Overview

Modeling plant–water interactions: an ecohydrological overview from the cell to the global scale

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Vegetation and the water cycles 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 nutrient cycles. To better understand and model plant–water interactions, highly interdisciplinary approaches are required. 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, 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: (1) models of plant hydraulics that mechanistically simulate stomatal controls and/or water transport at the tree level; (2) ecohydrological models that simulate plot- to catchment-scale water, energy, and carbon fluxes; and (3) terrestrial biosphere models that simulate carbon, water, and nutrient dynamics at the regional and global scales and address feedback 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 have led to key scientific findings are also 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. © 2015 Wiley Periodicals, Inc.

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INTRODUCTION

Transpiration is the process of water transfer from the 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,[1–3] and the corresponding 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 is the same pathway 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 feedback 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

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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, 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).[13–16] 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 (Figure 1). This has also been the result of the emphasis placed on water-vegetation interactions in a series of seminal works.[21–24] Ecohydrology has been less recognized as an emerging field in ecology because many ecologists and ecophysiologists would have regarded themselves as 'ecohydrologists' well before this term was popularized by hydrologists.[25] Despite this, 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, on regional and global scales, have appeared within the realm of 'biogeosciences' under the growing pressure to better understand the carbon cycle feedback to climate change.[26–28] There are recent studies 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 in addressing other relevant questions, for example in the assessments of land-use change impacts,[17] evaluation of ecosystem services,[29] soil resources, and

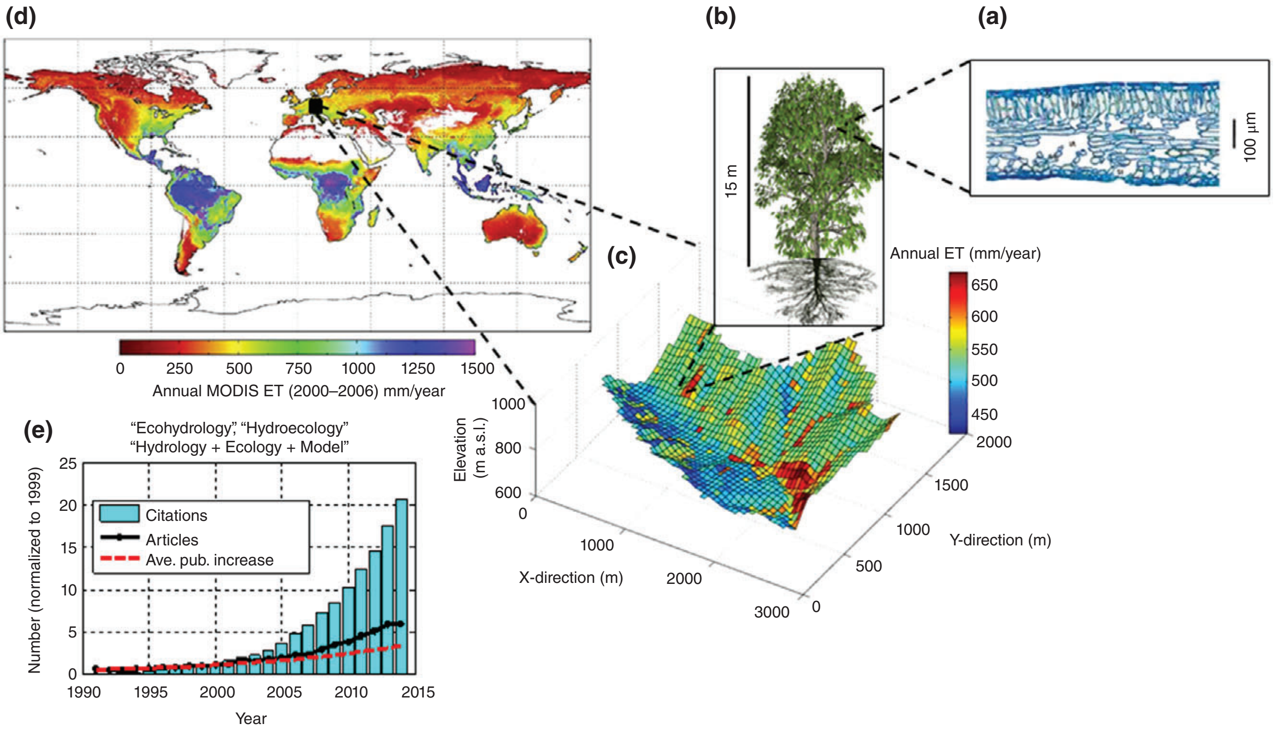

FIGURE 1 | Plant–water interactions occurr over a broad range of spatial scales from (a) leaf interior (≈ μm), to (b) individual plant (≈ m), to (c) catchments (≈ km), up to (d) the entire Earth. A map of annual evapotranspiration (ET) on the Rietholzbach catchment[17] and the annual global estimate of annual evapotranspiration (ET) from the MOD16 product[18] 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 a benchmark.[19] The MOD16 map is reprinted with permission from Ref 18. Copyright 2011 Elsevier; the leaf section is reprinted with permission from Ref 20. Copyright 2013 John Wiley and Sons.

landscape formation[30] as well as crop productivity.[31] These are all topics where water availability interacts with plant ecophysiology to produce complex dynamics that are unlikely to be uncovered with narrowly disciplinary approaches that ignore or trivialize either hydrological or vegetation components. Clearly, the perception of the significance and integration of vegetation processes into various fields of environmental research has recently undergone a considerable 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 for the purpose of representing vegetation and approaches that involve multiple processes and feedbacks are unlikely to considerably improve predictive capabilities or specific design criteria. However, when the focus shifts toward land-surface climate feedback, 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, the feedbacks between vegetation and the 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 the potential effects that model complexity and explicit consideration of elevated CO_2 feedback can have while evaluating drought trends[32,33] or aridity projections in a changing climate.[34,35] A too simple representation of vegetation has been shown to provide misleading assessments. Another example is the study of the effects of land-cover change (e.g., deforestation, grassland management) on evapotranspiration and streamflow. Detailed numerical analyses[17,36] and actual observations[37–39] suggest that the impact of land-cover change on the hydrological cycle may typically be less pronounced in comparison with the results obtained with model simulations using simplified approaches (e.g., Ref 40) or from small-scale manipulation experiments.[41] However, if the effects of disturbances or long-term analyses (≈multiple decades) are sought, then the water cycle is more tightly connected to the vegetation cover (e.g., Refs 42,43). For instance, shifts in forest composition because of species-specific mortality have been shown to produce hydrologically relevant consequences.[44] This is the result of processes that are 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 the water cycle is vegetation–snow interaction. Plant canopy that intercepts snow typically favors sublimation, thereby reducing the amount of snowpack on 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.[45–47] Additionally, the presence of vegetation affects the turbulent exchanges, modifying the wind profile.[48,49] All of these processes are highly nonlinear and can contribute to the increase or decrease of total snow melt below vegetation when compared to cleared areas.[50]

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 to the integrating scales of a watershed, region, and the globe (Figure 1). We treat only terrestrial ecosystems and do not consider aquatic plants in water bodies and oceans.[51] Water controls are also regarded from the plant's perspective and, therefore, issues related with vegetation such as a mechanical roughness element and its effect on modulating river and overland flows[52–54] 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 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). Because of this constraint, we do not explicitly discuss steady-state models and analytical derivations (e.g., Refs 55–60), 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 to simulate long-term (≈century) forest succession and management[61,62] are also excluded because of the rather minimalistic representation of hydrological processes. Finally, we favor models with a certain degree of generality that can be applied beyond the specific conditions for which they were derived. Furthermore, examples where plant–water interactions are especially important and have already led to key scientific findings are highlighted. We also present various data sources that are currently available to force and validate the current 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.[63] 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[64]) and concentrations of osmotic substances.[65] The mechanisms for water entering the roots and leaving the leaves are described in the 'Stomatal Controls' and 'Root Controls' section, while in the 'Plant Vascular Transport' section, 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 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.[8,66–70]

