height, root biomass.

**Soil biogeochemistry**

Water, energy and carbon fluxes are additionally connected through soil biogeochemistry and nutrient dynamics (Fig. 6). Soil biogeochemistry is typically simulated accounting for a given number of carbon and nitrogen pools[279]. Other nutrients, such as phosphorous, sulphur, or potassium are not typically included in ecohydrological models and rarely so in ESMs (see section "Terrestrial Biosphere Models"). The number of pools varies with model complexity, but a typical approach is to explicitly represent the carbon and nitrogen contents in plant litter material and soil organic matter (SOM), partitioned into various subcomponents, as well as inorganic nutrients in mineral pools, which are directly available for plant uptake (e.g.,[280,281,282,283,284]). In more recent model formulations, the SOM pool is partitioned among the substrate (available SOM) and the microbial biomass (bacteria, mycorrhiza) that feeds on the substrate[285], while soil fauna is typically neglected. In some models, extracellular enzymes catalyzing the decomposition reactions are also explicitly represented[286,287,288]. Exchanges between the different pools are typically simulated as the first-order kinetics processes, that account for temperature and soil moisture effects, or as higher order kinetics of the type described by the Michaelis-Menten equation[279,289,290]. A fraction of carbon is lost in the decomposition process as $CO_2$ through heterotrophic respiration. This is controlled by the capacity of the soil microbial biomass to assimilate carbon, defined as Carbon Use Efficiency (CUE). The production of mineral nutrients (e.g., $NO_3^-$, $NH_4^+$) is mostly connected to the dynamics of the carbon pools and to the stoichiometry (e.g., carbon-nitrogen ratio) of litter and SOM[291,292]. Part of nutrients can be lost through deep leakage, erosion, or in the case of nitrogen through denitrification and volatilization, the remaining can be taken up by roots. Plant nutrient uptakes represent an essential component of the vegetation functioning. Nutrient uptake depends on availability of mineral

13

nutrients, root density, mycorrhiza symbiosis, plant requirements, but exact mechanisms are not fully understood and their simulation is typically quite simplified[284,285,293,294]. The link with the carbon cycle is evident since soil biogeochemistry regulates the amount of heterotrophically respired $CO_2$, and controls the nutrients accessible to the plants. Nutrient availability affects plant development because of stoichiometric constraints in building plant tissues[295] and because leaf nitrogen is known to affect photosynthetic capacity[296,297,298,299]. The linkage with plant development offers an important feedback on water and energy exchanges because plant structure (e.g., LAI, vegetation height) modifies boundary conditions at the land surface[300].

## Spatial representation of processes

The description of how models deal with the water, energy, carbon, and nutrient cycles is weakly related to the spatial dimension of the domain of simulation. In other words, the discussed processes can be used for a domain of 5x5 $m^2$ as well as 100x100 $km^2$, changing only the climate forcing and boundary conditions but largely preserving the same model structure. Although, the process importance and heterogeneity clearly changes with the spatial scale, the conceptualization remains the same and similar approaches have been used at very different scales. A main issue with increasing spatial scale is the difficulty of prescribing appropriate boundary conditions and parameter values with a consequent problem related to the "fallacy of average", i.e., the false assumption that the mean of a nonlinear function of several variables equals the function of the means of these variables[301,302]. Regardless of the scale, a spatial domain has a well-defined topography that needs to be accounted for because it affects climatic inputs such as shortwave and longwave radiation[303,304,305,306] and rainfall[307], and because lateral exchanges of water, and nutrients may become significant. Lateral exchanges of energy are believed to be less important but they are essentially unstudied. Distributed ecohydrological models are typically designed to account for lateral exchanges of water[307,308] and sometime nutrients[309,310], even when process description is simplified in a comparison to mechanistic solutions[266]. The spatial re-distribution of these resources in the simulated domain allows for an emergence of topographically controlled patterns in vegetation dynamics (e.g., different species composition in southern and northern exposed hillslopes, higher plant density near the stream network, etc.) that can eventually feedback to water and energy exchanges.

Another important aspect of the spatial dimension is represented by competition, establishment and mortality of vegetation. There are few ecohydrological models that aim to reproduce this specific behavior, and they are especially developed to study vegetation patterns in semi-arid environments [311,266,312]. These models typically compromise in the rigorousness of process description in terms of water, energy and carbon dynamics but they explicitly introduce ways, mostly based on stochastic approaches, to simulate seed dispersal, plant establishment and mortality and their interaction with resource availability (water, radiation), which are absent in more complex models. At an even simpler level, models have been proposed to describe self-organized (or self-emergent) vegetation patterns in semi-arid environments using systems of partial differential equations, borrowed from

14

dynamic systems theory (e.g., [313]). While these studies are quite distant from the representation of the physical processes, they are important to put forward hypotheses on the controls of vegetation spatial organization and regular patterns observed in semi-arid ecosystems[314,315,316,317,318,319,320].

## Global scale

### Terrestrial biosphere models

The request for quantifications of global carbon and water cycles and plant biogeography, especially in the context of understanding consequences of climate change was conducive to the development of models able to simulate vegetation dynamics (Box 2) at the global scale[13,321,322,323,324,325]. These models are indicated with various names: Dynamic Global Vegetation Models (DGVMs), Terrestrial Biosphere Models, Terrestrial Ecosystem Models, and more recently, as vegetation components of Earth System Models (e.g.,[14,326,327,328,329,330]). Here, the term terrestrial biosphere models is used to refer to this family of models[13]. Typically, terrestrial biosphere models simulate water, energy, carbon, and nutrient cycles using an approach similar to the ecohydrological models described earlier. As a matter of fact, in most cases formulations of carbon dynamics and soil biogeochemistry have been first developed for these models (e.g.,[15,331,332]) and subsequently adopted into ecohydrological models. A detailed description of terrestrial biosphere models can be found in recent reviews by Prentice et al. 2007[333], Levis 2010[334], Quillet et al. 2010[335], Medlyn et al 2011[336], Fisher et al. 2014[13] and a list of popular models is presented in Table 2 along with a summary of the specifications of each model. The simulated biophysical and biochemical processes are to a large extent similar to the processes described in Section "Plot to catchment scale". We rather emphasize the main differences in comparison to ecohydrological models, related to (i) spatiotemporal scale of application, (ii) model initialization and boundary conditions, and (iii) biogeography and forest demography. We acknowledge that there is a tendency toward convergence in process description between certain ecohydrological and terrestrial biosphere models and in the future the separation may become semantic or mostly a function of the type and scale of application.

