

Ecohydrological advances and applications in plant–water relations research: a review

Heidi Asbjornsen^{1,*}, Gregory R. Goldsmith², Maria S. Alvarado-Barrientos¹, Karin Rebel³, Floortje P. Van Osch³, Max Rietkerk³, Jiquan Chen⁴, Sybil Gotsch¹, Conrado Tobón⁵, Daniel R. Geissert⁶, Alberto Gómez-Tagle⁷, Kellie Vache⁸ and Todd E. Dawson²

¹ Department of Natural Resources and the Environment, University of New Hampshire, Durham, NH 03824, USA

² Department of Integrative Biology, University of California Berkeley, Berkeley, CA 94720, USA

³ Department of Environmental Sciences, Copernicus Institute of Sustainable Development, Utrecht University, Utrecht 3508TC, The Netherlands

⁴ Department of Environmental Sciences, University of Toledo, OH 43606, USA

⁵ Department of Forest Sciences, National University of Colombia, Medellín, Colombia

⁶ Department of Functional Ecology, Institute of Ecology, Xalapa 91070, Mexico

⁷ Department of Earth Sciences, University of Michoacán, Morelia, Michoacán 58330, Mexico

⁸ Department of Biological and Ecological Engineering, Oregon State University, Corvallis, OR 97331, USA

*Correspondence address. Department of Natural Resources and the Environment, University of New Hampshire, Durham, NH 03824, USA; Tel: 603-862-2341; Fax: 603-862-4976; E-mail: heidi.asbjornsen@unh.edu

Abstract

Aims

The field of ecohydrology is providing new theoretical frameworks and methodological approaches for understanding the complex interactions and feedbacks between vegetation and hydrologic flows at multiple scales. Here we review some of the major scientific and technological advances in ecohydrology as related to understanding the mechanisms by which plant–water relations influence water fluxes at ecosystem, watershed and landscape scales.

Important Findings

We identify several cross-cutting themes related to the role of plant–water relations in the ecohydrological literature, including the contrasting dynamics of water-limited and water-abundant ecosystems, transferring information about water fluxes across scales, understanding spatiotemporal heterogeneity and complexity, ecohydrological triggers associated with threshold behavior and shifts between alternative stable states and the need for long-term data sets at multiple scales. We then show how these themes are embedded

within three key research areas where improved understanding of the linkages between plant–water relations and the hydrologic cycle have led to important advances in the field of ecohydrology: upscaling water fluxes from the leaf to the watershed and landscape, effects of plant–soil interactions on soil moisture dynamics and controls exerted by plant water use patterns and mechanisms on streamflow regime. In particular, we highlight several pressing environmental challenges facing society today where ecohydrology can contribute to the scientific knowledge for developing sound management and policy solutions. We conclude by identifying key challenges and opportunities for advancing contributions of plant–water relations research to ecohydrology in the future.

Keywords: ecohydrology • plant water use • regime shift • thresholds • scaling • transpiration

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INTRODUCTION

The role of plant–water relations is of central interest to the field of ecohydrology because plants occupy a key component of the hydrologic cycle. On the one hand, we know that plants need water to survive, and thus, the distribution, composition and structure of plant communities are directly influenced by

spatiotemporal patterns in water availability. On the other hand, plants are a primary conduit for returning terrestrial water to the atmosphere (Chapin *et al.* 2002) while mediating albedo and roughness (Pielke *et al.* 1998), thereby exerting a strong effect on hydrologic fluxes of the terrestrial-atmospheric system. The pivotal role plants play in modulating many hydrologic processes has long been recognized by both

ecologists and hydrologists, leading to efforts to refine and deepen understanding of water fluxes, flows and transport within these respective disciplines. However, collaboration and integration across these disciplines has historically been limited or isolated. In the early 20th century, the first scientific investigations focused on understanding the linkages between vegetation–water relationships and watershed scale response were conducted (e.g. Engler 1919; Hursh and Brater 1941). Yet ecohydrology has only recently been recognized as a separate, highly interdisciplinary, field that explicitly studies the interactions between ecological and hydrological processes (e.g. Smettem 2008). The timeliness and increasing interest in the field is reflected by its rapid growth and maturation over the past 10 years. A query of *Web of Science* using “ecohydrology” as the search term revealed 305 publications between 2001 and 2010, compared to only 18 for the previous decade, and zero publications prior to 1991. The recently established journal *Ecohydrology* ([http://onlinelibrary.wiley.com/journal/10.1002/\(ISSN\)1936-0592](http://onlinelibrary.wiley.com/journal/10.1002/(ISSN)1936-0592)), together with several foundational textbooks (e.g. Eagleson 2002; Rodriguez-Iturbe and Porporato 2005), have undoubtedly propelled the discipline forward through interdisciplinary collaboration and the formation of several ecohydrology-centered graduate research and degree programs worldwide.

Ecohydrological studies typically focus on understanding the linkages, interactions and feedbacks between hydrologic flows and ecosystem processes, as well as how these interconnections are manifested and exert distinct controls across multiple scales (e.g. Porporato and Rodriguez-Iturbe 2002; Smettem 2008). Given the growing urgency of declining global water supply and quality (UNESCO 2009), combined with the recognized relationship between land use change and water resources (Bonell and Bruijnzeel 2005), one of the major offerings of ecohydrology is its potential to address these pressing environmental issues (Kundzewicz 2002). This is especially important considering that conventional approaches based on watershed management, conservation or technological solutions to address water-related issues have often either failed or fallen short of their goals (e.g. Anderies *et al.* 2006; National Academy of Sciences 2008; Zalewski 2000). The science and practice of ecohydrology offers a scientific basis for designing more holistic and integrative approaches better suited to the complexity of environmental problems at the interface between hydrology and ecosystem science (Wagener *et al.* 2010; Wilcox 2010; Zalewski 2006).

Recently, ecohydrological investigations are placing increased emphasis on understanding plant–water relations, especially as related to patterns in vegetation water use and mechanisms controlling responses to environmental change. As vegetation manipulations are one of the primary tools available to watershed managers, improved understanding of how plants influence the hydrologic cycle across multiple scales provides a foundation for more effective watershed management. In this paper, we highlight significant advances in ecohydrology and identify key challenges and opportunities for future work, with

an emphasis on plant–water relations. We begin by providing a general overview of five cross-cutting themes related to the role of plant–water relations within the context of ecohydrologic research. We then discuss how these themes are revealed in greater depth within key research areas, with an eye on major scientific advances and remaining knowledge gaps. We conclude by identifying major knowledge gaps and offering a proposed research agenda for ecohydrology in the future.

CROSS-CUTTING THEMES IN ECOHYDROLOGY

Dynamics and emergent properties of contrasting water-controlled ecosystems

Although it might be argued that all ecosystems are to some extent controlled by water, the specific mechanisms controlling water fluxes and pathways may vary greatly. In water-limited environments, such as arid and semiarid deserts, grasslands and savannas, plant growth is often controlled by stochastic pulses of water that directly affect plants' ability to adapt and survive; in turn, species composition and structure affect water fluxes at larger scales (Schwinning and Sala 2004). Conversely, in humid environments where wetlands or saturated soils are prevalent, the predominant controls on ecosystem functions are often water table fluctuations and hydroperiod and their interaction and feedbacks with vegetation water use and successional processes (Rodriguez-Iturbe *et al.* 2007). In between these extremes lie seasonal environments where water availability and scarcity fluctuate sharply and plants may exhibit unique adaptations to and effects on the hydrologic cycle that differ from more continuously water-limited or water-abundant environments (Jacobsen *et al.* 2008). These different mechanisms by which water interacts with vegetation across hydroclimatic gradients are often associated with very different plant–water relations and functions (e.g. Allen *et al.* 1996; Jackson and Colmer 2005; Loik *et al.* 2004; van der Moezel *et al.* 1988). Although ecohydrological research has tended to emphasize dryland systems (e.g. Jackson *et al.* 2009; Newman *et al.* 2006), humid lands have received growing interest in recent years (Rodriguez-Iturbe *et al.* 2007). Deciphering the different mechanisms and processes that characterize ecosystems along hydroclimatic gradients, and understanding their contrasting sensitivities and responses to environmental perturbations, are important challenges in ecohydrology (e.g. Sun *et al.* in press).