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 (Box 1), 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[71–73] (Figure 2). 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 (Figure 2). Stomatal size and density and leaf venation have been recognized to be important for plant functioning and evolution.[20,74,75] At the same time, the bulk of the resistance to water transport in the leaf occurs outside the venation network.[76–78] Transpiration to the external atmosphere takes place through stomatal apertures of few micrometers in size (~ 2–40 μm), mostly located on the lower side of the leaf.[7,79] 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 apertures, such as light, temperature, CO_2, vapor pressure deficit,[80–83]

BOX 1

PLANT PHYSIOLOGY: DEFINITIONS

Concise definitions of plant physiological terms are provided to guide readers. **Xylem** refers to the non-living vascular conduits of plants that transport water from the roots to the leaves (Figure 4). **Phloem** refers to the vascular conduits that transport sugars produced by photosynthesis to other tissues in the plant (Figure 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 matric effects such as capillary action. **Cavitation** is the processes induced by a change of pressure, that leads to the formation of vapor bubbles in a liquid; in plants, it occurs within the xylem. **Non-structural carbohydrates** (NSC) are the free, low molecular weight sugars (glucose, fructose, and sucrose) plus starch that are readily available for transport and plant metabolism. **Abscisic acid** (ABA) is a plant hormone involved in many plant processes, including stomatal closure, bud dormancy, and 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.

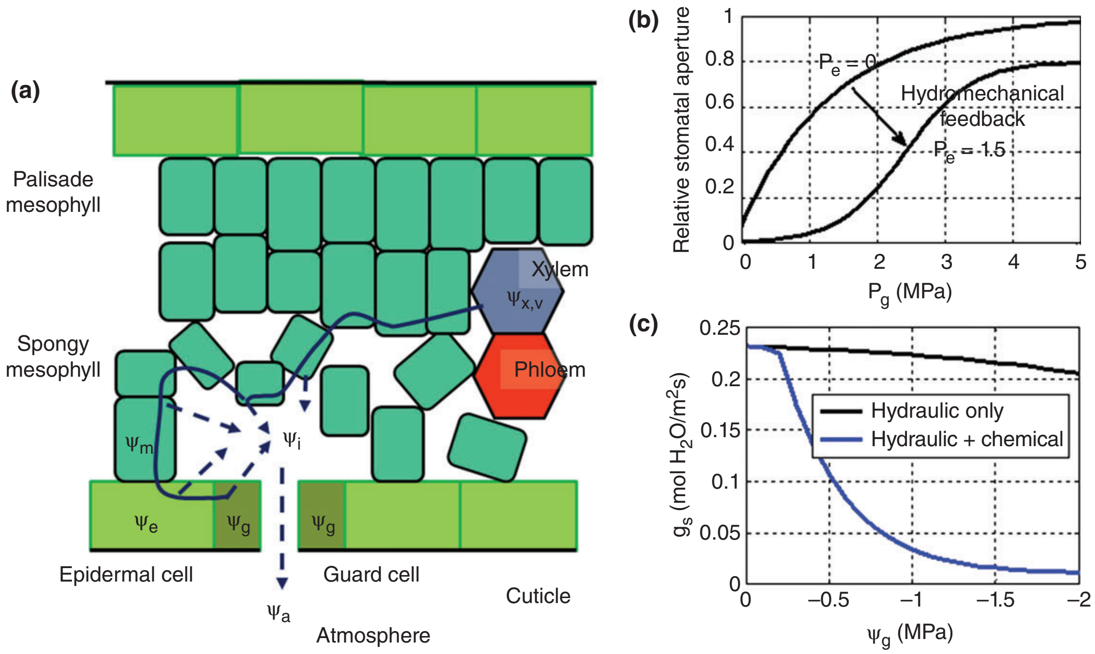

FIGURE 2 | A leaf is mostly composed of mesophyll and epidermal cells. The mesophyll is subdivided into palisade and spongy mesophyll. The epidermis secretes a waxy substance called the cuticle to separate the leaf interior from the external atmosphere. Among the epidermal cells, there are pairs of guard 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 exits the xylem is evaporated in the leaf interior (dashed lines). The terms Ψx,v Ψm, Ψe, Ψg, Ψi, and Ψa are the water potential in the xylem of the 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 because of a combination of hydraulic and chemical factors.

but despite the critical role that stomata play, the details of their regulation are still not fully understood.[84] Ultimately, stomata are largely regulated biologically, and it is through these tiny apertures (or lack 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 (Figure 2). Stomata tend to open when guard cells increase their turgor (the sum of water potential and osmotic pressure, see Eq. (4)), while an increase in epidermal cell turgor results in the opposite reaction, exerting a hydromechanically negative feedback[85–87] (Figure 2(b)). As the guard cell turgor is the sum of osmotic pressure and water potential, stomatal apertures are controlled by both hydraulic and chemical factors[88] (Figure 2(c)). Stomata close when water potential in the leaf drops because of a large transpiration flux or low water potential in the upstream xylem conduits.[89–91] The hydraulic control acts directly in the reduction of guard cell turgor, while chemical signals are less well quantified.[92] However, it is well established that chemical factors are essential for stomata opening in response to light.[93–95] Furthermore, chemical compounds, such as ABA, are typically released in response to water stress from the leaves and roots[96–98] and contribute to a reduction in the stomatal aperture.[99] Release of ABA is an important evolutionary trait as in early plants such as lycophyte and ferns, stomatal closure is purely hydraulically controlled.[100] 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 behavior’), while others tend to keep stomata open to favor carbon assimilation, experiencing larger fluctuations and lower values of the leaf water potential (‘anisohydric behavior’).

Models have been presented to mechanistically describe stomatal behavior and reproduce the hydraulic dynamics in the leaf[86,101–108] or simply to reproduce functional relations in agreement with observations.[80,109,110] Models that represent the exact mechanisms through which stomata respond to the external environment and chemical signals[111–113] still represent 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[80] 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 a function of relative humidity or vapor pressure deficit (VPD). These are, for instance, the structures of the Ball-Berry[114] and Leuning equations[115,116]:

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

where g_0 is the residual (or 'leakage') stomatal conductance, when A_n is equal to zero, a is an empirical parameter, and Γ is the CO_2 compensation point, i.e., the concentration of CO_2 at which the rate of CO_2 uptake is exactly balanced by the rate of CO_2 release in respiration. The Leuning equation (Eq (1)) is widely used and 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.[117–121]

An alternative approach to characterizing stomatal regulation is to assume that stomatal apertures are regulated to maximize carbon gain, while minimizing water loss.[122,123] These approaches, known as 'optimality arguments', are appealing from a theoretical standpoint because they are based on ecological evolutionary principles and appear to be corroborated by observed stomatal behavior.[123] However, they require specific assumptions for the optimality function and temporal and spatial scales of integration, which have all been questioned.[84] Specific formulations of the optimality principle lead to different analytical expressions for leaf-scale conductance,[124–126] and the approach has also started to be adopted in ESMs.[127]

Note that most of the models referenced above do not directly account for the effects induced by plant water stress beyond VPD, which need to be introduced empirically by either directly modifying g_s, the parameters of the biochemical photosynthesis model,[128,129] or some of the terms in the analytical form of optimal stomatal conductance.[130]