A major distinction between ecohydrological and terrestrial biosphere models relies on the different spatiotemporal scales of their applications, and thus the generality that the latter are meant to achieve. Terrestrial biosphere models are not tailored to any particular place or catchment and have to simulate vegetation occurring in the entire Earth surface. In addition, terrestrial biosphere models typically address research questions for longer time scales, when compared to the time horizons of ecohydrological studies, even though exceptions exists and some ecohydrological models have been also developed for long-term analyses[263,309]. This implies that their structure needs to be flexible enough to include various processes and parameterizations and to simulate vegetation response across a large range of climatic conditions and time scales. However, structural and parameterization issues may emerge due to simplified assumptions introduced for the sake of generality and flexibility, as pinpointed recently by Pappas et al. 2013[337]. Furthermore, because the spatial representation in terrestrial biosphere models is in the order of several $km^2$, they cannot account

15

explicitly for topography. Each computational element may receive a different climate forcing, but, in essence, terrestrial biosphere models are one-dimensional since they do not exchange laterally mass and nutrient fluxes and the effect of local topography in controlling meteorological inputs is not accounted for.

The large spatiotemporal scales of the typical applications carried out with terrestrial biosphere models, requests a different philosophy for assigning the initial conditions (state variables) for the numerical simulations. While for ecohydrological models a initialization period of few years is typically able to bring the examined ecosystem to a representative state (since the vegetation component is often assumed to be in a mature state), longer spin-up periods are required for the initialization of terrestrial biosphere models that simulate short- and long-term soil biogeochemical processes (e.g., soil organic matter and nutrient dynamics). All terrestrial biosphere models account for soil carbon dynamics, many of them for nitrogen (e.g.,[283,284,338]) and a minor fraction for phosphorous cycle[339,340,341]. It is worth underlying that, although often unrealistic, the assumption of vegetation in equilibrium with the observed environmental conditions (climate, nutrient deposition, weathering rates) is commonly and unavoidably applied for the spin-up of terrestrial biosphere models (e.g.,[302]). In addition, contrary to the confined spatial extent (i.e., plot and catchment scales) and to the relatively short time-scales (i.e., less than 30 years) of the ecohydrological applications, the applications of terrestrial biosphere models address research questions at the regional or global scales with time horizons of several decades or centuries. Therefore, land use and vegetation cover are often not pre-assigned, as typically done in ecohydrological applications, but are prognostic variables computed by the model. For the same reasons, processes such as forest demography, natural or anthropogenic disturbances, e.g., fire, windthrow, plant diseases, insect attacks, forest management, and plant competition needs to be represented. Feedbacks on vegetation dynamics due to nutrient cycles are also much more relevant at those temporal scales than are for ecohydrological applications, at least in forests[342]. Forest demography in terrestrial biosphere models is similar or identical to the one developed for forest-gap models in forestry research[343,58]. Forest demography can be handled evolving in time an average tree individual[344,345,346], or by simulating cohorts of individuals with different age classes and size in the stand (e.g.,[58,302,347,348,349]). This allows, for instance, an explicit representation of early and late successional species and more generally of heterogeneous forests with gaps, uneven stand height and density[350,351]. Disturbances are typically very difficult to simulate mechanistically, even though recently a general framework has been presented[352], and are mostly simulated removing a certain amount of biomass in a given domain with a given probability of disturbance occurrence. Plant competition is often simulated implicitly assigning "bioclimatic limits" of existence (temperature, soil moisture, or light thresholds for establishment) to specific species or plant functional types, or removing plants that are underperforming from a carbon balance perspective (e.g.,[344,353]). Mortality is far from being mechanistically simulated[354] and is typically related to plant negative carbon balances or prescribed with given constant probabilities or as a function of plant age or size[355,356]. This background mortality is typically summed with the probability of disturbance occurrence.

**Vegetation feedbacks to the climate system**

There are several examples of successful applications of terrestrial biosphere models, which elucidate feedbacks between vegetation dynamics and climate or hydrological cycle at the global and regional scales. One example is represented by the predictions of the fate of the Amazon forest. Early findings suggested potential dieback of the Amazon rainforest in response to projected droughts, with huge implications for the future of Earth's climate[357]. While these extreme projections have been moderated using more refined models, the response of the Amazon forest to a changing climate remains very uncertain (e.g.,[358,359,360,361,362]). There is a large community effort dedicated to better understand the effect of drought on the Amazon forest (e.g., [363,364,365,366]) because current observations and future predictions are suggesting a potential lengthening of the dry intervals and an increase of drought risk[367,368]. At local scales, Amazon deforestation has been demonstrated to affect cloud formation and convective precipitation, because it changes the partition of net radiation into sensible and latent heat, thus affecting boundary layer development. This has the possibility to increase or decrease convective precipitation downwind of the cleared patches as a function of the deforestation extent[369,370,371].

Another significant example is represented by the observed tree and shrub encroachment at high latitudes. The prognostic nature of vegetation cover in terrestrial biosphere models allows them to simulate shrub encroachment and tree line shifts following, for example, Earth warming. While the exact causes of tree and shrub encroachment are still uncertain[372,373], shrub presence in previously non-vegetated or poorly vegetated areas of the Arctic has the capacity to modify the hydrology and the energy exchanges between the land and the atmosphere. If shrubs grow taller than typical winter snowpack height, the albedo of the surface is substantially decreased, and at the same time the longwave radiation regime is modified[374]. These changes in vegetation have a positive feedback on local and global warming with the potential to further push shrub encroachment or northern tree line expansion[375].

A final example of important interactions between plants and the water cycle is related to the consequences of increasing atmospheric $CO_2$ concentration. Elevated $CO_2$ concentration has a well-known direct physiological effect at the leaf level, increasing photosynthesis and reducing stomatal conductance[376,377]. The increased plant productivity associated with elevated $CO_2$ is typically indicated as $CO_2$ fertilization effect (e.g.,[378]). The integration of this effect from leaf to the global scale is still debated[379,380] but it has been postulated to have contributed to increase runoff[381,382] and be largely responsible for the terrestrial carbon sink with direct feedbacks on Earth climate[23,383,384]. While the magnitude of $CO_2$ fertilization at the ecosystem scale and the persistence of the carbon sink in time are still open research areas[362,385,386,387], it represents one additional example that robust long-term projections of future water cycle cannot be made without accounting for vegetation physiology.