Measuring and transferring information across scales

Issues of scale comprise a central feature and challenge in ecohydrological research. Relevant scale issues range from choosing the appropriate measurement scale and how to best transfer information across different scales (Chang *et al.* 2006; Miller *et al.* 2004), to the quantification of how error, variation and parameter uncertainty are affected by measurement scale and scaling procedures (Anderson *et al.* 2003). While mechanisms controlling water fluxes often need to be examined

at the scale of individual leaves, whole plants or within spatially explicit points or plots within the soil profile, the effects of accumulated fluxes are often best understood at larger watershed and landscape scales as manifested by streamflow, evapotranspiration (ET) and recharge. It is also at these larger scales where ecohydrological processes are most relevant for society through their impacts on water provisioning and quality. The availability and refinement of several powerful technologies, such as portable laser spectroscopy for determining water stable isotope ratios (Berman *et al.* 2009; Lee *et al.* 2005), micrometeorological approaches for direct measurement of ET (Chen *et al.* 2004) and high-resolution remote sensing technologies for assessing vegetation water stress (Berni *et al.* 2009) greatly enhance our ability to integrate data from a range of spatial scales. Simultaneously, more advanced theoretical and statistical approaches (Hwang *et al.* 2009) and modeling frameworks (Popp *et al.* 2009) are being developed to better account for increasing complexity associated with scaling. In this paper, we explore two major challenges related to measuring and transferring information across scales: upscaling plant water fluxes from leaves to watersheds or landscapes and linking vegetation water use to streamflow regime.

Heterogeneity and complexity in time and space

Quantifying and characterizing variability in space and time is a cornerstone of hydrological and ecological research (Caylor *et al.* 2005; Levin 1992); the same is true for interdisciplinary explorations in ecohydrology. For example, ecohydrological research reveals how spatial patterns in vegetation exert strong controls on horizontal and vertical gradients in soil moisture (Breshears *et al.* 2009; Duniway *et al.* 2010; Potts *et al.* 2010) and infiltration (Thompson *et al.* 2010), on the amount and distribution of throughfall (Holwerda *et al.* 2010; Zimmermann *et al.* 2007, 2009) and stemflow (Hildebrandt *et al.* 2007; Li *et al.* 2009) and on ET and streamflow (Jothityangkoon *et al.* 2001; Flerchinger *et al.* 2010). Soil moisture patterns feed back to affect vegetation dynamics through their effects on plant establishment and growth (Breshears and Barnes 1999), leaf phenology (Choler *et al.* 2010) and competitive interactions and successional processes (Asbjornsen *et al.* 2004a; Booth *et al.* 2003). For instance, water use by vegetation changes dramatically with stand age (Vertessy *et al.* 2001), which in turn can have important consequences for streamflow (Scott and Prinsloo 2008). More advanced measurement techniques are allowing for the detection of spatiotemporal patterns with greater resolution at both fine (e.g. time domain reflectometry, sapflow techniques) and broad (e.g. satellite thermal multi-spectral imagery, eddy covariance [EC] technologies) scales.

Ecohydrological triggers of non-linear relationships, thresholds and stable states

Non-linear relationships resulting in threshold behavior and shifts to alternate stable states are being increasingly recognized by ecologists (Groffman *et al.* 2006; Rietkerk and van

de Koppel 1997; Scheffer and Carpenter 2003; Suding *et al.* 2004; van Nes and Scheffer 2003). Similarly, hydrologists have documented the existence of thresholds for runoff generation and streamflow response in relation to factors such as hydrologic connectivity and land cover change (James and Roulet 2007; Li *et al.* 2007; Vivoni *et al.* 2009). Such shifts can be triggered by either gradual change or abrupt events in the external system conditions (Scheffer and Carpenter 2003). Mechanisms underlying threshold behavior and alternate stable states are often related to positive feedbacks that also drive self-induced spatial heterogeneity and complex interactions. Positive feedbacks are self-reinforcing changes, independent of the direction of change and are particularly pronounced in ecosystems where water stress is important for limiting plant growth. For instance, in arid ecosystems, positive feedbacks operate between increased vegetation biomass, rainwater infiltration into the soil and increased lateral root spread, leading to more vegetation biomass and thus alternate stable vegetated and desert states (Rietkerk *et al.* 2002, 2004a; von Hardenberg *et al.* 2001). While the dynamics of threshold behavior and regime shifts within ecohydrology are only beginning to be investigated, such research may have far-reaching implications for managing and restoring watersheds (Briggs *et al.* 2005; Contamin and Ellison 2009; Mayer and Rietkerk 2004), especially when threshold responses are influenced by disturbances or extreme climate events to create unexpected surprises (e.g. Gordon *et al.* 2008; Mulholland *et al.* 2009). We highlight examples of the contribution of ecohydrological research to our understanding of threshold behavior and regime shifts, within the context of watershed management.

Need for long-term data sets at multiple scales

Effectively addressing key questions in ecohydrology requires long-term data sets (including both physical and biological variables) from plot to landscape scales and under contrasting climatic and biophysical conditions (Moran *et al.* 2008). Only a few sites worldwide have been instrumented for long-term (>10 years) streamflow monitoring at the catchment scale, as reflected by the emphasis in hydrology on modeling approaches for estimating streamflow from ungauged catchments (Perrin *et al.* 2007; Winsemius *et al.* 2009; Yadav *et al.* 2007). In contrast, ecologists have often had access to data sets on vegetation dynamics that span relatively long time frames (e.g. Bresee *et al.* 2004; John *et al.* 2009; Lauenroth and Sala 1992; Tape *et al.* 2006; Willis *et al.* 2008), although long-term physiological data on plant water fluxes are notably scarce (e.g. Vertessy *et al.* 2001; Conner *et al.*, 2011). Many discoveries leading to significant theoretical advancements in ecohydrology are based on relatively long-term data sets, including the ecohydrological effects of woody encroachment in the southeastern USA (Wilcox *et al.* 2008, 2010), of wetland restoration on fens in the UK (Large *et al.* 2007) and of reforestation in South Africa (Scott and Prinsloo 2008). More generally, long-term data have contributed to understanding time lags in ecohydrological responses to environmental change

(Breshears *et al.* 2005; Hannah *et al.* 2007; Moran *et al.* 2008; Newman *et al.* 2006; Scott and Prinsloo 2008). However, the availability of sufficient data to conduct such long-term ecohydrological assessments is poor and represents an important area for future work.

KEY CHALLENGES IN ECOHYDROLOGY AND PLANT-WATER RELATIONS

Scaling plant water use from leaves to watersheds and landscapes

The ability to assess plant water use across scales relies not only on the identification and mechanistic understanding of the processes involved at each level but also on capturing variability at each scale. The question of how to “tell the forest from the trees” (Denmead 1984), in the context of extrapolating leaf-level or whole-plant water use to stand-level water use, remains a central challenge for ecohydrology (Mackay *et al.*

2010). Traditionally, the issue has been a “bottom-up” scaling issue (cf. Hinckley *et al.* 1998), as water fluxes and their controlling mechanisms are mainly studied at the leaf or whole-plant levels. However, it is logistically difficult to measure a large number of plants, and therefore, scaling approaches must be built on a sound understanding of the plant water flux processes at different levels of organization (Fig. 1).