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.[131–134] Roots with diameters smaller than 2 mm are generally defined as 'fine roots', while roots of a 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.[135,136] Water flows into the roots because the water potential is typically larger in the soil than inside the plants.[137] Situations of reverse flow from roots to soil may also occur and are typically referred to as 'hydraulic redistribution'.[138,139] There is still a debate as to whether the phenomenon is a part of a typical plant life process or confined to specific conditions; however, it is generally believed that it is of considerably smaller magnitude than water uptake.[140] Water moves from the soil to the inner part of fine roots overcoming a barrier called the Casparian strip, which is mostly composed of suberin for isolating the plant interior and preventing, for instance, the entrance of pathogens. Afterwards, water movement continues across cell cytoplasm (sympalstic pathway) or through cell walls (apoplastic pathway) and reaches the xylem and, therefore, the vascular network where it can flow to the main stem.[141–143] 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.[144–146] The axial and especially the radial conductivities to water flow are not constant but vary with water potential and can be partially controlled chemically by the plant through aquaporins[147,148] even though the exact mechanisms underlying this control are still uncertain. Nutrient uptake can be passive and follow 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.[149–151]

The variability in soil water potential, axial and radial conductivities, and three-dimensional root architecture (Figure 3) is preserved in a number of plant-scale models that generally have a specific emphasis on root processes.[154–161] The most common approach in ecohydrological models and ESMs is to only consider root depth (zero-dimensional model) in combination with some empirical function of water content or water potential limiting water

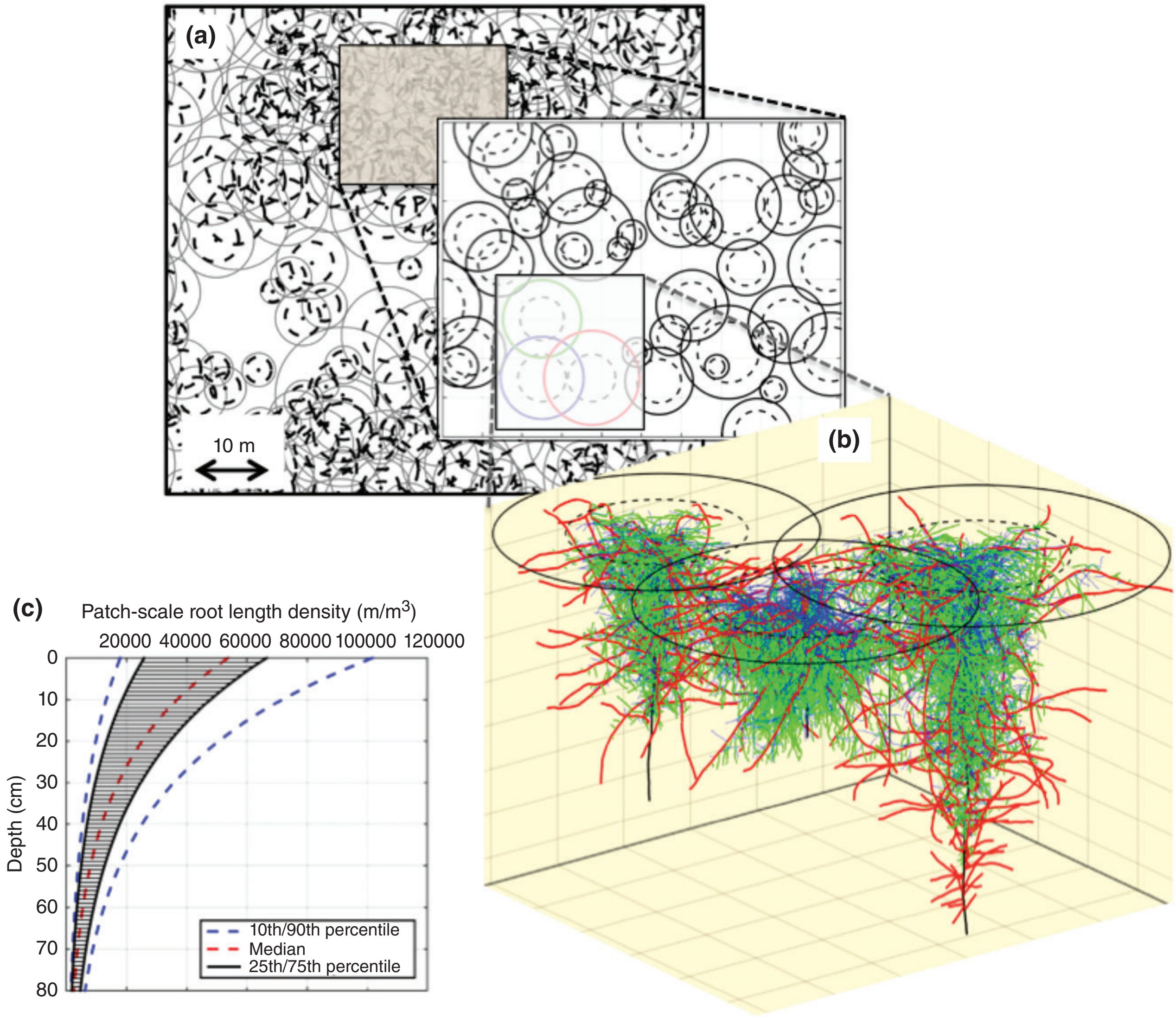

FIGURE 3 | Representation of plant- and patch-scale root systems suitable for explicit 3-D hydraulic models of plant water and nutrient uptake. (a) Spatial distribution of tree stems and their root systems based on measurements at the University of Michigan Biological Station[152]: the central dot is tree stem (diameter ≥ 10 cm); the solid line shows the maximum lateral root extent, while the 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.[153] 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[152] converted to the length density from variations of root diameters and root specific density. For each depth, the median density, 25–75%, and 10–90% ranges of the obtained distribution are shown.

uptake or transpiration in conditions considered to be ‘water stress’.[161–163] Several models started also considering the vertical distribution of root biomass (one-dimension[164,165]), and others include a bulk soil-to-root conductance,[166,167] which is a function of soil hydraulic conductivity and the amount of roots expressed through some index such as root-length-index or root-area-index.[168] A hybrid approach has recently been developed that preserves three-dimensional information and hydraulic conductivities in a simplified form[145] and may represent an important way forward in representing the hydraulic relations (and constraints) of describing the process of plant water uptake. However, an important limitation of the studies of root functioning and uptake capacity, which has likely prevented the development of a larger number of models or conceptualization of intermediate complexity, is the immense challenge of instrumenting and monitoring roots in field conditions.

Plant Vascular Transport

It is currently accepted by the scientific community that water movement in the xylem is governed by the cohesion-tension theory,[63,169,170] while the flow of water in the phloem follows the Münch hypothesis.[171–173] 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 remain 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 the formation of air bubbles (the process of cavitation), and, thus, the plant's vascular transport becomes impaired.[170]

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

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

where the xylem conductivity K_{xyl} is a plant/tissue-specific parameter that 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,[174–177] typically indicated as percentage loss of conductivity (PLC) (Figure 4). The xylem vulnerability curve (PLC vs Ψ_{xyl}) can be described by the knowledge of the water potential at 50% loss of conductivity ($\Psi_{\mathrm{xyl,50}}$) and of another characteristic value (e.g., $\Psi_{\mathrm{xyl,12}}$), typically correlated to $\Psi_{\mathrm{xyl,50}}$.[178,179] The term J_{xyl} is called sap flow and can be measured directly in the plants with various methods.[180]

Similarly, following the Münch hypothesis of a turgor-pressure driven flow, the water flux in the phloem in the vertical downward direction (J_{phl}) in a conduit of length (ΔL) is driven by the gradient of turgor (ΔP_{phl}) plus the gravitational potential ($\rho g \Delta z$) times the phloem conductivity (K_{phl}), which depends on temperature and on the concentration of sucrose in the phloem (C_{phl}) because sucrose concentration affects the fluid viscosity[181] (Figure 4):

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

The turgor (P) is defined as the sum of osmotic pressure (Π), directly related to the concentration of osmotic solutes through the Van't Hoff relation or other empirical functions[182,183] and water potential[184,185]:

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

Conversely to sap flow, phloem flow is particularly challenging to measure because of the size of the phloem tissue and the disturbances induced by the measurement itself. It has only been measured in laboratory experiments,[68,186] although promising techniques for field measurements are emerging.[187]