**Process up-scaling**

17

**Forcing and boundary conditions**

The models described in the previous sections (plant hydraulic, ecohydrological, and terrestrial biosphere models) are designed to address scientific quesons at different spatiotemporal scales. Plant hydraulic models are typically forced with very detailed meteorological inputs and boundary conditions (e.g., soil type, tree height and diameter, root depth, plant hydraulic traits, etc.) but they are used to simulate a single tree or a specific forest stand and for a relative short period of time (a growing season, few years). It would be in fact unrealistic to simulate each individual tree at the continental scale. At larger spatiotemporal scales, different model types are typically applied. Ecohydrological models are normally employed from the plot to the catchment scale, while terrestrial biosphere models are used from the plot to the global scale. As described previously, terrestrial biosphere models cannot account for fine-scale heterogeneities (e.g., topography, climate) because the spatial resolution at which they usually operate is in the order of several $km^2$. This limitation has been shown to be more relevant than previously thought because the mean response obtained with meteorological forcing and boundary conditions mediated over a large area can be different from the mean of the responses obtained with a detailed treatment of input and boundary conditions[302]. In other words, the non-linear dynamics inherent to hydrological and vegetation processes play a considerable role. In an analogy, the temporal resolution of the model is also very important[388,389] because coarse temporal resolutions do not allow solving non-linear effects produced by short-term variability in the forcing (e.g., shortwave radiation). In this regard, however, differences among models are less marked, most of the ecohydrological and terrestrial biosphere models are using an hourly or half-hourly time-step for the forcing, at least to solve hydrological and energy dynamics, with few models still using daily or longer scales (e.g.,[348]). Plant growth, soil biogeochemistry and forest demography processes have typically slower dynamics that can be simulated at the daily time scale or even annually for processes such as forest demography.

**Vegetation heterogeneity**

A very important "boundary condition" in any model that deals with vegetation is how the vegetation itself is parameterized. Historically, the existing diversity in species and plant traits (e.g., [390]) has been summarized using a given number (~8-25) of Plant Functional Types (PFTs), that aimed to distinguish climatic zone (e.g., temperate, boreal, tropical), phenology (evergreen, deciduous), and leaf morphology (e.g., needleleaves, broadleaves) of the plant[391]. This approach has been utilized in both ecohydrological and terrestrial biosphere models because it allowed a synthesis of important differences in plant properties as well as phenological behaviour without entering in the details of exact species or intra-species variability. Recently, the PFT approach has been widely criticized and new approaches based on the definition of plant traits and their distributions are becoming progressively popular (e.g.,[33,392,393,394,395]). These approaches rely on the knowledge of observed distributions of plant properties, "traits", which correspond or can be related to model parameters, such as, maximum photosynthetic capacity, leaf nitrogen content, specific leaf area, root depth and turnover rates, leaf dimension, etc. Beyond the distribution of the values of a given

18

plant trait, there are several ecological studies that show a certain degree of coordination between many of these traits[396,397,398]. An illustrative example is the "leaf economics spectrum" that suggest that leaf traits co-vary in a continuum from leaves with a high photosynthetic capacity, nitrogen content, and specific leaf area index and short lifespan typical of fast growing species to the opposite combination typical of slow growing species[399,396]. While cross-correlations have been mostly studied for leaf traits, there is emerging evidence that this holds true for many plant traits[400] and such information can be transferred to the model parameters. Observed trait distributions and cross-correlation can be used to create "proxy species", which do not correspond exactly to an observed species but are deemed as realistic within the range of observed natural variation. Models can then use a large number of these "proxy species" to investigate the importance of variability in plant traits in carbon and water dynamics in a given region, or directly use observed distributions of plant traits as input. Note that the latter should be typically weighted for the occurrence of a given species in a specific place or region. Despite the huge amount of biodiversity, forest biomass and productivity are in fact mostly controlled by a limited number of dominant species[401]. A great advantage of the probabilistic approximation of plant trait diversity, based on multivariate distributions of whole-plant trait spectra, rather than on few PFTs or species, is that it allows for a probabilistic assessment of ecosystem response and thus provides a framework for quantifying uncertainties related to vegetation spatiotemporal heterogeneity[33,393].

## Data for model parameterization and confirmation

Any model, regardless of the scale, needs climate forcings as well as data that can be used for confirmation of model results. Meteorological forcing requirements are similar in most of the models and include air temperature, precipitation, relative humidity, wind speed, atmospheric pressure, $CO_2$ concentration, and shortwave and longwave radiation. Boundary conditions consist of soil properties, such as soil depth, soil texture or soil hydraulic properties (e.g.,[402,403]), and vegetation properties represented by functional and morphological plant traits (see Section "Vegetation heterogeneity"). In the case of distributed simulations, land-cover, topographic and geologic information is also required. Modelling of soil biogeochemistry and nutrient cycle theoretically needs additional data about initial values of nutrient content, nutrient deposition and primary minerals weathering together with a number of parameters that characterize kinetics and turnover rates of microbial biomass and organic substrate in the soil (e.g.,[288,404,405]).

There are multiple measurements that can potentially be used in models and that are carried out directly at the plant scale in one or multiple individuals. These are  leaf and stem water potential, sapflow, stem diameter changes, leaf turgor, leaf temperature, gas exchange measurements at leaf, root and stem level (Table 3). Additionally, plant hydraulic traits such as stem capacitance and vulnerability curves or biochemical traits such as the ones related to photosynthesis are necessary for accurate parameterization of stomata and plant hydraulic models (e.g.,[249]). When combined together these measurements do provide a rather complete characterization of plant behaviour, with a notable exception represented by short term carbon allocation dynamics (phloem transport,

19

tissue growth and respiration), which are currently very difficult or impossible to measure in the field and mostly limited to leaf growth and point measurements of non-structural carbohydrates repeated few times during a season[406].