At the leaf level, stomata are the “gateway” for plant gas exchange in all vascular plants. The need to acquire atmospheric CO₂ in order to fix carbon for growth, reproduction, defense and maintenance comes at the unavoidable cost of losing water through open leaf stomata via the process of transpiration (T). The rate of T is dictated by a number of environmental factors, including the amount of plant available water from soils as indicated by plant water potential, as well as the difference in the water vapor pressure of the air inside and outside of a leaf (Δw) (Buckley 2005; Lambers and Chapin 2008). Drier air resulting from lower atmospheric relative humidity reduces the water vapor saturation of air outside leaves relative

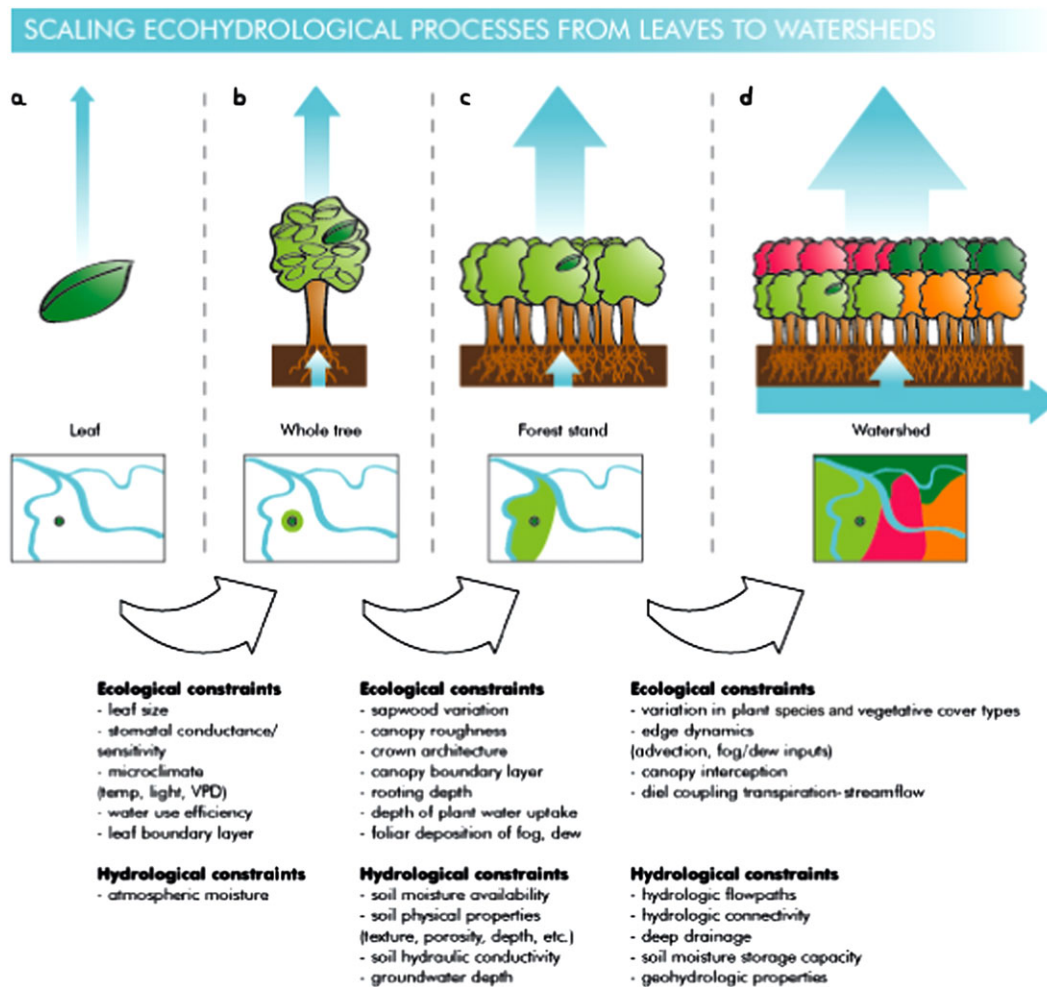


Figure 1. conceptual model for scaling ecohydrological processes from leaves to whole trees to forest stands to watersheds, with emphasis on the ecological and hydrological controls on water fluxes that must be understood and quantified when transferring ecohydrologic information across scales.

to that inside the stomatal cavity; if stomatal aperture remains constant as the difference in humidity increases between outside and inside of the leaf, then transpiration also increases (Buckley and Mott 2002). This occurs until water loss exceeds water availability, at which point leaf-level regulation of water loss begins via a decrease in stomatal aperture (Meinzer *et al.* 1993). Differences or changes in Δw are driven by a range of microclimatic conditions (e.g. air and leaf temperatures, humidity) and have been described directly or by variations of the Jarvis Model (Jarvis 1976).

Microclimatic influences on plant gas exchange can occur on the scale of a single leaf, a plant crown, as well as forest canopy, and can vary greatly between water limited, water abundant and seasonal environments. Leaf size, crown architecture and canopy roughness can all, individually and together, impose important boundary layer effects that if large can decouple a leaf from the surrounding air (Jarvis and McNaughton 1986; Meinzer *et al.* 1993). If this occurs, overall water loss at leaf and landscape scales will be influenced. Additionally, microclimate conditions known to influence T can vary over small spatial and temporal scales, leading to large differences among species and individual plants in whole-plant carbon fixation (A), water use and their ratio, A/T , or water use efficiency (Bauerle *et al.* 2009; Golluscio and Oesterheld 2007). It follows that when scaling from leaf to landscape, interactions between microclimate and plant physiological controls on transpiration will ultimately impact on ecohydrology with respect to water used from the soil and returned to the atmosphere (Fig. 1).

Estimates of T in plant ecophysiological studies have often been based on leaf-level measurements, but these approaches are limited in their scaling utility due to their instantaneous nature, high variability and extremely small scales (Ansley *et al.* 1994; McDermitt 1990). Thus, an increasingly popular approach is the use of heat as a tracer for sap movement in xylem. A distinct advantage of this approach is that it provides continuous integrated water flux measurements for the whole plant.

Heat tracer techniques appropriate for larger stems generally measure sap velocity at a single or a few depths within the xylem, and these data can be scaled to the whole tree by multiplying velocity by the cross-section area of sapwood. Accounting for radial variation in sap velocity is essential for accurate estimates of whole-plant water use (Čermák *et al.* 2004; Nadezhdina *et al.* 2002; Pausch *et al.* 2000). Overestimates of up to 154% can result if this variability is overlooked (Ford *et al.* 2004), particularly for trees with large sapwood areas. Furthermore, radial patterns of sap velocity may vary with species (Gebauer *et al.* 2008), across individuals within a species (Kumagai *et al.* 2005; Poyatos *et al.* 2007), throughout the day (Cohen *et al.* 2008; Ford *et al.* 2004; Saveyn *et al.* 2008) and with environmental conditions, including air vapor pressure deficit (VPD, Nadezhdina *et al.* 2002), radiation (Fiora and Cescatti 2006; Saveyn *et al.* 2008), wind (Herbst *et al.* 2007; Taylor *et al.* 2001) and soil moisture (Phillips *et al.* 1996). To

account for radial variability, multiple point measurements of sap velocity across the sapwood are needed to fit polynomial functions to integrate sap velocity across the entire sapwood depth (e.g. Ford *et al.* 2004; Gebauer *et al.* 2008; but see Saveyn *et al.* 2008). These approaches have the disadvantage of being based on the limits of the empirical analysis. Moreover, there is no consensus regarding how to best account for radial profiles in sap flow to address the variation with sapwood depth. Innovative approaches involving theoretical frameworks that integrate normalized values of sap velocity and stem conductance into predictive species-specific mathematical models may improve the accuracy and broad applicability of upscaling procedures (Caylor and Dragoni 2009).