In order for 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 also move radially between the phloem and xylem and between storage reserves (mostly composed by living parenchyma cells residing near xylem conduits) and the xylem. These exchanges make the xylem and phloem hydraulically coupled[188,189] and confer on the plant a given capacitance for absorbing fluctuations between the water demand of the leaves (transpiration) and the water uptake from the roots.[190–194] Capacitance is typically more significant in stems of larger trees,[195] and it is because of a combination of the elastic shrinkage and swelling of the phloem, living bark, and xylem tissue and because of 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 used 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.[196,197] In both young and old trees, the elastic behavior of the xylem and phloem is large enough to be clearly measured with high-resolution dendrometers[187,198,199] that can provide important information on plant hydraulic behavior.[200–202] 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

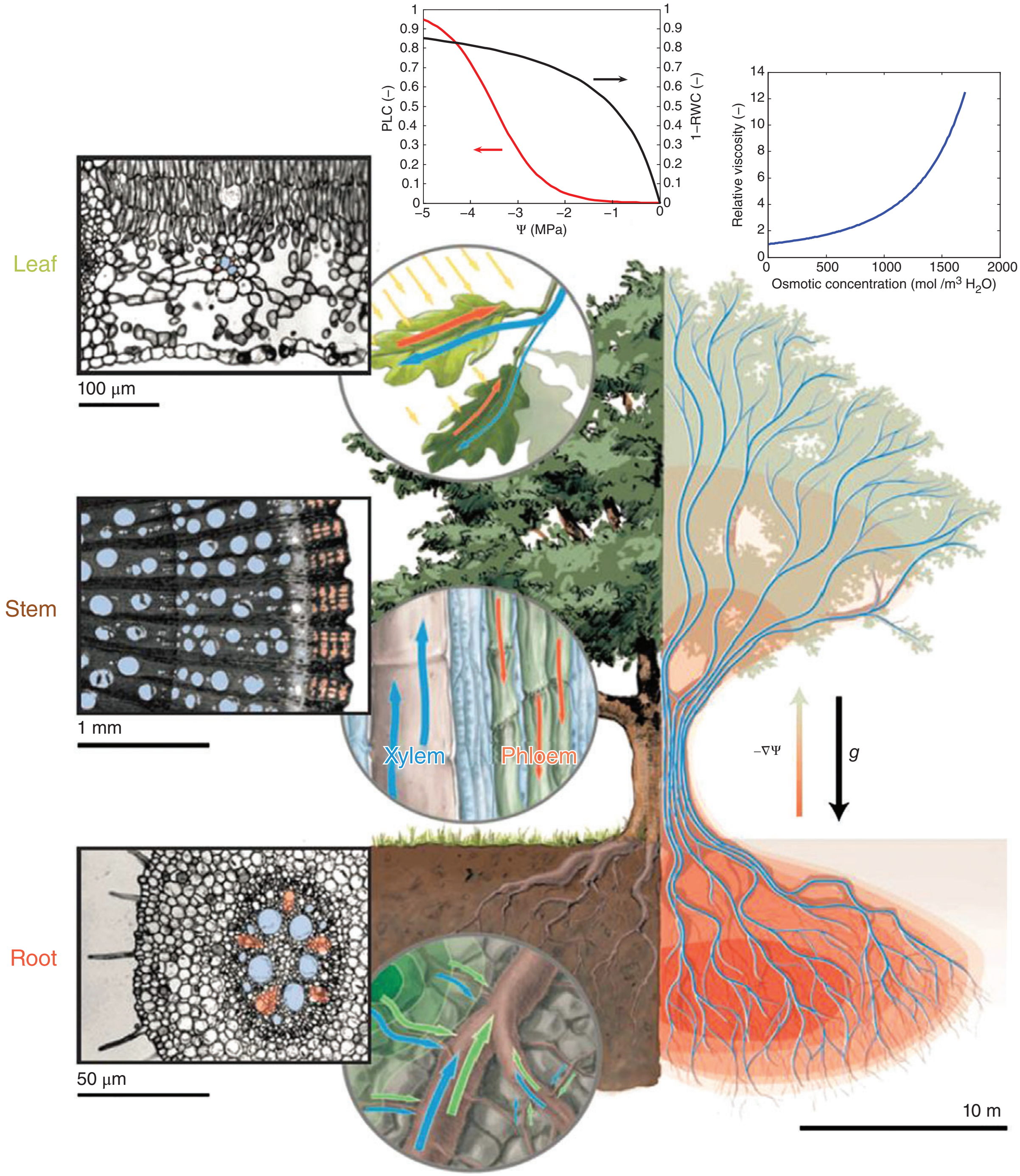

FIGURE 4 | Global view of long-distance water and carbohydrate transport pathways in a vascular plant. The xylem mediates the net transfer of water from the soil to the atmosphere down a gradient in water potential, $\nabla\Psi$. The phloem carries a flow of sugars and other metabolites down the plant 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). Root nutrient uptake is also shown (green). Typical curves for changes in stem relative water content (RWC) (black line) and xylem cavitation (red line) 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 (blue line). (Reprinted with permission from Ref 69. Copyright 2014 Annual Reviews)

trees and several hours, or even days during droughts, for large, old trees.[194,203]

Only a few models have been currently presented to describe plant vascular transport in detail as the prevalent option has been to lump the entire plant system into a single conductance or resistance term[204] 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 Ref 127). Important exceptions are the Sperry model[142] and the TREES model,[205,206] which use a series of resistances from the soil to the leaves and xylem vulnerability curves to describe plant hydraulic behavior. The FETCH model,[207] the XWF model,[208–210] and the model presented by Chuang et al.,[211] describe 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[181,212–218] as a follow-up of the first pioneering attempts.[219]

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 in water potential throughout the various plant compartments, accompanied by a reduction of turgor in living tissues, as the plant is only partially able to compensate for low water potentials through osmotic adjustments.[220–222] The first process to be affected by the low water potentials is growth (Figure 5). Cell growth is mostly the result of cell division, enlargement, and cell wall synthesis.[223,224] Cell enlargement is a function of turgor pressure.[185,225–227] A small reduction of water potential can significantly decrease or stop growth well before photosynthesis or stomatal conductance are affected.[228–230] As the growth stops, respiration associated with the growth also ceases.[231,232] Growth impairment has been neglected by ecohydrological literature and models, but, in fact, it represents the first consequence of the onset of water stress.

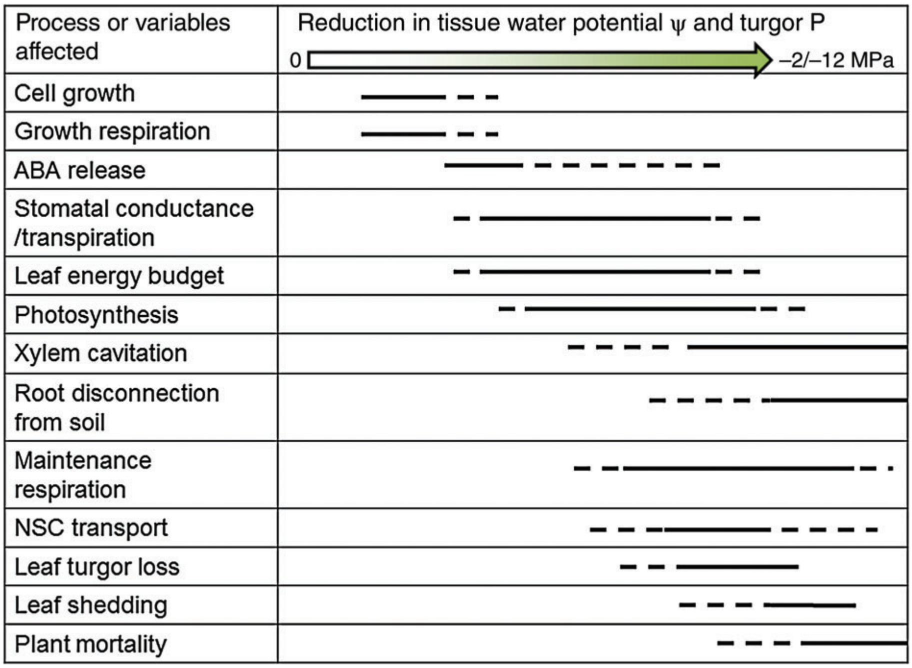

FIGURE 5 | Effects on plant physiology caused by a decrease in water potential and turgor. The length of the horizontal lines represent the range of stress levels within which a process becomes first affected. Two different levels of minimum water potential, Ψ, are given: –2 and –12 MPa. These are indicative, and the former corresponds to a value characteristic for drought intolerant plants/crops and the latter for drought-adapted plants in deserts. Dashed lines signify an incipient or vanishing effect. The figure is inspired by Hsiao et al.[220] and Porporato et al.[22]