Moving from the plant to the plot/stand scale, measurements are not typically carried out anymore on the individual plants but express an integrated quantity over a given area. This type of measurements includes: (i) energy and mass exchange between the land surface and the atmosphere obtained with flux-tower monitoring systems that employ the eddy covariance technique[407,408,409,410,411] (ii) soil water content and temperature, and soil respiration at different locations. Measurements of soil water content provide a direct quantification of one of the key variable in the water-vegetation interaction but are difficult to upscale from the sensor level to stand scale due to considerable spatial heterogeneities[412,413,414,415]. Flux-tower measurements are instead an up-scaled quantity but have problems of continuity and interpretation[416,417]. Despite well-recognized issues[418,419], flux-tower observations have represented and still represent the major source for validation of ecohydrological and terrestrial biosphere models, since they provide values for variables such as latent and sensible heat, net radiation and mass fluxes of water vapour and carbon. Lysimeters can be also used to measure directly leaching of water and nutrients and the water content variation in soil monoliths, and, therefore, evapotranspiration[420,421]. This measurement is probably the most precise and continuous estimate of evapotranspiration fluxes but it is very expensive to set-up and maintain. Moving from fluxes to stocks, forest inventories represent an important source of information to characterize standing and dead biomass, and plant demography (age, size, and species). When inventories are repeated systematically in time, they also provide information on plant turnover rates, mortality and growth (e.g.,[422,423]) and they can be used for model testing (e.g.,[351,302]). Recently, tree ring dendrochronology has been presented as a possibility to test simulations of carbon accumulation as well as the effect of infrequent disturbances[424]. Despite the numerous problems, existing in the scaling from single trees to areal estimates, it represents a potential additional source for model validation.

An alternative way to test models is the recourse to observations carried out during ecological manipulation experiments, e.g., rainfall exclusion and addition, warming, $CO_2$ enrichment (FACE), girdling, and nutrient additions. Such experiments can be used to test whether models can reproduce the effect of treatment at least in terms of observed sensitivity (e.g.,[365,425,426,427,428]). When models are able to do so without changing their parameterization, this represents an important validation of their predictive skills for conditions different from the current climate. Manipulation experiments have been mostly focused in measuring vegetation productivity, especially in grassland, but other metrics can be also monitored and used for model validation, especially if new experiments will be designed with this additional scope in mind[428,429,430]. In fact, despite their potential importance, manipulation experiments have been seldom used for model testing so far.

Moving to larger spatial scales, direct observations become more challenging and remote sensing as LIDAR and hyperspectral cameras have been recently employed. Observational devices can be

20

placed over land or aircraft platforms or on satellites[431,432]. Remote sensing observations can be carried out with optic or radar sensors and are mostly used to measure vegetation reflectivity indices, carbon stocks, and soil moisture. Carbon stocks are typically observed with radar sensors and at the regional scale (e.g.,[433,434]). Optic observations in multiple spectral bands are typically mapping the entire Earth and they are used to derive vegetation indices as the Enhanced Vegetation Index (EVI), the Normalized Difference Vegetation Index (NDVI), or chlorophyll fluorescence[435,436]. Signals in multiple bands can be also processed and converted into variables such as LAI, carbon assimilation[437,438] or nutrient contents of the leaves[439,] although the reliability of these estimates is still uncertain (e.g.,[440,441]). A few remote sensing products are also available for near surface soil water content (e.g.,[442]), as well as promising results in this direction are expected from campaigns as Soil Moisture Active Passive (SMAP)[443]. Finally, anomalies of atmospheric $CO_2$ concentration are an important source of information to estimate the net carbon uptake or release over very large areas and at the seasonal and annual time-scale[384,444], and they may become even more so in the future[445].

## Conclusion

The examined literature suggests that approaches to simulate the intertwined dynamics of water, energy, carbon, and nutrients cycles are becoming widely available and that a number of models of different complexity has been presented to address problems at various scales. While the combination of hydrology and ecology can be considered a reality, additional efforts need to be devoted to integrate solutions developed for different scales.

The issue of scales is not merely an operational one related to finding better parameterizations but requires innovative approaches to preserve key physical and ecological mechanisms operating locally as well as heterogeneities into larger-scale applications. We do not mean that the entire complexity of plant-hydraulic or detailed biogeochemistry models should be retained into ecohydrological or terrestrial biosphere models but there is a wide margin to better use insights gained at local scales into watershed, regional and global applications (see[125]). For instance, models simulating mechanistically plant hydraulic and carbon dynamics are still rare and confined to specialized studies[202,208,209,214], but they have the potential to improve considerably representation of fundamental aspects such as plant growth, response to elevated $CO_2$, response to severe droughts or pathogen attacks, and ultimately plant mortality. These are subjects where we still have gaps in process understating and where a well-structured combination of modelling and observations is likely to provide insights well beyond model improvements, potentially increasing fundamental knowledge of plant-water interactions. Modelling plant mortality has been regarded as one of the great scientific challenge[446] and surely it is, but we should not forget that current models still struggle to simulate correctly the response to water limitations[447]and have limited flexibility to accommodate diverging response across species or within a landscape[33,302].

Most of the processes underlying plant-water interactions are highly non-linear, this implies that averaging significant heterogeneities in space and time may lead to considerable biases. While the importance of solving ecohydrological processes at the sub-daily temporal scales is progressively

21

recognized[388,389,448] and implemented in most of the models, the relevance of being spatially explicit has been less emphasized in literature[302]. Few studies presented process-based simulations accounting explicitly for topographic attributes and lateral water and mass exchanges[300,307,308,449]. Applications at regional or continental scale of ecohydrological models or the introduction of topography in terrestrial biosphere models will represent possible solutions. These solutions bring along operational issues related to computational resources and accurate model parameterizations. Large spatial and long temporal scales pose great challenges for model initialization and validation, since current available data are typically inadequate when compared to the diversity of model outputs. A better integration of data from multiple platforms and scales and especially of remote sensing estimates is thus essential for improving distributed and/or continental scale models. A more rigorous treatment of uncertainty with stochastic analyses and probabilistic predictions should also represent an important avenue for the future, since many model parameters (e.g., plant and microbial traits) are unlikely to be known with a high accuracy everywhere and vary, not only in space but also in time[33]. Studies and modelling of plant-water interactions have seen great advancements in the past years but current shortcomings and the challenges pose by environmental changes and preservation of water resources and ecosystem services are suggesting that exciting times are still ahead.