Plant water use expressed on a ground area basis is usually the primary variable of interest in ecohydrology studies, and biometric scalars such as sapwood area or leaf area are often used to convert flux estimates to the stand or ecosystem level (e.g. Čermák *et al.* 2004; Wullschleger *et al.* 1998). A critical challenge for scaling from plant to stand is accounting for spatial variability in plant water use due to factors such as age-related decline in leaf-specific conductance (Irvine *et al.* 2004; Ryan *et al.* 2000, 2006), structural characteristics associated with edges (Detto *et al.* 2008; Taylor *et al.* 2001), forest fragmentation (Giambelluca *et al.* 2003), and stand density (Simonin *et al.* 2006), variation in soil moisture and depth (Tromp-van Meerveld and McDonnell 2006; Wullschleger and Hanson 2006), and physiological adaptations and growth characteristics related to water use (Licata *et al.* 2008; Dierick and Holscher 2009; Fernandez *et al.* 2009; Kagawa *et al.* 2009). A comparison of water use among 10 co-occurring tropical angiosperm species showed a twofold difference in transpiration between different trees species of similar size (Dierick and Holscher 2009). These findings challenge earlier theories proposing a strong linear relationship between tree size and daily water use that outweighs interspecific differences in water use patterns (e.g. Meinzer *et al.* 2001; Motzer *et al.* 2005; McJannet *et al.* 2007; Wullschleger *et al.* 2001).

While the above discussion points to the importance of measuring sap flow in as many trees and species as possible to adequately scale whole-tree transpiration to the stand (Kumagai *et al.* 2005), only limited measurements are typically conducted due to both time and resource constraints. A review of 90 sap flow studies in trees revealed ≤ 8 trees per species per plot are typically measured in 1 or 2 plots to represent areas from 8 to 6 000 m² (Mackay *et al.* 2010). Given the large degree of spatial heterogeneity described above, a critical focus of research has been determining the representativeness of these limited observations (e.g. Kumagai *et al.* 2007; Kume *et al.* 2010; Mackay *et al.* 2010). Collectively, this work suggests that a more accurate characterization of stand-level transpiration is accomplished by biased rather than random sampling, in which plots are located in structurally representative areas within the stand.

Other approaches to estimating plant water use on larger scales while avoiding the complications of using biometric

scalars involve the use of distributed SVAT models (Blöschl and Sivapalan 1995, Raupach and Finnigan 1995). Model structure and design often depends on the model developer, the study objective, the scale of interest and data availability. Further, models can be aggregated into a hierarchical framework to identify significance of processes in the form of parameterizations to be incorporated into models of the next larger scale (Anderson *et al.* 2003). For instance, the spatially explicit 3D model MAESTRA computes radiation absorption, photosynthesis and transpiration at the scale of a leaf within the crown of individual trees within a stand, using spatial and temporal leaf-level biochemical properties linked with stomatal gas regulation and the Penman–Monteith equation (Bowden and Bauerle 2008; Medlyn *et al.* 2007). Estimates of species-specific transpiration for five deciduous hardwood species compared well with short-term sap flow measurements; however, longer term measurements have not been examined (Bowden and Bauerle 2008). Meiresonne *et al.* (2003) compared a stand-level (physiological) process model (SECRETS; Sampson and Ceulemans 1999) and a soil water balance model (WAVE; Vancloster *et al.* 1994) with both sap flow and EC measurements and found that estimated seasonal trends and annual transpiration were similar to empirical data.

Another promising approach for upscaling plot-based measurements to landscapes is the use of remote sensing techniques. Extrapolation is possible providing that an acceptable relationship between actual plant water and a measured variable (e.g. reflectance of foliage in tree canopies) is extractable from a remote sensing data set (Chiesi *et al.* 2002, Waring and Landsberg, 2011). Glenn *et al.* (2008) used leaf area index, fractional vegetation cover and enhanced vegetation index derived from MODIS satellites to scale up T from individual shrubs to the landscape (Mu *et al.* 2007). Such approaches are now widely used to estimate ET at regional and global scales from thermal images (Bastiaanssen *et al.* 1998; Zhang *et al.* 2010).

A final approach to quantify ecosystem and landscape-level water fluxes is through tower- and aircraft-based measurement of ET. Moreover, interest in quantifying carbon fluxes as part of climate change research has promoted the establishment of EC towers at which ET is also measured (Baldocchi 2008). EC flux towers have been used to measure continuous ET in a large range of climate and biome types and provide details of ecosystem-level exchange of water spanning diurnal, synoptic, seasonal and interannual time scales since the early 1990s (Chen *et al.* 2004). These towers are now coordinated by several networks (e.g. AmeriFlux, FLUXNET, USCCC) where thousands of site-year data are compiled (Papale *et al.* 2006), allowing examination of regional, continental and global ET patterns at the scale of 10s of meters to kilometers. To examine ET over regions or continents, EC flux measurements must be upscaled by combining *in situ* data with ecosystem models and/or remote sensing technology (Yuan *et al.* 2010).

Major lessons are being learned using EC to explore ecosystem-level mechanisms for changes of ET at various temporal

scales. In the semiarid regions of Inner Mongolia (China) and Wyoming (USA), Wilske *et al.* (2010) used EC flux data to demonstrate the importance of VPD and soil water potential on regulating ET fluxes. To address the controversial question of how disturbance regulates ET losses, Miao *et al.* (2009) used EC methods in four grasslands of different grazing intensity in Inner Mongolia and concluded that grazing significantly reduced ET. Synthesis of these findings using FLUXNET data is also elucidating how both terrestrial ecosystem ET (Yuan *et al.* 2010) and plant–water relationships (Jung *et al.* 2010) vary across different time periods and among continents and biomes. For example, the declining trend between 1998 and 2008 in ET for Australia and Africa showed clear ET differences compared to other continents due to effects of high soil moisture limitation on regional plant productivity (Jung *et al.* 2010). However, application of EC data at all scales faces many challenges, such as analytical methods for analysis, data quality control, gap filling, uncertainties and scaling protocols.

Some major advances and challenges involved in scaling leaf level water fluxes to larger spatial scales are highlighted the growing body of research on the interactions between atmospheric water (e.g. fog, cloud and dew), plant–water relations and site water balance. Atmospheric water can reduce the amount of atmospheric losses of water from leaf surfaces by lowering the saturation vapor pressure at a given temperature and thereby suppressing transpiration (Burgess and Dawson 2004; Simonin *et al.* 2009). Studies using sapflow techniques to quantify the suppression effect of fog on plant transpiration have typically documented reductions of plant transpiration by 40–60% in fog, as compared to fog-free conditions (Hildebrandt *et al.* 2007; Reinhardt and Smith 2008; Ritter *et al.* 2009). When atmospheric water has saturated all plant surfaces and exceeded canopy storage capacity, additional water may drip to the ground and contribute to both plant available water (Burgess and Dawson 2004; Dawson 1998) and the overall ecosystem water budget (Cavelier *et al.* 1996; Dawson 1998; Ewing *et al.* 2009; Holder 2004; Holwerda *et al.* 2010), with maximum contributions in some cases exceeding total rainfall inputs (Buijnzeel *et al.* in press). Finally, plants in temperate and tropical ecosystems are capable of direct uptake of water through leaves (Breshears *et al.* 2008; Burgess and Dawson 2004; Limm *et al.* 2009; Stone *et al.* 1950; Yates and Hutley 1995), which can account for 2–11% of leaf water content following 3 h of leaf wetness (Limm *et al.* 2009) and may have implications for stand-level water balance due to reduced plant stress and consequently greater total water use. Application of EC approaches in these cloud-affected regions helps explain how interactions between atmospheric moisture, other microclimate variables and canopy water fluxes for large-scale processes affect the water balance (Holwerda *et al.* 2006; Ritter *et al.* 2009; Schellekens *et al.* 2000). Innovative approaches based on integrating individual tree sapflow measurements with stand-level water use using a combination of biometric scalars, hydrometeorological monitoring and modeling are enhancing ecohydrologic

understanding of vegetation–water linkages in these systems (Katata *et al.* 2010; Muñoz-Villers *et al.* in press; Wu *et al.* 2006). Nevertheless, more work is needed to resolve large errors in estimates of total water inputs from fog and/or cloud deposition.