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 the 'Stomatal Controls' section). A reduction of stomatal conductance typically leads to a decrease in gas exchanges, e.g., photosynthesis and transpiration. These are the controls that have been typically placed at the foundation of ecohydrology[22] and embedded in ESMs.[16] The decrease in turgor and photosynthesis further modifies plant metabolism and carbon allocation strategies.[233,234] 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 also observed at the canopy or larger spatial scales.[235]

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 cavitation and, thus, the formation of emboli in the xylem conduits ('Plant Vascular Transport' section, Figure 5). At relatively low water potentials, leaves lose turgor, and the photosynthetic machine starts to be structurally damaged.[222,236,237] At this stage, roots can also become completely disconnected from the soil, a process typically unaccounted for in models (but see Ref 206). Maintenance respiration has also been found to decrease as the drought progresses.[232,238] This is probably because of the slowing down of metabolic activities, although specific mechanisms are yet not fully understood. It is not rare that plants start to shed leaves when exposed to a long severe drought.[239,240] For some plants, such as drougth-deciduous trees, this is a routinely adopted strategy.[241–243]

The decrease or even cessation of photosynthesis poses a challenge for the plant that is called to rely only on NSC reserves for its maintenance. The permanent hydraulic failure of vascular transport and carbon starvation because of exhaustion or impossibility to access NSC or a combination of these mechanisms have been hypothesized as reasons for plant mortality.[244,245] Recent evidence supports an earlier occurrence of hydraulic failure and a consequent blockage of NSC transport.[238,246] 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.[247–249] This is particularly relevant as drought stress conditions can be potentially exacerbated by higher temperatures and VPD in the future.[250–252] Given the fact that the exact mechanisms that lead to plant mortality are still unknown, its modeling is a daunting task[253,254] and represents an important challenge to improving 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.[38,39,255]

PLOT TO CATCHMENT SCALE

Historically, a representation of vegetation was included in land-surface and hydrological models because it affects transpiration through surface roughness, albedo, and canopy resistance $r_c = r_s/\mathrm{LAI}$, 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. It may offer a larger resistance between the soil and atmosphere with respect to bare ground in well-water conditions or a lower resistance in dry conditions, accessing water storages through relatively deep roots. The well-known Penman–Monteith equation[11,256] 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., Refs 164,257) but still provides a reasonable approximation for many other studies.[258] Consequently, models that explicitly and simultaneously solve hydrological and vegetation dynamics (Box 2) have been presented in the last 15 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, in time and, eventually, space, evolve 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., Refs 55,60). Rather than describing each ecohydrological model separately, a non-exhaustive list of models is

BOX 2

VEGETATION DYNAMICS

The term ‘vegetation dynamics’, when referred to models, may have different meanings according to the context in which it is used. In a large fraction of terrestrial biosphere model literature, vegetation dynamics is used to refer 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, and disturbances that may modify the amount and type of vegetation occurrence. In ecohydrological model literature, vegetation dynamics typically refer to models that prognostically simulate vegetation attributes such as LAI, 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 simulates the temporal evolution of processes connected to vegetation but not directly linked to the plant structure such as photosynthesis, respiration, or stomatal conductance. For the 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 the temporal evolution of plant properties.

presented in Table 1. In the following, we summarize the processes that these models represent. Ecohydrological models typically solve water, energy, carbon, and, quite rarely, nutrient cycles at the land surface (Figure 6).

Water Budget

In terms of water budget, models use precipitation as an 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 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 a snowpack, where it melts or sublimates. Water in the soil undergoes vertical and horizontal redistribution following gravitational and soil matric potential gradients, typically modeled with the Richards equation.[278–281] Depending on the vertical profile of soil water potential and plant demand, water is evaporated from the surface as ground evaporation and/or taken up by plants and transpired. As 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 to plants (but see Ref 282) 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 the channel network downstream to a specified outlet.

Energy Budget

Latent heat flux is the energy equivalent of the sum of all water vapor fluxes (transpiration and evaporation); therefore, it makes the water and energy cycles tightly coupled. Models that explicitly solve the energy budget compute the latent heat flux and its partition into different components (evaporation and transpiration) concurrently with the water budget (e.g., Refs 164,165,259,264,275,283). Latent heat flux (λE) is typically solved assuming conservation of energy in a given domain:

$$R_n - H - \lambda E - G - \lambda_p A_n - A_H = \frac{dS}{dt}, \qquad (5)$$

where R_n is the net radiation, H is the sensible heat flux, G is the ground heat flux, λ_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 in 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 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

TABLE 1 | A Non-Exhaustive List of Ecohydrological Models

Model	Key Reference	Water Budget	Energy Budget	Carbon Pools	Nutrients	Photosynthesis and Stomata	Spatial Representation	Water Routing	Plant Spatial Dynamics
Tethys-Chloris (T&C)	Fatichi et al.[17,165]	Y (Richards -Multilayer)	Y (1 prognostic temp.)	Y (7 Pools)	N	Y (Biochemical + Leuning)	Y (Grid)	Y	N
tRIBS-VEGGIE	Ivanov et al.[164]	Y (Richards -Multilayer)	Y (2 prognostic temp.)	Y (4 pools)	N	Y (Biochemical + Leuning)	Y (TIN)	Y	N
MLCan	Drewry et al.[259]	Y (Richards -Multilayer)	Y (Multilayer temp.)	N	N	Y (Biochemical + Ball-Berry)	N	N	N
RHESSys	Tague and Band, Tague et al.[260,261]	Y (Two layers)	N (Penman-Monteith)	Y (3 pools)	Y	Y (Empirical)	Y (Semi-distributed)	Y	N
CATHY/NoahMP	Niu et al.[262]	Y (Richards -Multilayer)	Y (2 prognostic temp.)	N	N	N	Y (Grid)	Y	N
PAWS+CLM	Shen et al.[263]	Y (Richards -Multilayer)	Y (3 prognostic temp.)	Y (4 Pools)	Y	Y (Biochemical + Leuning)	Y (Grid)	Y	N
Geotop-dv	Della Chiesa et al.[264]	Y (Richards -Multilayer)	Y (1 prognostic temp.)	Y (3 Pools)	N	Y (Empirical)	Y (Grid)	Y	N
CATGraSS	Zhou et al.[265]	Y- Bucket	N (Penman-Monteith)	Y (3 pools)	N	Y (Empirical)	Y (Grid)	N	Y
—	Van Wijk and Rodriguez-Iturbe,[266]	Y (Bucket)	N	N	N	N	Y	N	Y
VELMA	Abdelnour et al.[40]	Y (Four layers)	N (Empirical)	Y	Y	N	Y	Y	N
CANOAK	Baldocchi and Wilson,[267]	Y (Multilayer)	Y (Multilayer temp.)	N	N	Y (Biochemical + Ball-Berry)	N	N	N
—	Nouvellon et al.[268]	Y (Three layers)	N (Penman-Monteith)	Y (3 Pools)	N	Y (Empirical)	N	N	N
VDM	Montaldo et al.[269]	Y (Bucket)	N (Penman-Monteith)	Y (3 Pools)	N	Y (Empirical)	N	N	N