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**Box 1: Plant physiology: definitions**

Definitions of plant physiological terms are provided to guide readers. **Xylem** refers to non-living vascular conduits of plants that transport water from the roots to the leaves (Fig. 4). **Phloem** refers to vascular conduits that transport sugars produced by photosynthesis to other tissues in the plant (Fig. 4). **Water potential** is the potential energy of water per unit volume relative to pure water in reference conditions. Water potential quantifies the tendency of water to move from one area to another due to osmosis, mechanical pressure, or matrix effects such as capillary action. **Cavitation** is the processes that leads to formation and growth of vapour bubbles in a liquid, in the case of plants it occurs within the xylem. **Non-structural carbohydrates** (NSC) are the free, low molecular weight sugars (glucose, fructose and sucrose) plus starch, readily available for transport and plant metabolism. **Abscisic acid** (ABA) is a plant hormone involved in many plant processes, including stomatal closure, bud dormancy, leaf abscission. **Aquaporins** are integral membrane proteins that form pores in the membrane of biological cells and allow for the selective passage of water. **Cytoplasm** is the portion of the cell that is enclosed within the cell membrane and is composed by organelles and a gel-like substance. **Suberin** is a waterproofing waxy substance present in the cell walls of certain plant tissue.

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**Box 2: Vegetation dynamics**

The term "vegetation dynamics" when referred to models may have different meanings according to the context where it is used. In a large fraction of terrestrial biosphere model literature, *vegetation*

22

*dynamics* is used for referring to models where the vegetation type (e.g., PFT or species) is prognostic in space and time. In other words, vegetation dynamics are related to processes such plant establishment and mortality, forest demography, disturbances that may modify the amount and type of vegetation occurrence. In ecohydrological model literature, *vegetation dynamics* typically refer to model that simulate prognostically vegetation attributes such as leaf area index, root density, carbon allocation or more generally a number of carbon pools. Finally, in some context *vegetation dynamics* may simply refer to a model that is simulating the temporal evolution of processes connected to vegetation but not directly linked to the plant structure such as photosynthesis, respiration or stomatal conductance. For sake of generality, in the article we use the broadest definition of *vegetation dynamics* that includes both fast and slow processes through which models simulate temporal evolution of plant properties.

**Notes**

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**Figure captions**

**Fig. 1** Plant-water interactions are occurring over a broad range of spatial scales from (a) leaf interior (≈ μm) to (b) individual plant (≈ m), to (c) catchments (≈ km) up to (d) the entire Earth. Map of evapotranspiration on the Rietholzbach catchment[25] and the annual global estimate of evapotranspiration from the MOD16 product[450] are shown. (e)The increasing attention that is paid by the scientific community to ecohydrology is reflected in the number of published articles and the citations they received during the last 16 years (Source: ISI Web of knowledge, August 2015). The average increasing rate of publication in scientific literature is also shown as benchmark[451]. The MODIS map is reproduced by permission of Elsevier[450], the leaf section is reproduced by permission of John Wiley and Sons[71].

**Fig. 2** A leaf is mostly composed of mesophyll and epidermal cells. The mesophyll is subdivided in palisade and spongy mesophyll. The epidermis secretes a waxy substance called the cuticle to separate leaf interior from the external atmosphere. Among the epidermal cells, there are pairs of guard cells. Each pair of guard cells forms a pore called stoma. Water and $CO_2$ enter and exit the leaf mostly through the stomata. The vascular network of the plant is composed of xylem (blue) that transports water to the leaf cells and of phloem (red), which transports sugars from the leaf to the rest of the plant. Water that get off the xylem is evaporated in the leaf interior (dashed lines). The term $\Psi_{x,v}$ $\Psi_m$, $\Psi_e$, $\Psi_g$, $\Psi_i$, and $\Psi_a$ are the water potential in the xylem of leaf vein, mesophyll cell, epidermal cell, guard cell, leaf interior, and atmosphere, respectively. Stomatal aperture responds positively to guard cell turgor pressure ($P_g$) and negatively to epidermal cell turgor pressure ($P_e$) (hydromechanical feedback). The conductance of the stomatal aperture ($g_s$) decreases with water potential in the leaf due to a combination of hydraulic and chemical factors.

**Fig. 3** Representation of plant- and patch-scale root systems suitable for explicit 3-D hydraulic models of plant water and nutrient uptake. (a) Spatial distribution of tree stems and their root systems based on measurements at the University of Michigan Biological Station[414]: the central dot is tress stem (diameter ≥ 10 cm), the solid line shows the maximum lateral root extent, while the

63

dashed line delineates distance corresponding to 95% of vertically and radially integrated root length. (b) Plant-scale properties of root distribution are controlled by using explicit root architecture obtained with the RootBox software[452]. Roots of different order (color-coded) as well as overlapped areas where competition for soil water and nutrients occurs are shown for three exemplary trees. (c) Patch-scale property of root distribution with depth is inferred from in situ observations of the bulk biomass density[414] converted to the length density from variations of root diameters and specific density. For each depth, the median density, 25-75%, and 10-90% ranges of the obtained distribution are shown.

**Fig. 4** Global view of long-distance water and carbohydrate transport pathways in a vascular plant. The xylem mediates the net transfer of water from the soil to the atmosphere down a gradient in water potential, $\nabla\Psi$. The phloem carries a flow of sugars and other metabolites down the plant from the leaves to the tissues. Optical micrographs show cross sections of a leaf, stem, and root with the approximate location of the xylem (blue) and phloem (orange). Typical curves for changes in stem relative water content (RWC) and xylem cavitation expressed as Percentage Loss of Conductivity (PLC) as a function of water potential are shown along with the increase in fluid viscosity as a function of sucrose osmotic concentration. The figure is copied and adapted from[66]. Permission will be acquired for the final manuscript version.

**Fig. 5**. Effects on plant physiology caused by a decrease in water potential and turgor. The length of the horizontal lines represent the range of stress levels within which a process becomes first affected. Two different levels of minimum water potential $\Psi$ are given: -2 and -12 MPa, these are indicative and correspond to a value characteristic for drought intolerant plants/crops and one for drought-adapted plants in deserts. Dashed lines signify an incipient or vanishing effect. The figure is inspired to Hsiao et al. 1976[216] and Porporato et al. 2001[18].

**Fig. 6** Ecohydrological and terrestrial biosphere models have components and parameterizations to simulate the (i) surface energy exchanges; (ii) the water cycle, (iii) the carbon cycle and (iv) soil biogeochemistry and nutrient cycles. Many models do not include all the components presented in the figure.