Threshold responses can be observed at different scales in terms of how individual plants and whole ecosystems regulate water fluxes and respond to biophysical controls. At the individual leaf scale, transpiration generally increases in response to increasing VPD up to a threshold level, after which stomata begin to close and transpiration declines. However, this threshold–response relationship varies markedly among species and ecosystems due to different adaptive strategies and physiological mechanisms that regulate stomatal functions (Sperry *et al.* 2002; Damour *et al.* 2010; Zweifel *et al.* 2007). At landscape scales, transpiration is controlled largely by interactions between microclimate variables and the saturation deficit experienced by the canopy. This may be very different than the saturation deficit at the leaf scale, even though the two are usually assumed to be the same (Jarvis and McNaughton 1986). Threshold responses at large scales are generally not as sharp or dramatic since changes occur more slowly. Nevertheless, dramatic and rapid dieback and mortality of vegetation in response to extreme droughts (e.g. Breda *et al.* 2006) suggests that strong thresholds and shifts in ecosystem state may operate on larger scales and deserve greater attention. These processes may be examined most effectively by modeling changes in saturation deficit across scales, while incorporating appropriate site-specific values for reference saturation deficit (Jarvis and McNaughton 1986) as well as species- and ecosystem-level information on the dynamics of the different threshold responses and potential for shifts in ecohydrologic functions.

Effects of plant–soil interactions on soil moisture dynamics

In most ecosystems, except perhaps extremely dry deserts where environmental conditions preclude establishment of extensive vegetative cover, plants form a critical pathway for water fluxes between the soil and atmosphere. Hydropedology—the science of understanding water flow and transport processes, variability and mass-energy interactions in the structured unsaturated soil zone (Lin 2003; Lin and Rathbun 2003)—depends strongly on knowledge of the controls exerted by vegetation on soil moisture dynamics. The intersection of plant ecophysiology, hydropedology and hydrology is leading to an enhanced understanding of how interactions and feedbacks between vegetation and soil influence the hydrologic cycle (e.g. Fig. 1). One area receiving increased attention is the relationship between spatiotemporal patterns in water fluxes within the soil profile and the distribution, structure and physiological functions of plant communities.

In dryland (water-limited) ecosystems characterized by patchy vegetation, soil moisture varies vertically with soil depth and horizontally with varying vegetation structure

(e.g. subcanopy, edge, intercanopy positions), with complex and changing seasonal and annual variability (e.g. Breshears *et al.* 2009), and in response to water pulses (Loik *et al.* 2004). For example, tree and shrub canopies mediate soil moisture fluctuations by reducing evaporative losses through shade and by reducing rainfall inputs through canopy interception, resulting in buffering against extreme fluctuations in soil moisture in the upper soil profile (Asbjornsen *et al.* 2004b; Potts *et al.* 2010). Stemflow and preferential flow along root channels into deeper soil layers can contribute to soil moisture heterogeneity and enhance desert shrub water relations (Li *et al.* 2009). Stemflow has also been shown to create saturated areas within the vadose zone extending to the water table beneath canopy trees (Durocher 1990). Moreover, vegetation can exert reciprocal feedbacks on the vertical and horizontal distribution of plant available water through diverse mechanisms (Breshears and Barnes 1999; Caylor *et al.* 2006). In semiarid mixed grass–shrublands, preferential redistribution of water from rainfall pulses to grass canopies was shown to enhance grass transpiration, whereas no response was observed in shrubs (Pockman and Small 2010). Furthermore, plant water uptake patterns from different soil depths, which often vary spatially and temporally between different plant functional types, can directly influence soil water dynamics during the growing season (Asbjornsen *et al.* 2008; Dalsgaard *et al.*, 2011; Lu *et al.*, 2011; Nippert and Knapp 2007a, 2007b; Ryel *et al.* 2008; Schwinning 2010).

Humid ecosystems are often characterized as being strongly controlled by interactions between vegetation water use and groundwater dynamics. Where vegetation has either constant or intermittent groundwater access, groundwater uptake or ‘discharge’ by the vegetation responds to variability and recharge processes to cause seasonal and annual water table fluctuations (Jackson and Colmer 2005; Naumburg *et al.* 2005; Ridolfi *et al.* 2006). Groundwater access can greatly enhance water use to levels above rainfall input, such that it may comprise a large proportion (>50%) of annual transpiration, and in some cases, annual water use may approach theoretical potential ET once the canopy has closed (Benyon *et al.* 2006). In turn, water table fluctuations can exert controls on vegetation depending on different plant species’ tolerance to anoxic and/or saline conditions (Kozłowski 1997, 2002; Naumburg *et al.* 2005; Shafroth *et al.* 2000). A decline in the water table below the rooting zone can lead to increased plant moisture stress, reduced growth and increased mortality (Scott *et al.* 1999, 2000; Sperry *et al.* 2002). Conversely, excessively high levels of soil water can lead to reduced transpiration, such as in tropical montane cloud forests where highly organic soils may become saturated (Santiago *et al.* 2004), or in mangrove swamps subjected to frequent flooding (Krauss *et al.* 2007).

In both dryland and humid land systems, plants can directly influence soil water dynamics, as well as the growth and competitive interactions of plant communities, through the active redistribution of water by plant roots. This so-called ‘hydraulic lift’ (Richards and Caldwell 1987) or ‘hydraulic redistribution’

(HR; Burgess *et al.* 1998) has been shown to occur in a wide range of ecosystems (Bleby *et al.* 2010; Caldwell *et al.* 1998; Dawson 1993, 1996; Domec *et al.* 2010; Hultine *et al.* 2003; Meinzer *et al.* 2004; Oliveira *et al.* 2005). While HR is commonly considered to cause an increase in soil moisture at shallow depths due to lift from ground water sources, water can also flow from shallow to deep soil layers following the onset of rain in seasonal systems (Burgess *et al.* 1998). HR can maintain steady soil water availability despite seasonality in rainfall, facilitating greater carbon fixation and increased rates of ET, where transpiration rates can increase by 30–50% (Domec *et al.* 2010; Lee *et al.* 2005). This raises interesting questions about the capacity for HR to affect changes in plant-atmosphere processes such as convective rainfall generation (Siqueira *et al.* 2009).

Vegetation can also exert a positive effect on infiltration rates and soil hydraulic conductivity due to organic matter accumulation, increased root activity and improved physical properties (Bonell *et al.* 2010; Germer *et al.* 2010). This affects overland water flow, source–sink relationships and plant productivity (Ludwig *et al.* 2005; Popp *et al.* 2009; Reid *et al.* 1999). Plants directly modulate spatiotemporal fluxes of water within the soil by influencing the connectivity of water flow on the soil surface and subsurface (Bartos and Campbell 1998). Connectivity occurs after a given soil water content threshold is exceeded, such that saturated zones grow to meet one another, connecting the hillslope hydrologically and generating runoff (Bond *et al.* 2002, 2007; Fitzjohn *et al.* 1998; McNamara *et al.* 2005).