TABLE 1 | Continued

Model	Key Reference	Water Budget	Energy Budget	Carbon Pools	Nutrients	Photosynthesis and Stomata	Spatial Representation	Water Routing	Plant Spatial Dynamics
Topog-IRM	Vertessy et al.[270]	Y (Richards -Multilayer)	N (Penman-Monteith)	Y (3 pools)	N	Y (Empirical + Leuning)	Y (Flow-net)	Y	N
—	Cervarolo et al.[271]	Y (Richards -Multilayer)	Y (1 prognostic temp.)	Y (3 pools)	N	Y (Empirical + Jarvis)	Y (Grid)	Y	N
CABALA	Battaglia et al.[272]	Y (Bucket)	N (Penman-Monteith)	Y (6 pools)	Y	Y (Biochemical + Ball-Berry)	N	N	N
CenW 3.1	Kirschbaum et al.[273]	Y (Multilayer)	N (Penman-Monteith)	Y (10 pools)	Y	Y (Biochemical + Ball-Berry)	N	N	N
CASTANEA	Dufrene et al.[274]	Y (Three layers)	Y (2 prognostic temp.)	Y (5 pools)	N	Y (Biochemical + Ball-Berry)	N	N	N
MuSICA	Ogée et al.[275]	Y (Two layers)	Y (1 prognostic temp.)	N	N	Y (Biochemical + Leuning)	N	N	N
WEB-DHM	Wang et al.[276]	Y (Richards -Multilayer)	Y	N	N	Y (Biochemical + Ball-Berry)	Y (Grid)	Y	N
BEPS-TerrainLab	Govind et al.[277]	Y (Two layers)	N (Penman-Monteith)	Y (4 Pools)	Y	Y (Biochemical + Empirical)	Y	Y	N

The presence or absence of specific processes is indicated with a yes (Y) or no (N) and with additional specifications.

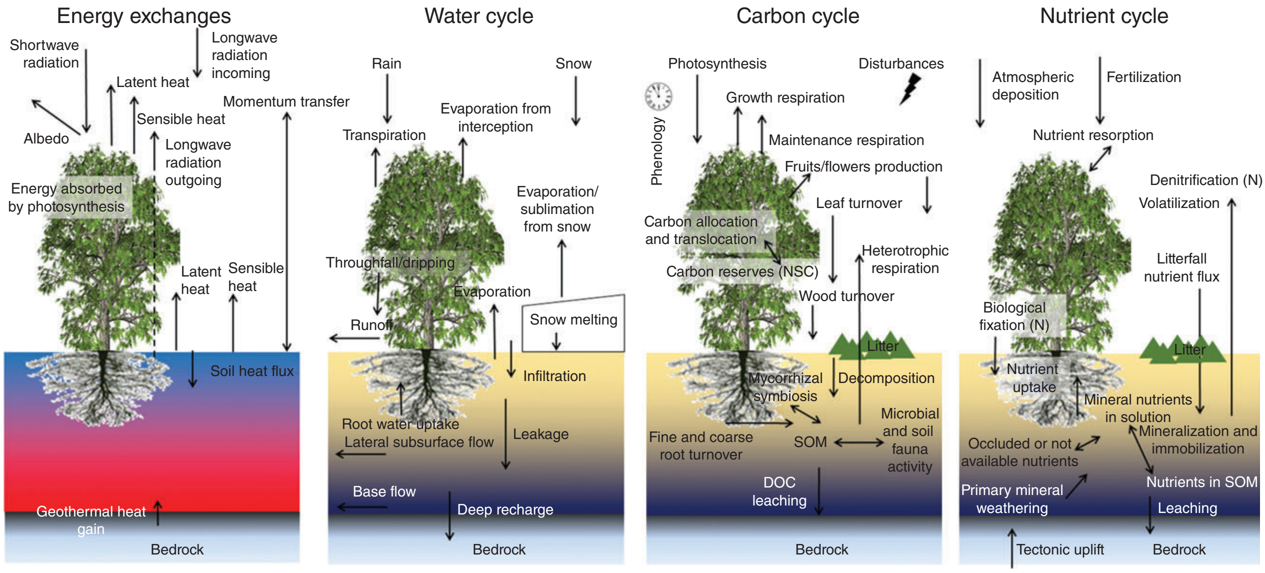

FIGURE 6 | Ecohydrological and terrestrial biosphere models have components and parameterizations to simulate the (1) surface energy exchanges, (2) the water cycle, (3) the carbon cycle, and (4) soil biogeochemistry and nutrient cycles. Many models do not include all the components presented in the figure.

computationally demanding. Therefore, several ecohydrological models still use simplified solutions of the energy budget such as the Penman–Monteith or Priestley-Taylor equations (e.g., Refs 260,265,269,273).

Carbon Budget

The carbon cycle is linked to the water and energy cycles because carbon assimilated through photosynthesis uses the same pathway between the outer atmosphere and leaf interior as transpired water (see the 'Stomatal Controls' section) and because changes in vegetation properties (e.g., plant height and LAI) modify boundary conditions for energy and water exchanges (Figure 6). For instance, a 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., Refs 164,165,259,275,276); others have simpler approaches exploiting the water use efficiency (WUE; i.e., the ratio between net carbon assimilation and transpiration[284]) or light use efficiency (LUE; i.e., the efficiency through which radiation absorbed by vegetation is converted into carbon[285]) concepts that empirically link carbon assimilation to the transpired water or intercepted light (e.g., Refs 264,265,271,286,287). In some ecohydrological models, vegetation dynamics are essentially reduced to the simulation of carbon assimilation only (e.g., Refs 262,276). 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 account for the size and dynamics of different plant compartments.[288] The number of carbon pools varies from model to model, but a typical set is composed of at least of a foliage pool, a fine-root pool, a sapwood or stem pool, and, more recently, a carbon reserve pool (e.g., Refs 165,273). Carbon reserves have been ignored in early ecohydrological models and ESMs with rare exceptions (e.g., Ref 289), but it is currently recognized that plant dynamics cannot be simulated meaningfully without accounting for carbon reserves.[290–292] Models that use carbon pools can also simulate the dynamics of the biophysical structure of vegetation, e.g., LAI, vegetation height, and root biomass.

Soil Biogeochemistry

Water, energy, and carbon fluxes are additionally connected through soil biogeochemistry and nutrient dynamics (Figure 6). Soil biogeochemistry is typically simulated to account for a given number of carbon and nitrogen pools.[293] Other nutrients, such as phosphorous, sulfur, or potassium, are not typically included in ecohydrological models and rarely so in ESMs (see the 'Terrestrial Biosphere Models' section). 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., Refs 294–298). 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,[299] while soil fauna is typically neglected. In some models, extracellular enzymes catalyzing the decomposition reactions are also explicitly represented.[300–302] Exchanges between the different pools are typically simulated as 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.[293,300,303,304] 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.[305,306] Part of the nutrients can be lost through deep leakage, erosion, or, in the case of nitrogen, through denitrification and volatilization; the remaining can be absorbed by roots. Plant nutrient uptakes represent an essential component of vegetation functioning. Nutrient uptake depends on the availability of mineral nutrients, root density, mycorrhiza symbiosis, and plant requirements, but exact mechanisms are not fully understood, and their simulation is typically quite simplified.[298,299,307,308] The link with the carbon cycle is evident as 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[309] and because leaf nitrogen is known to affect photosynthetic capacity.[310–313] The linkage with plant development offers important feedback on water and energy exchanges because plant structure (e.g., LAI, vegetation height) modifies boundary conditions at the land surface.[263]

Spatial Representation of Processes

The description of how models deal with 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 5 × 5 m^2 as well as 100 × 100 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 on very different scales. The main issue with an 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 non-linear function of several variables equals the function of the means of these variables.[314,315] 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[316–319] and rainfall[320] 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 the lateral exchanges of water[320,321] and, sometimes, nutrients[322,323] even when process description is simplified in a comparison with mechanistic solutions.[265] The spatial redistribution 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 provide feedbacks about water and energy exchanges.