**Tables**

**Table 1.** A non-exhaustive list of ecohydrological models. The presence or absence of specific processes is indicated with a yes (Y) or no (N) and with additional specifications.

| MODEL | Key Reference | Water Budget | Energy Budget | Carbon Pools | Nutrients | Photosynthesis and stomatal | Spatial Representation | Water Routing | Plant spatial dynamics |
|-------|--------------|--------------|---------------|--------------|-----------|----------------------------|------------------------|---------------|------------------------|
| T&C Tethys-Chloris | *Fatichi et al 2012; 2014,* [161,25] | Y (Richards -Multilayer) | Y (1 prognostic temp.) | Y (7 Pools) | N | Y (Biochemical + Leuning) | Y (Grid) | Y | N |

64

| Model | Reference | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| tRIBS-VEGGIE | *Ivanov et al 2008,* [160] | Y (Richards-Multilayer) | Y (2 prognostic temp.) | Y (4 pools) | N | Y (Biochemical + Leuning) | Y (TIN) | Y | N |
| MLCan | *Drewry et al 2010,* [261] | Y(Richards-Multilayer) | Y (Multilayer temp.) | N | N | Y (Biochemical + Ball-Berry) | N | N | N |
| RHESSys | *Tague and Band 2004, Tague et al 2013 ,* [263, 449] | Y (Two layers) | N( Penman-Monteith) | Y (3 pools) | Y | Y( Empirical) | Y (Semi-distributed) | Y | N |
| CATHY/NoahMP | *Niu et al 2014,* [273] | Y(Richards-Multilayer) | Y (2 prognostic temp.) | N | N | N | Y (Grid) | Y | N |
| PAWS+CLM | *Shen et al 2013,* [300] | Y (Richards-Multilayer) | Y (3 prognostic temp.) | Y( 4 Pools) | Y | Y (Biochemical + Leuning) | Y (Grid) | Y | N |
| Geotop-dv | *Della Chiesa et al 2014,* [262] | Y (Richards-Multilayer) | Y (1 prognostic temp.) | Y( 3 Pools) | N | Y( Empirical) | Y (Grid) | Y | N |
| CATGraSS | *Zhou et al 2013,* [266] | Y- Bucket | N( Penman-Monteith) | Y (3 pools) | N | Y( Empirical) | Y (Grid) | N | Y |
| ---- | *Van Wijk and Rodriguez-Iturbe 2002,* [311] | Y (Bucket) | N | N | N | N | Y | N | Y |
| VELMA | *Abdelnour et al 2011,* [37] | Y (Four layers) | N(Empirical) | Y | Y | N | Y | Y | N |
| CANOAK | *Baldocchi and Wilson 2001,* [453] | Y(Multilayer) | Y (Multilayer temp.) | N | N | Y (Biochemical + Ball-Berry) | N | N | N |
| --- | *Nouvellon et al 2000,* [454] | Y (Three layers) | N( Penman-Monteith) | Y( 3 Pools) | N | Y (Empirical) | N | N | N |
| VDM | *Montaldo et al 2005,* [264] | Y (Bucket) | N( Penman-Monteith) | Y (3 Pools) | N | Y (Empirical) | N | N | N |
| Topog-IRM | *Vertessy et al 1996,* [455] | Y (Richards-Multilayer) | N( Penman-Monteith) | Y ( 3 pools) | N | Y (Empirical + Leuning) | Y ( Flow-net) | Y | N |
| --- | *Cervarolo et al 2010,* [271] | Y (Richards-Multilayer) | Y (1 prognostic temp.) | Y ( 3 pools) | N | Y (Empirical+Jarvis) | Y (Grid) | Y | N |
| CABALA | *Battaglia et al 2004,* [456] | Y (Bucket) | N( Penman-Monteith | Y ( 6 pools) | Y | Y (Biochemical + Ball-Berry) | N | N | N |
| CenW 3.1 | *Kirschbaum et al 2007,* [265] | Y (Multilayer) | N( Penman-Monteith | Y (10 pools) | Y | Y (Biochemical + Ball-Berry) | N | N | N |
| CASTANEA | *Dufrene et al 2005,* [457] | Y (Three layers) | Y (2 prognostic temp.) | Y (5 pools) | N | Y (Biochemical + Ball-Berry) | N | N | N |
| MuSICA | *Ogée et al 2002,* [259] | Y (Two layers) | Y (1 prognostic temp.) | N | N | Y (Biochemical + Leuning) | N | N | N |
| WEB-DHM | *Wang et al 2009,* [288] | Y (Richards-Multilayer) | Y | N | N | Y (Biochemical + Ball-Berry) | Y (Grid) | N | N |
| BEPS-TerrainLab | *Govind et al 2009,* [458] | Y (Two layers | N( Penman-Monteith) | Y( 4 Pools) | Y | Y (Biochemical + Empirical) | Y | Y | N |

**Table 2.** A non-exhaustive list of terrestrial biosphere models. The presence or absence of specific processes is indicated with a yes (Y) or no (N).

| MODEL | Key Reference | Energy Fluxes | Water Fluxes | Carbon model | Nitrogen Model | Plant Establ./Mortality/Disturbances | Carbon reserves | Root exudation | Mychorrizal |
|---|---|---|---|---|---|---|---|---|---|
| CN-CLASS | *Arain et al 2006,* [338] | Y | Y | Y | Y | N | Y | N | N |
| JULES-TRIFFID | *Clark et al 2011,* [459] | Y | Y | Y | N | Y | N | N | N |
| Noah-MP | *Niu et al 2011,* [460] | Y | Y | Y | N | N | N | N | N |
| LPJ | *Sitch et al 2003,* [344] | N | Y | Y | N | Y | N | N | N |
| ORCHIDEE | *Krinner et al 2005,* [345] | Y | Y | Y | N | Y | Y | N | N |
| CLM-DGVM | *Levis et al 2004,* [461] | Y | Y | Y | N | Y | N | N | N |
| CLM4CN | *Lawrence et al 2011,* [462] | Y | Y | Y | Y | N | N | N | N |
| IBIS | *Kucharick et al 2000,* [463] | Y | Y | Y | Y | Y | N | N | N |
| ISAM | *Yang et al 2009,* [464] | Y | Y | Y | Y | N | N | N | N |
| DLEM | *Tian et al 2010,* [465] | Y | Y | Y | Y | Y | N | N | N |
| Biome-BGC | *Thornton et al 2002,* [466] | Y | Y | Y | Y | Y | N | N | N |
| ED2 | *Medvigy et al 2009,* [349] | Y | Y | Y | Y | Y | Y | N | N |
| Ecosys | *Grant et al 2009,* [467] | Y | Y | Y | Y | N | Y | N | Y |
| MOSES-TRIFFID | *Cox 2001,* [468] | Y | Y | Y | N | Y | N | N | N |
| JSBACH | *Goll et al 2012,* [340] | Y | Y | Y | Y | N | Y | Y | N |
| LPJ-DyN | *Xu-Ri and Prentice 2008,* [283] | N | Y | Y | Y | Y | N | N | N |
| O-CN | *Zaehle and Friend 2010,* [284] | Y | Y | Y | Y | Y | Y | N | N |
| Hybrid3.0 | *Friend et al 1997,* [275] | Y | Y | Y | Y | Y | Y | N | N |
| ANAFORE | *Deckmyn et al 2008,* [163] | Y | Y | Y | Y | Y | Y | N | N |
| SEIB-DGVM | *Sato et al 2007,* [469] | N | Y | Y | N | Y | Y | N | N |
| Sheffield-DGVM | *Woodward and Lomas 2004,* [470] | N | Y | Y | Y | Y | N | N | N |
| LPJ-GUESS | *Smith et al 2001,* [348] | N | Y | Y | N | Y | N | N | N |
| aDGVM2 | *Scheiter et al 2013,* [471] | N | Y | Y | N | Y | N | N | N |
| FoBAAR | *Keenan et al 2012,* [472] | N | N | Y | N | N | Y | N | N |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| CASA | *Carvalhais et al 2008,* [473] | N | Y | Y | Y | N | | N | N | N |
| JeDi-DGVM | *Pavlick et al 2013,* [353] | N | Y | Y | N | Y | | Y | N | N |