The dynamic regulation of water fluxes resulting from interactions and feedbacks between vegetation and soils can produce non-linear behavior and rapid, unexpected changes in response to certain ecohydrological triggers. In arid and semi-arid regions, these processes are clearly illustrated by desertification. Conceptual models propose two alternate ecosystem states (e.g. grassland vs. shrubland and vegetated vs. desert) that, in part, are controlled by changes in ecohydrologic functions leading to state shifts (e.g. Rietkerk and van de Koppel 1997; Walker *et al.* 1989). For example, in the southwestern USA, stable coexistence of herbaceous vegetation with widely dispersed trees (e.g. savanna) is suggested to represent a dynamic equilibrium between shallow-rooted grasses and deep-rooted shrubs and trees (Scholes and Archer 1997), with shifts to the alternate (degraded) woodland state occurring with increased grazing pressure and/or altered fire regime (Archer 1989). Studies suggest that the threshold at which a shift occurs from grassland to degraded states is primarily determined by the increased exposure of soil surfaces with increasing shrub cover and decreasing grass cover, such that raindrop impacts form surface crusts and limit infiltration rates, resulting in a positive feedback of accelerated degradation (Ludwig *et al.* 2005; Petersen *et al.* 2009; Whisenant 1999). Petersen *et al.* (2009), studying sagebrush (*Artemisia tridentata*) communities encroached by juniper (*Juniperus occidentalis*) in the western USA, found that once juniper cover exceeds 20%, the

system crosses an abiotic threshold where increased bare ground, accelerated erosion and decreased infiltration prevent recovery. Although long-term studies on recovery following such regime shifts are generally lacking, some evidence suggests that removing livestock from degraded grasslands may enable native, perennial grass reestablishment and associated hydrologic functions (Allington and Valone 2010; Castellano and Valone 2007; Wilcox and Thurow 2006).

Another example of water-vegetation feedbacks resulting in shifts between alternate stable states is observed in regions vulnerable to salinization. Such processes are often triggered in response to a reversal of the recharge–discharge balance of soil water and groundwater caused by land use/cover change (Jobbágy and Jackson 2007). Interestingly, salinization can occur under two seemingly contrasting conditions: planting of deep-rooted trees on former grasslands and replacing deep-rooted trees with crops. The first case is well documented for the native, non-phreatophytic humid grasslands of Argentina, where discharge of groundwater and soil water by ET is less than recharge by precipitation such that saline water remains at deeper levels. In this system, establishment of phreatophytic tree plantations reverses this recharge–discharge relationship, causing salt concentrations of groundwater and soils to increase due to solute transport to the rooting zone and salt exclusion by plants during water uptake (Engel *et al.* 2005; Jobbágy and Jackson 2007). Salinity levels under tree plantations can reach levels 15–30% greater than under adjacent grasslands (Jackson *et al.* 2005). A switch in water balance from positive to negative resulting in salinization may be a function of a climatic threshold, only occurring on sites where mean annual precipitation is <1100 mm, and thus, drainage is insufficient to remove and prevent the accumulation of solutes (Nosetto *et al.* 2008). Further, plants may directly modulate the intensity of salinization because of differences in species' salinity tolerances, and hence, in the amount of water extracted from saline groundwater (Nosetto *et al.* 2008).

An apparently contrasting situation with similar ecohydrological implications, but different mechanisms, is observed in Australia, where conversion of the native, deep-rooted woodland vegetation to shallow-rooted agriculture has led to increased deep drainage and a rise in the saline groundwater and severe salinization problems (Archibald *et al.* 2006; Peck 1978). High solute concentrations in the shallow groundwater and vadose zone can produce a positive feedback response from the vegetation by reducing plant growth, leaf area and in turn transpiration, thereby further increasing groundwater rise and salinization (Peterson *et al.* 2009). Positive feedbacks can also be exacerbated on lands already experiencing salinization by planting trees that exclude dissolved salts during water uptake, thereby further increasing the salt concentrations (Archibald *et al.* 2006). Such positive feedbacks can cause a rapid transition to an alternate stable state comprised of structurally and floristically impoverished vegetation communities (Cramer and Hobbs 2002; Wright and Chambers 2002), which may be irreversible (Cramer and Hobbs 2005; Ridolfi

et al. 2006). Ecohydrologic models developed to simulate salinization processes have demonstrated the plausible existence of several attractors that result in multiple stable states, which is contrary to most hydrologic models that assume only one attractor and therefore a steady-state water table (Peterson et al. 2009). A modeling approach applied to an intensive agricultural system in southeastern Australia showed that the threshold at which a switch to the alternate salinized state was a function of the percent of native vegetation cleared in the mid-catchment (Anderies et al. 2006). However, there are still many unanswered questions regarding the drivers and thresholds that trigger movement to an alternate stable state, as well as the potential for reversing such transitions once they occur, leaving an open area for future study.

Linking plant water use, hydrologic flow paths and streamflow regime

One important contribution of ecohydrological research is enhanced understanding of the connections between plant water use, hydrologic flow paths throughout the soil–plant–atmosphere continuum and streamflow regime. Central to this discussion is the water balance equation, which can be expressed as:

$$P = ET + R + S + D, \text{ where } ET = I + E + T \quad (1)$$

where P is precipitation, R is runoff, S is soil water storage, D is deep leakage of water below the root zone, I is canopy interception and evaporation and E is evaporation of water from the soil and litter layer. In general terms, in water-limited ecosystems, ET accounts for a large proportion of P (often >90%, Wilcox et al. 2003), whereas in high rainfall regions ET represents a much smaller fraction of P . Soil moisture can be considered an integrating factor of ecohydrological processes (Rodríguez-Iturbe and Porporato 2005) because it reflects the net effects of the different water balance components (Breshears et al. 2009). The water balance equation (1) directly links vegetation water use to streamflow regime. Plant transpiration determines water losses from the soil to the atmosphere, and canopy interception can greatly increase the surface area for evaporation relative to the soil alone. The remaining soil water is available for streamflow generation through different hydrologic flow paths. Understanding these linkages requires quantifying how the interactions between plant water use and soil water dynamics scale up to influence hydrologic flow paths and streamflow response (Fig. 1).

Over daily time scales, direct links between vegetation and streamflow is expressed as a transpiration signal in diel streamflow fluctuation. Such signals generally occur with a time lag of 4–6 h between maximum transpiration and minimum streamflow (Bren 1997; Bond et al. 2002; Federer 1973; Gribovszki et al. 2008; Szilagyi et al. 2008). In a forested hillslope in western Oregon, the strongest coupling (i.e. shortest lag) between vegetation water use and streamflow was observed in early summer, becoming weaker as the summer drought progressed, attributed to increasing depth of the plant available water in the soil profile (Bond et al. 2002). Working at

this same site, Barnard et al. (2010) used an irrigation experiment to show that time lags between maximum transpiration and minimum hillslope discharge decreased from 6.5 h pre-irrigation to 4 and 2 h during steady-state irrigation and post-irrigation conditions, respectively. The authors suggest that these changes in transpiration–streamflow relationships are likely due to the influence of soil pore size distribution, soil filling and draining processes, the degree of hydraulic conductivity and flow velocity and uptake of water by plants from pores of different sizes. This interpretation was further researched by Brooks et al. (2009), who used stable isotopes to suggest that water from the first rainfall after a dry period was held in small pores where it was not displaced by subsequent rainfall and was only removed by ET (plants). Their conceptual model postulates two soil water domains: tightly bound water available to plants and mobile water entering the stream. A two-domain flow system, in which macropores facilitate slow, lateral subsurface flow that is not in chemical or hydrological equilibrium with the soil matrix, has also been suggested to exist in semiarid environments (Newman et al. 1998). These type of studies highlight the need for deeper mechanistic understanding between what drives plant water uptake (water potential) and how it might be linked to soil hydraulic properties like soil pore sizes and soil type and diel streamflow patterns across different ecosystems and climatic regions. To date, none of the aforementioned investigations has accomplished this.