Another important aspect of the spatial dimension is represented by competition, establishment, and mortality of vegetation. There are a few ecohydrological models that aim to reproduce this specific behavior, and they are especially developed to study vegetation patterns in semi-arid environments.[265,266,324] These models typically compromise 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 the dynamic systems theory (e.g., Refs 325). While these studies are quite distant from the representation of the physical processes, they are important as they put forward hypotheses on the controls of vegetation spatial organization and regular patterns observed in semiarid ecosystems.[326–332]

GLOBAL SCALE

Terrestrial Biosphere Models

The request for quantifications of global carbon and water cycles and plant biogeography, especially in the context of understanding the consequences of climate change, was conducive to the development of models able to simulate vegetation dynamics (Box 2) on a global scale.[13,333–337] These models appear with various names: dynamic global vegetation models (DGVMs), terrestrial biosphere models, terrestrial ecosystem models, and more recently, as vegetation components of ESMs (e.g., Refs 14,338–342). Here, the term terrestrial biosphere model 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., Refs 15,343,344) and subsequently adopted by ecohydrological models. A detailed description of terrestrial biosphere models can be found in recent reviews by Prentice et al.,[345] Levis,[346] Quillet et al.,[347] Medlyn et al.,[348] and Fisher et al.[13]; 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 the 'Plot to Catchment Scale' section. We rather emphasize the main differences in comparison to ecohydrological models related to (1) spatiotemporal scale of application, (2) model initialization and boundary conditions, and (3) biogeography and forest demography. We acknowledge that there is a tendency toward convergence in process descriptions 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 on the entire Earth's surface. In addition, terrestrial biosphere models typically address research questions for longer time scales when compared with the time horizons of ecohydrological studies, even though exceptions exist, and some ecohydrological models have also been developed for long-term analyses.[260,322] 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 because of simplified assumptions introduced for the sake of generality and flexibility (e.g., Ref 371). Furthermore, because the spatial representation in terrestrial biosphere models is in the order of several km^2, they cannot account explicitly for topography. Each computational element may receive a different climate forcing, but, in essence, terrestrial biosphere models are one-dimensional as they do not exchange mass and nutrient fluxes laterally, 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 follow a different philosophy for assigning the initial conditions (state variables) for the numerical simulations. For ecohydrological models, an initialization period of a few years is typically able to bring the examined ecosystem to a representative state (as 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., Refs 297,298,349), and a minor fraction for phosphorous cycles.[363,372,373] It is worth noting 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., Refs 315). 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 on 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 many ecohydrological applications, but are prognostic variables

TABLE 2 | A Non-Exhaustive List of Terrestrial Biosphere Models

Model	Key Reference	Energy Fluxes	Water Fluxes	Carbon Module	Nitrogen Module	Plant Establ./Mortality/ Disturbances	Carbon Reserves	Root Exudation	Mychorrizal
CN-CLASS	Arain et al.[349]	Y	Y	Y	Y	N	Y	N	N
JULES-TRIFFID	Clark et al.[350]	Y	Y	Y	N	Y	N	N	N
Noah-MP	Niu et al.[351]	Y	Y	Y	N	N	N	N	N
LPJ	Sitch et al.[352]	N	Y	Y	N	Y	N	N	N
ORCHIDEE	Krinner et al.[353]	Y	Y	Y	N	Y	Y	N	N
CLM-DGVM	Levis et al.[354]	Y	Y	Y	N	Y	N	N	N
CLM4CN	Lawrence et al.[355]	Y	Y	Y	Y	N	N	N	N
IBIS	Kucharick et al.[356]	Y	Y	Y	Y	Y	N	N	N
ISAM	Yang et al.[357]	Y	Y	Y	Y	N	N	N	N
DLEM	Tian et al.[358]	Y	Y	Y	Y	Y	N	N	N
Biome-BGC	Thornton et al.[359]	Y	Y	Y	Y	Y	N	N	N
ED2	Medvigy et al.[360]	Y	Y	Y	Y	Y	Y	N	N
Ecosys	Grant et al.[361]	Y	Y	Y	Y	N	Y	N	Y
MOSES-TRIFFID	Cox[362]	Y	Y	Y	N	Y	N	N	N
JSBACH	Goll et al.[363]	Y	Y	Y	Y	N	Y	Y	N
LPJ-DyN	Xu-Ri and Prentice[297]	N	Y	Y	Y	Y	N	N	N
O-CN	Zaehle and Friend[298]	Y	Y	Y	Y	Y	Y	N	N
Hybrid3.0	Friend et al.[289]	Y	Y	Y	Y	Y	Y	N	N
ANAFORE	Deckmyn et al.[167]	Y	Y	Y	Y	Y	Y	N	N
SEIB-DGVM	Sato et al.[364]	N	Y	Y	N	Y	Y	N	N
Sheffield-DGVM	Woodward and Lomas[365]	N	Y	Y	Y	Y	N	N	N
LPJ-GUESS	Smith et al.[366]	N	Y	Y	N	Y	N	N	N
aDGVM2	Scheiter et al.[367]	N	Y	Y	N	Y	N	N	N
FoBAAR	Keenan et al.[368]	N	N	Y	N	N	Y	N	N
CASA	Carvalhais et al.[369]	N	Y	Y	Y	N	N	N	N
JeDi-DGVM	Pavlick et al.[370]	N	Y	Y	N	Y	Y	N	N

The presence or absence of specific processes is indicated with a yes (Y) or no (N).

computed by the model. For the same reasons, processes such as forest demography and natural or anthropogenic disturbances such as fire, windthrow, plant diseases, insect attacks, forest management, and plant competition needs to be represented. Feedback on vegetation dynamics caused by nutrient cycles is also much more relevant at those temporal scales than they are for ecohydrological applications, at least in forests.[374] Forest demography in terrestrial biosphere models is similar or identical to the one developed for forest-gap models in forestry research.[61,375,376] Forest demography can be handled by an average tree individual[352,353,377] evolving in time or by simulating cohorts of individuals with different age classes and size in the stand (e.g., Refs 61,315,360,366,378–380). This allows, for instance, an explicit representation of the early and late successional species and more generally of heterogeneous forests with gaps, uneven stand height, and density.[381,382] Disturbances are typically very difficult to simulate mechanistically even though a general framework has been recently presented[383]. They are mostly simulated by removing a certain amount of biomass in a given domain with a given probability of disturbance occurrence. Plant competition is often simulated by 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., Refs 352,370). Mortality is far from being mechanistically simulated[384] and is typically related to plant-negative carbon balances or prescribed with given constant probabilities or as a function of plant age or size.[385,386] This background mortality is typically summed with the probability of disturbance occurrence.

Vegetation Feedback to the Climate System

There are several examples of the successful applications of terrestrial biosphere models, which elucidate the feedback between vegetation dynamics and climate or hydrological cycles on global and regional scales. One example is the predictions of the fate of the Amazon forest. Early findings suggested the potential dieback of the Amazon rainforest in response to projected droughts with huge implications for the future of Earth's climate.[387] 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., Refs 388–391). There is a large community effort dedicated to better understand the effect of drought on the Amazon forest (e.g., Refs 392–395) because current observations and future predictions are suggesting a potential lengthening of the dry intervals and an increase of drought risk.[396,397] On local scales, the Amazon's deforestation has been demonstrated to affect cloud formation and convective precipitation because it changes the partition of net radiation into sensible and latent heat, affecting boundary layer development. This could possibly increase or decrease convective precipitation downwind of the cleared patches as a function of the extent of deforestation.[398–400]

Another significant example is represented by the tree and shrub encroachment observed 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's warming. While the exact causes of tree and shrub encroachment are still uncertain,[401,402] 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.[403] These changes in vegetation have a positive effect on local and global warming with the potential to further push shrub encroachment or northern tree line expansion.[43]

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.[404,405] The increased plant productivity associated with elevated CO_2 is typically indicated as the CO_2 fertilization effect (e.g., Ref 406). The integration of this effect from the leaf to the global scale is still debated,[407,408] but it has been postulated to have contributed to an increase runoff[409,410] and be largely responsible for the terrestrial carbon sink with direct feedback on Earth's climate.[27,411,412] While the magnitude of CO_2 fertilization on the ecosystem scale and the persistence of the carbon sink in time are still open research areas,[413–415] the expected consequences of elevated CO_2 represent one additional example that robust, long-term projections of future water cycles cannot be made without accounting for vegetation physiology.