**Table 3**. List of variables that can be potentially observed at different scales.

| Scale | Variable | Instrument/Product |
|---|---|---|
| Plant | Sapflow | Sap flow meter |
| Plant | Leaf Water Potential | Pressure chamber |
| Plant | Stem Water Potential | Psychrometer |
| Plant/Stand | Tree/Branch Diameter | Forest Inventory |
| Leaf | Photosynthesis Stomatal conductance | Gas analyzers |
| Leaf/Stand | Leaf/Canopy temperature | IR Thermometers, Thermocouple, Thermal cameras |
| Leaf | Turgor | Turgor probes or estimated from water potential and osmolyte concentration |
| Plant | Plant Respiration | Gas analyzers |
| Plant | Stem water content | Coring, Moisture probe |
| Stand | Evapotranspiration | Lysimeter, Flux-tower |
| Point/Stand | Soil Respiration | Gas analyzers |
| Plant/Stand/Global | Leaf Area Index | Direct sampling, Optical sensors, Remote Sensing |
| Plant | NSC dynamics (leaves and branches and fine roots) | Sampling and laboratory analysis |
| Point/Stand | Soil water potential (tensiometers) and volumetric water content | Soil moisture probe and tensiometer, Remote sensing |
| Point/Stand | Soil temperature | Thermometers |
| Stand | Energy fluxes (LE, H) | Flux towers |
| Stand | Carbon fluxes (NEE) | Flux towers |
| Stand/Regional | Aboveground carbon stocks | Forest Inventories, Remote Sensing |
| Stand/Regional | Tree Height | Forest Inventories, Remote Sensing |
| Regional/Global | Vegetation reflectivity Indices (NDVI, EVI, chlorophyll fluorescence) | Remote Sensing |
| Regional/Global | Surface temperature | Remote Sensing, IR Thermometers |
| Regional/Global | $CO_2$ anomalies | Remote Sensing, Stations |
| Regional/Global | Albedo | Remote Sensing |

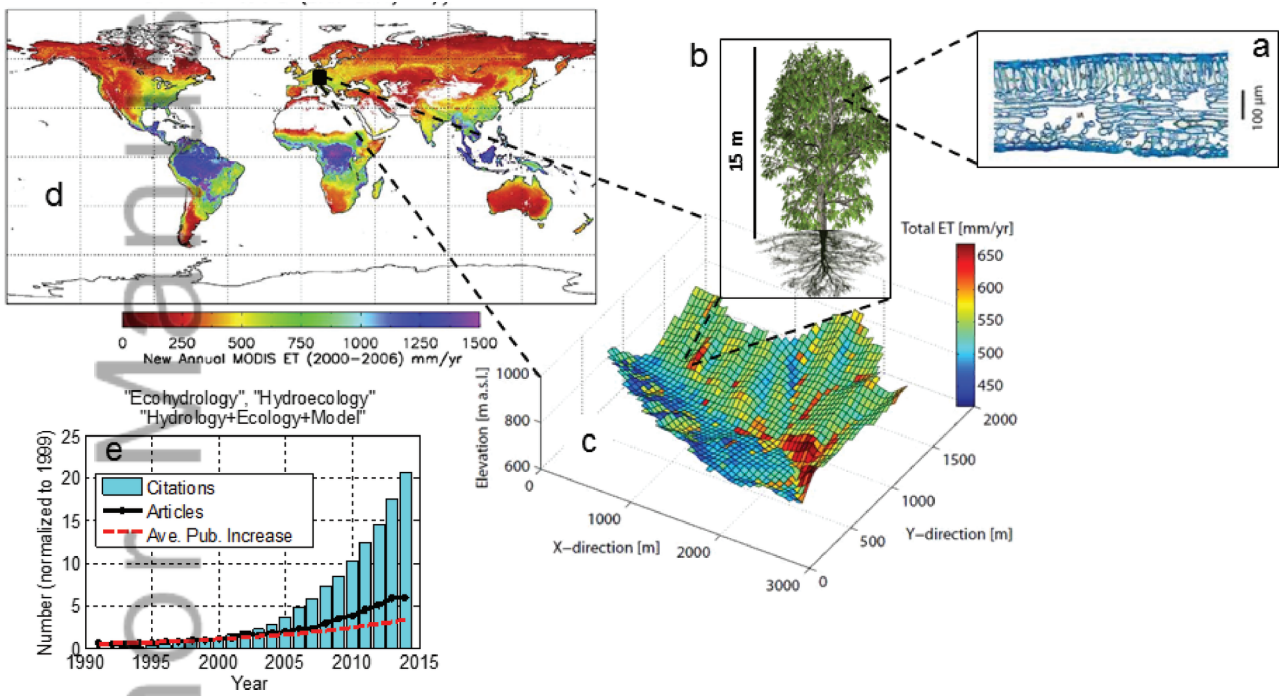## Further Reading/Resources

[--]