Over annual time scales, vegetation water use and plant–soil interactions have a strong effect on streamflow. Early watershed scale hydrology studies using a ‘black box’ approach demonstrated that forest removal generally leads to an increase in total water yield (e.g. Bosch and Hewlett 1982), which is generally attributed to decreased canopy ET (e.g. Zhang et al. 2004). However, decreased dry season or ‘low’ flows have also been attributed to deforestation (e.g. Bewket and Sterk 2005; Kashaigili 2008; Madduma Bandara and Kuruppuarachchi 1988; Sinukaban and Pawitan 1998). Such low flows may be explained by the effects of intensive land use practices on increasing soil compaction and reducing soil hydraulic conductivity, infiltration rate and water storage capacity (Ilstedt et al. 2007; Turnbull et al. 2008; Ziegler et al. 2004; Zimmermann and Elsenbeer 2008), leading to larger proportions of overland and subsurface flow during the wet season and reduction in recharge of deep soil and groundwater stores that feed streams during the dry season (Bruijnzeel 2004). Reforestation generally causes a reduction in water yield due to greater water uptake by trees (Farley et al. 2005; Scott et al. 2005; Locatelli and Vignola 2009). Moreover, some studies suggest that the rate and magnitude of stand-level water use varies by species composition (Dierick and Holscher 2009; Kagawa et al. 2009) and that young fast-growing tree plantations use more water compared to native vegetation (Bren et al. 2010; Kagawa et al. 2009; Licata et al. 2008; Little et al. 2009). However, a meta-analysis of water use of invasive and native plants found that while leaf level stomatal conductance was on average 136% greater for invasives compared to

natives, they were equally likely to have higher water use at the whole-plant scale. This analysis also suggested that T was greater for ecosystems dominated by invasives, while ET was similar for invasive and native dominated stands. Nevertheless, these latter conclusions were based on only three and two studies, respectively. Additional research is needed to elucidate how transpiration–streamflow relationships may vary depending on species and site conditions. Further, general patterns of reduced transpiration with increasing stand age (e.g. Delzon and Loustau 2005; Macfarlane *et al.* 2010; Vertessy *et al.* 2001) suggest that negative effects on streamflow may eventually be reversed. One long-term ecohydrological study in South Africa showed a reduction in low flows following establishment of eucalyptus and pine plantations on degraded lands, with reestablishment of baseflows once stands reach 15–30 years (Scott and Prinsloo 2008). In contrast, Bren *et al.* (2010) reported continued declines in catchment water yield up to 34 years after clearfelling and regeneration of native *Eucalyptus regnans* relative to catchments with mature *E. regnans* in Australia. These differing results may reflect species and ecosystem variation in disturbance dynamics, canopy structure, partitioning of stand ET and changes in the sapwood area to basal area ratio (Bren *et al.* 2010; Macfarlane *et al.* 2010), as well as to climatic fluctuations (Bren and Hopmans 2007). It is also important to consider potential positive effects of vegetation regrowth and reforestation on increasing soil infiltration, hydraulic conductivity and water holding capacity (Istedt *et al.* 2007; Zimmermann *et al.* 2009), which may offset the additional water losses by increased transpiration, thereby improving low flows on (formerly) degraded sites (Bruijnzeel 2004). Understanding the interconnection between vegetation, soil hydraulic properties and hydrologic flows will provide valuable information for management aimed at improving water availability to human population centers in lower lying regions.

In contrast to humid lands, relatively high proportions of ET with respect to P characterize the water balance of dryland ecosystems, such that losses to subsurface flow and soil moisture storage are typically low (Raz Yaseef *et al.* 2010; Wilcox *et al.* 2006). There is generally little contribution by precipitation to streamflow, except when site conditions allow for deep infiltration and soil and groundwater recharge, such as on karst topography or sandy textured soils (Wilcox *et al.* 2008). The effects of plant water use and soil hydraulic properties on dryland hydrology are highlighted by considering the seemingly paradoxical effects of vegetation change on streamflow regime in the semiarid rangelands of the southwestern USA. In some regions, replacement of native shrublands with pasture clearly increases streamflow, while encroachment by shrubs after abandonment of grazing reduces streamflow (Huang *et al.* 2006). In other areas, woody encroachment combined with decreased grazing pressures results in increased streamflow and baseflow (Wilcox and Huang 2010). These contrasting findings were attributed to the relatively deep soils with high soil water storage capacity on sites with reduced streamflow

since these conditions result in less groundwater recharge and greater opportunity for soil water discharge by plant transpiration, leading to reduced streamflow (Huang *et al.* 2006). Conversely, on sites with karst geology that offer the potential for deep infiltration, encroachment by woody vegetation may result in increased soil hydraulic conductivity and thereby increased groundwater recharge (Turnbull *et al.* 2008), while rapid infiltration and deep drainage prevents plants from taking up large amounts of water and results in a net increase in flows (Wilcox *et al.* 2008).

The close coupling and complex feedbacks between vegetation and streamflow dynamics are often manifested most clearly when a system approaches or surpasses thresholds of functioning. Following on earlier discussion of regime shifts associated with desertification, ecohydrological research in Africa has revealed the watershed implications of these desertification processes. Sahelian Africa has experienced severe desertification accompanied by a decrease in mean rainfall by 25–40% between 1931–1960 and 1968–1997 (Nicholson 2000). However, hydrological responses vary greatly depending on geographic and anthropogenic factors. In southwestern Niger, increasing population pressures have led to large-scale expansion of rain-fed crops and degradation of the native savanna vegetation. This has led to increased surface runoff and groundwater recharge, attributed to lower ET by crops and reduced soil infiltration capacity of degraded soils (Leblanc *et al.* 2008). In less intensively used areas, surface water area increased over the past three decades despite similarly declining rainfall, as attributed to direct vegetation feedbacks to the severe 1970–1980 droughts, whereby drought-induced reduction in vegetative cover reduced ET sufficiently to trigger increased runoff (Claussen 1997; Gardelle *et al.* 2010; Wang and Eltahir 2000a, 2000b). In both cases, interactions between vegetation and the hydrologic cycle contributed to landscape scale alterations in hydrologic flows, but the underlying causes differed.

Shifts between alternate vegetated and desertified states in Africa may also, in part, involve self-propelled change and positive feedbacks associated with ecohydrological controls. Vegetation has lower surface *albedo* than bare soil, and it increases the land–ocean thermal gradient and thus amplifies summer monsoon rainfall. Consequently, two alternate stable states can emerge based on initial vegetative cover: dry and bare or wet and vegetated (Claussen 1997). These may explain abrupt regime shifts from vegetated to desert state, such as observed by paleo-reconstructions in the mid-Holocene in the Sahel/Sahara (Claussen *et al.* 1999; de Menocal *et al.* 2000). Interestingly, more fine-scale positive feedbacks in this region between vegetation and soil water should influence ET and surface *albedo* at larger scales, suggesting that feedbacks at disparate spatial scales may influence one another. Modeling studies suggest that the fine-scale feedbacks greatly amplify nonlinear feedbacks at larger scales (Dekker *et al.* 2007; Jansen *et al.* 2008; Scheffer *et al.* 2005). Similarly, modeling and observational studies demonstrate how primarily large-scale

climatic drivers (e.g. atmospheric CO₂, temperature, precipitation) change vegetation patterns and water use efficiency at finer scales (Barbier *et al.* 2006; Kefi *et al.* 2008).