PROCESS UP-SCALING

Forcing and Boundary Conditions

The models described in the previous sections (plant hydraulic, ecohydrological, and terrestrial biosphere models) are designed to address scientific questions on 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 relatively short period of time (a growing season, few years). It would be unrealistic to simulate each individual tree on 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.[315] 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[416,417] because coarse temporal resolutions do not allow the solving of 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 use an hourly or half-hourly time step for the forcing, at least to solve hydrological and energy dynamics, with a few models still using daily or longer scales (e.g., Ref 366). Plant growth, soil biogeochemistry, and forest demography processes have typically slower dynamics that can be simulated on 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 vegetation itself is parameterized. Historically, the existing diversity in species and plant traits (e.g., Ref 418) has been summarized using a given number (~8–25) of plant functional types (PFTs) that aimed to distinguish climatic zones (e.g., temperate, boreal, tropical), phenology (evergreen, deciduous), and leaf morphology (e.g., needle leaves, broadleaves) of the plant.[419] 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 behavior 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., Refs 36,420–422). These approaches rely on the knowledge of the observed distributions of plant properties, ‘traits’, which can correspond or 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 plant trait, there are several ecological studies that show a certain degree of coordination between many of these traits.[423–425] An illustrative example is the ‘leaf economics spectrum’ that suggests that leaf traits co-vary in a continuum from leaves with a high photosynthetic capacity, nitrogen content, specific LAI, and a short lifespan typical of fast-growing species to the opposite combination typical of slow-growing species.[423,426] While cross-correlations have been mostly studied for leaf traits, there is emerging evidence that this holds true for many plant traits,[427] and such information can be transferred to the model parameters. Observed trait distributions and cross-correlations 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 of 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. In fact, despite the huge amount of biodiversity, forest biomass and productivity are mostly controlled by a limited number of dominant species.[428] 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.[36]

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 incoming shortwave and longwave radiation. Boundary conditions consist of soil properties, such as soil depth, soil texture, or soil hydraulic properties (e.g., Refs 429,430), and vegetation properties represented by functional and morphological plant traits (see the 'Vegetation Heterogeneity' section). In the case of distributed simulations, land cover, topographical, and geological information is also required. Modeling 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., Refs 300,431,432).

There are multiple measurements that can potentially be used in models and that are carried out directly on the plant scale in one or multiple individuals. These are leaf and stem water potential, sap flow, stem diameter changes, leaf turgor, leaf temperature, and gas exchange measurements at the 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 the accurate parameterization of stomata and plant hydraulic models (e.g., Ref 253). When combined together, these measurements provide a rather complete characterization of plant behavior with a notable exception represented by short-term carbon allocation

TABLE 3 | List of Variables That Can Be Potentially Observed on Different Scales

Scale	Variable	Instrument/Product
Plant	Sap flow	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 towers
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, optical sensor cable
Stand	Energy fluxes (λE, 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, ground long-term observatories
Regional/global	Albedo	Remote sensing

dynamics (phloem transport, 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 NSCs repeated a few times during a season.[433]

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 measurement includes: (1) energy and mass exchange between the land surface and the atmosphere obtained with flux-tower monitoring systems that employ the eddy covariance technique[434–438] and (2) 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 variables in the water-vegetation interaction but are difficult to upscale from the sensor level to stand scale because of considerable spatial heterogeneities.[152,439–441] Flux-tower measurements are instead an up-scaled quantity but have problems of continuity and interpretation.[442,443] Despite well-recognized issues,[444,445] flux-tower observations have represented and still represent the major source of validation for ecohydrological and terrestrial biosphere models as they provide values for variables such as latent and sensible heat, net radiation, and mass fluxes of water vapor and carbon. Lysimeters can also be used to directly measure the leaching of water and nutrients and the water content variation in soil monoliths, and, therefore, evapotranspiration.[446,447] 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 that characterizes 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., Refs 448–451), and they can be used for model testing (e.g., Refs 315,382). Recently, tree ring dendrochronology has been presented as a possibility to test simulations of carbon accumulation as well as the effect of infrequent disturbances.[452] Despite the numerous problems that exist 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., Refs 394,453–456). 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 mostly been focused on measuring vegetation productivity, especially in grasslands, but other metrics can also be monitored and used for model validation, especially if new experiments will be designed with this additional scope in mind.[456–458] 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 devices such as Lidar and hyperspectral cameras have been recently employed. Observational devices can be placed over land or aircraft platforms or on satellites.[459,460] Remote sensing observations can be carried out with optic or radar sensors and are mostly used to compute vegetation reflectivity indices, carbon stocks, and soil moisture. Carbon stocks are typically observed with radar sensors on a regional scale (e.g., Refs 461,462). Optic observations in multiple spectral bands typically map 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.[463,464] Signals in multiple bands can also be processed and converted into variables such as LAI, carbon assimilation,[465,466] or nutrient content of the leaves,[467] although the reliability of these estimates is still uncertain (e.g., Refs 468,469). A few remote-sensing products are also available for near-surface soil water content (e.g., Ref 470), and promising results in this direction are expected from campaigns such as Soil Moisture Active Passive (SMAP).[471] 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 on the seasonal and annual time scale,[412,472,473] and they may become even more so in the future.[474]

CONCLUSION

The examined literature suggests that approaches to simulate the intertwined dynamics of water, energy, carbon, and nutrient cycles are becoming widely available and that a number of models of different complexity has been presented to address problems on 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 scale 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 existing heterogeneities in larger-scale applications. We do not mean that the entire complexity of plant-hydraulic or detailed biogeochemistry models should be retained in ecohydrological or terrestrial biosphere models, but there is a wide margin to better use the insights gained at local scales in watershed, regional, and global applications (see Ref 127). For instance, models simulating plant-hydraulic and carbon dynamics mechanistically are still rare and confined to specialized studies,[206,212,213,218] but they have the potential to considerably improve the 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 modeling and observations is likely to provide insights well beyond model improvements, potentially increasing fundamental knowledge of plant–water interactions. Modeling plant mortality has been regarded as one of the great scientific challenges[475] and surely it is, but we should not forget that current models still struggle to correctly simulate the response to water limitations[476]and have a limited flexibility to accommodate diverging responses across species or within a landscape.[36,315]

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 recognized[416,417,477] and implemented in most of the models, the relevance of being spatially explicit has been less emphasized in literature.[315] Only a few studies presented process-based simulations accounting explicitly for topographic attributes and lateral water and mass exchanges.[261,263,320,321] Applications of ecohydrological models at a regional or continental scale or the introduction of topography in terrestrial biosphere models will represent possible solutions. These solutions lead to operational issues related to computational resources and accurate model parameterizations. Large spatial and long temporal scales pose great challenges to model initialization and validation as 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.[478,479] A more rigorous treatment of uncertainty with stochastic analyses and probabilistic predictions should also represent an important avenue for the future as 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.[36] Studies and modeling of plant–water interactions have seen great advancements in the past years, but current shortcomings and the challenges posed by environmental changes and preservation of water resources and ecosystem services suggest that exciting research opportunities are still ahead.

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