## Acwnoledgements

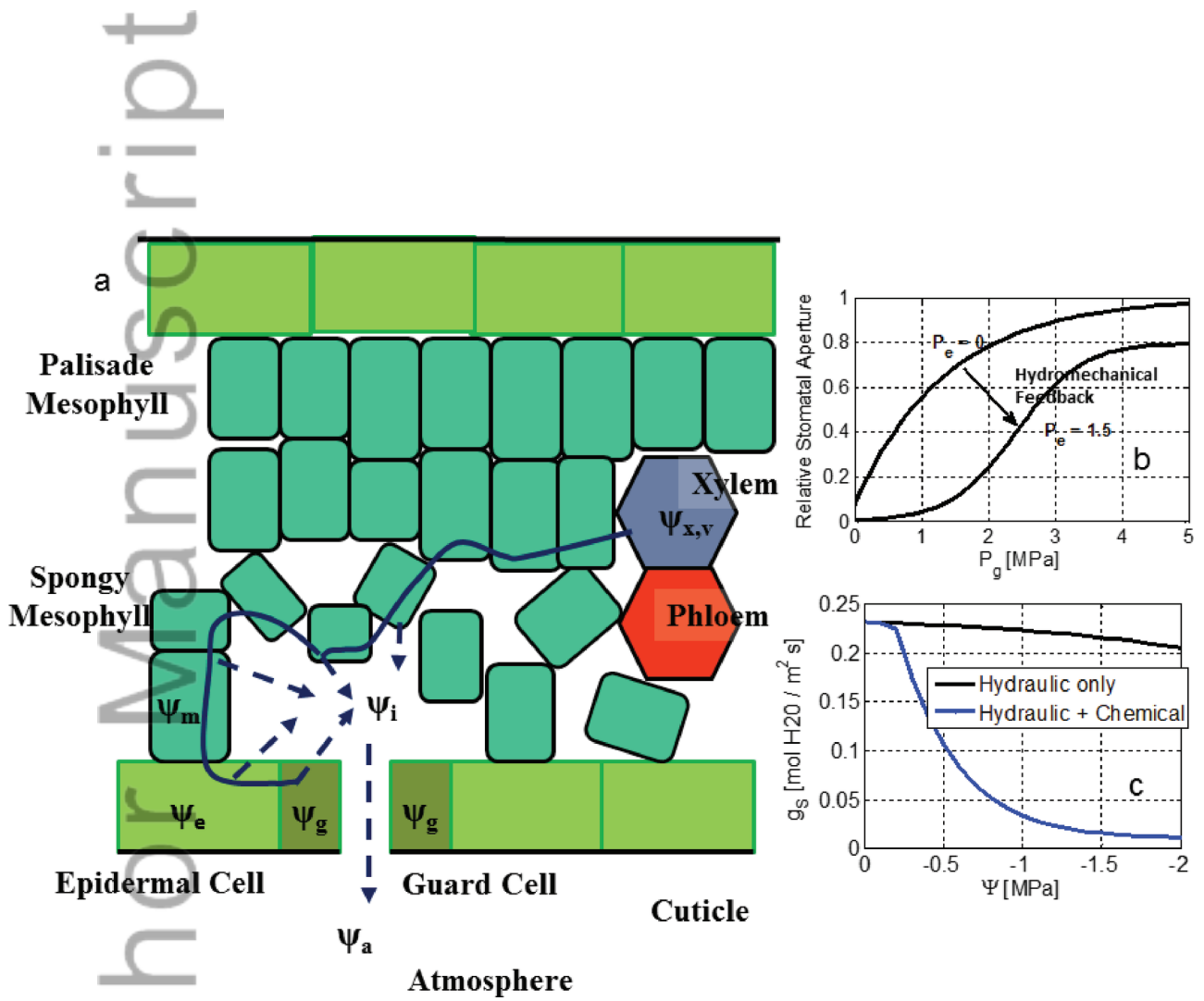## Related Articles

| DOI | Article title |
|---|---|
| | McDonnell Jeffrey J. The two water worlds hypothesis: ecohydrological |

| | |
|---|---|
| 10.1002/wat2.1027 | separation of water between streams and trees? WIREs Water 2014, 1: 323-329. doi: 10.1002/wat2.1027 |
| 10.1002/wcc.83 | Levis Samuel. Modeling vegetation and land use in models of the Earth System. WIREs Clim Change 2010, 1: 840-856. doi: 10.1002/wcc.83 |
| 10.1002/wcc.148 | Flato Gregory M.. Earth system models: an overview. WIREs Clim Change 2011, 2: 783-800. doi: 10.1002/wcc.148 |

68

a

b

15 m

c

Total ET [mm/yr]
650
600
550
500
450

Elevation [m a.s.l.]
1000
800
600

X−direction [m]
0
1000
2000
3000

Y−direction [m]
2000
1500
1000
500
0

d

New Annual MODIS ET (2000−2006) mm/yr
0    250   500   750  1000  1250  1500

"Ecohydrology", "Hydroecology"
"Hydrology+Ecology+Model"

e

Number (normalized to 1999)
25
20
15
10
5

Citations
Articles
Ave. Pub. Increase

Year
1990  1995  2000  2005  2010  2015

figu1f

a

Palisade
Mesophyll

Spongy
Mesophyll

$\Psi_m$

$\Psi_e$    $\Psi_g$

Epidermal Cell

Xylem

$\Psi_{x,v}$

Phloem

$\Psi_i$

$\Psi_g$

Guard Cell

Cuticle

$\Psi_a$

Atmosphere

Relative Stomatal Aperture

$P_e = 0$

Hydromechanical
Feedback

$P_e = 1.5$

b

$P_g$ [MPa]

$g_S$ [mol H20 / m$^2$ s]

Hydraulic only

Hydraulic + Chemical

c

$\Psi$ [MPa]

figu2f

figu3f

figu4f

| Process or Variables affected | Reduction in Tissue Water Potential Ψ and Turgor P |
|---|---|
| | 0 ⟶ -2/-12 MPa |
| Cell growth | |
| Growth respiration | |
| ABA release | |
| Stomatal conductance /Transpiration | |
| Leaf energy budget | |
| Photosynthesis | |
| Xylem cavitation | |
| Root disconnection from soil | |
| Maintenance respiration | |
| NSC transport | |
| Leaf Turgor Loss | |
| Leaf shedding | |
| Plant Mortality | |

figu5f

figu6f