Threshold dynamics are also evident in the manifestation of watershed scale streamflow response to small-scale changes. For example, the relationship between watershed area subjected to land use change and streamflow response is not linear, but rather, thresholds exist for the minimum proportion of a watershed that must be altered to elicit a detectable change in streamflow. In the early meta-analysis of paired catchment studies by Bosch and Hewlett (1982), forest cover changes of <20% could not be detected in streamflow response; however, they observed a 25-mm change in yield per 10% cover change for deciduous forests beyond this threshold that increased to 40 mm for coniferous forests. Similarly, research on the conversion of agricultural land dominated by annual row crops to perennial cover suggests a threshold of 10% of the area is required to significantly reduce runoff and nutrient and sediment losses (Xhou *et al.* in press; Hernández-Santana *et al.* in press). Advances in modeling approaches are providing new insights into these complex relationships (Fohrer *et al.* 2005). Using ecohydrologic modeling and Monte Carlo simulations, Eckhardt *et al.* (2003) predicted that conversion of 25–35% of a watershed from pasture to forest is required to detect a significant change in hydrologic response. Li *et al.* (2007), using terrestrial ecosystem and aquatic transport models, demonstrated that removal of tropical forest in West Africa occupying <5% of the basin resulted in a 35–65% increase in simulated annual streamflow, attributed mainly to a large decrease in transpiration outweighing a smaller increase in evaporation. Model simulations suggested that only after >50% removal did runoff and discharge change significantly because at low thinning levels, the combination of increased transpiration rate per unit leaf area and soil evaporation compensated for decreased total stand transpiration. However, after ~60% removal, the simulated evaporative demand was fully met, and any further removal of vegetation led to reduced transpiration, which was no longer compensated by increased evaporation (Li *et al.* 2007). Similarly, Ghaffari *et al.* (2010) reported that runoff increased dramatically when >60% of a rangeland was converted to rain-fed agriculture and bare ground. The precise mechanisms explaining the occurrence and characteristics of such thresholds are still unclear and require more detailed ecohydrological research (e.g. Zehe and Sivapalan 2009). Future efforts will need to take into account watershed size and parameter uncertainty when using models to scale information and make predictions across scales. For example, streamflow response in smaller catchments shows greater sensitivity to rainfall events compared to larger catchments (Seibert and McDonnell 2010), while simple scaling factors alone poorly represented the effects of small-scale phenomena across larger areas (Wilcox *et al.* 2008). Understanding non-linear behavior of lateral flow response in hillslopes due to factors such as random distribution of soil properties (Lehmann *et al.* 2007) and hydrologic connectivity and preferential flow paths (Molina *et al.* 2009; Detty and

McGuire 2010; Hrnčič *et al.* 2010; Nieber and Sidle 2010) may provide additional mechanistic capability for enhancing modeling efforts to explain threshold dynamics.

Another area where ecohydrologic research is revealing strong connections between vegetation water use, land use change and streamflow is in fog-affected regions. Fog water intercepted by forest canopies in cloud forests can provide significant hydrological inputs, and observations suggest potentially greater water yield in watersheds receiving significant fog or cloud inputs (Zadroga 1981; Ingwersen 1985). Application of isotope techniques is revealing the importance of fog and cloud water in plant–water relations (Corbin *et al.* 2005) and watershed hydrology (Scholl *et al.* 2007). These plant canopy–atmosphere interactions—and their manifestation at the watershed scale—are intricately linked to global changes in climate and hydrology. Ecosystems with frequent fog and cloud inputs may experience changes in frequency, intensity and duration of events as a function of climate and land use change (Johnstone and Dawson 2010; Lawton *et al.* 2001; Pounds *et al.* 2006; Still *et al.* 1999). These changes can have significant, yet still poorly understood, consequences for streamflow (e.g. Buijnzeel *et al.* in press). An important area for future ecohydrologic research is understanding threshold behavior related to changes in fog–plant interactions and how these scale up to affect watershed responses to larger-scale phenomena, such as lifting of the cloud base, land use change and restoration efforts.

Also important, models provide a key tool to evaluate how a changing climate may influence ecohydrological relationships (Rastetter 1996). For example, Coops *et al.* (2005) used results from the 3-PG model (Landsberg and Waring 1997) to conclude that the suitable habitat are for *P. ponderosa* should increase by 5–10% in the Northwestern USA over the next 100 years as a result of changes in ecohydrological conditions related to adaptations of *P. ponderosa* to seasonal and annual changes in soil moisture availability. The Regional Hydro-Ecological Simulation System (RHESSys) (Band *et al.* 1993) combines a productivity model with a hydrological model (similar to 3-PG), but is also spatially distributed, allowing for more full evaluation of how changes in ecohydrological flux dynamics associated with climate change may be manifested within watersheds. Zierl *et al.* (2007) showed that the RHESSys model acceptably captured streamflow across 5 watersheds (R^2 from 0.82 to 0.97 for monthly streamflow) and carbon fluxes at 15 EUROFLUX sites (R^2 from 0.26 to 0.96 for monthly net ecosystem exchange). These types of modeling frameworks, which combine hydrological accounting and productivity models, has considerable promise in evaluating how potential climate changes may influence ecohydrological relationships (also see Zhan *et al.*, 2011).

CONCLUSIONS

Summary of key findings

In this paper, we show how advances in plant–water relations research in the context of ecohydrological processes are

leading to enhanced theoretical frameworks for understanding complex interactions between vegetation and hydrologic flows. Although research has identified different mechanisms that mediate water fluxes in both water-limited and water-abundant environments, we are far from having a clear understanding of these processes across space and time. Feedbacks occurring within the soil–plant–atmosphere continuum are complex and represent important drivers of ecohydrologic functions that are highly sensitive to land use and climate change. In addition to unraveling the importance of these linkages between vegetation and hydrologic flow patterns, dynamic threshold behavior and regime shifts in response to ecohydrologic triggers can have potentially far-reaching implications for managing and restoring watersheds. As a young discipline, there are still far more questions than answers.

Major challenges and opportunities for future research

Improving capabilities for scaling plant water use data from individual leaves and whole trees to stands and landscapes must remain a central research topic. More work is needed to effectively account for spatial heterogeneity and variability in the controls on water fluxes across different scales. In particular, a greater understanding of the variation of sapwood area and radial profiles is crucial to refining calculations of whole-tree transpiration from point measures. Further, understanding the effects of multiple factors such as tree and stand age, edge and patch dynamics, stand density and species-specific physiological characteristics on water use patterns would greatly enhance the potential for scaling transpiration estimates from individual trees to stands and watersheds. Approaches that link field-based measurements of plant water use with modeling efforts that incorporate larger scale constraints on water fluxes offer particularly promising opportunities to advance understanding of the role of plant–water relations in ecohydrological processes.

Recent work has also highlighted important interactions between vegetation and soil moisture dynamics resulting in positive feedbacks that significantly alter plant water controls and can lead to shifts in ecohydrologic functioning. However, application of ecohydrologic investigations to understanding such regime shifts is still relatively new, and many unknowns remain regarding our understanding of threshold behavior in response to ecohydrologic triggers in both dryland and humid environments, particularly the mechanisms controlling the magnitude and direction of change. Depending on the environmental context, plants have been shown to buffer the effects of dry soil or create positive feedbacks leading to desertification or salination. Direct relationships have been documented between transpiration by vegetation and diel fluctuations in streamflow, although information is lacking regarding the more complex interactions between vegetation and soil hydraulic functions, hydrologic flows and watershed response. Future research should focus on unraveling the link-

ages between these components in response to land use and climate change and across a range of climatic and biophysical conditions.

Ecohydrology has progressed rapidly over the past decade, and new opportunities are emerging to apply the results to solving critical management issues related to water resources worldwide. For example, by understanding the species-specific effects of diurnal and seasonal patterns of transpiration on groundwater fluctuations and stream discharge, managers will be able to make decisions regarding which species to plant in reforestation efforts aimed at improving hydrologic functions. Furthermore, large-scale research on connections between upland vegetation and hydrologic flows will have important applications for how to best conserve habitats to protect downstream water supplies. Finally, by understanding potential threshold effects of land use change on water resources, land management policies can be developed to avoid undesirable surprises and to minimize negative impacts on hydrologic services.

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