

Ecohydrology of water-limited environments: A scientific vision

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[1] Water-limited environments occupy about half of the Earth's land surface and contain some of the fastest growing population centers in the world. Scarcity or variable distributions of water and nutrients make these environments highly sensitive to change. Given the importance of water-limited environments and the impacts of increasing demands on water supplies and other natural resources, this paper highlights important societal problems and scientific challenges germane to these environments and presents a vision on how to accelerate progress. We argue that improvements in our fundamental understanding of the links between hydrological, biogeochemical, and ecological processes are needed, and the way to accomplish this is by fostering integrated, interdisciplinary approaches to problem solving and hypothesis testing through placebased science. Such an ecohydrological approach will create opportunities to develop new methodologies and ways of thinking about these complex environmental systems and help us improve forecasts of environmental change.

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1. Definition and Need for an Ecohydrological Approach

[2] Multiple agencies, and the scientific community in general, recognize the necessity and potential benefits accruing from environmental research that crosses traditional scientific disciplines [Rodriguez-Iturbe, 2000; National Research Council, 2001a, 2001b; Harte, 2002; Nuttle, 2002; Infrastructure for Biology at Regional to Continental Scales Working Group, 2003; Newman et al., 2003]. This need for interdisciplinary research has heightened interest in the hybrid discipline of "ecohydrology", which seeks to elucidate (1) how hydrological processes influence the distribution, structure, function, and dynamics of biological communities and (2) how feedbacks from biological communities affect the water cycle (modified from Nuttle [2002])

(alternative definitions and in-depth discussions of ecohydrology are given by *Baird and Wilby* [1999], *Rodriguez-Iturbe* [2000], *Bonell* [2002], *Eagleson* [2002], *Kundzewicz* [2002], *Nuttle*, [2002], *Porporato and Rodriguez-Iturbe* [2002], *Zalewski* [2002], *Bond* [2003], *Hunt and Wilcox* [2003], *Newman et al.* [2003], *Van Dijk* [2004], *Hannah et al.* [2004], and *Breshears* [2005]). Implicit in the above definition is the recognition that vegetation, water, and nutrients are intimately coupled. Simply put, changes in one bring about changes in the others. Although these couplings have been studied for many years within various earth science and biological disciplines [*Bonell*, 2002], our understanding of the interdependencies and interaction of these three components is far from complete.

- [3] The reasons for adopting an ecohydrological perspective are compelling. For example, the extent to which scientists will be able to forecast the nature, magnitude, and rate of environmental changes, and thereby their effects on natural resources and socioeconomic systems, will determine how well societies adapt and function [Clark et al., 2001]. Reliable forecasting depends on obtaining and integrating a broad range of scientific information to understand environmental processes, particularly those in the "critical zone", the heterogeneous, near-surface environment in which complex interactions between rock, soil, water, air, and living organisms regulate the natural habitat and determine the availability of life-sustaining resources [National Research Council, 2001a].
- [4] Simply put, ecohydrology as a "discipline" involves linking hydrology and ecology. There are, however, multiple ways that this linkage can be achieved. One of the goals of this paper is to describe our perspectives on how this linkage might be forged and the potential benefits to science

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and society. The approach we advocate, while admittedly challenging, offers the potential for rapid advances in addressing applied problems within the critical zone, providing insights about coupled environmental processes that would not be obtained otherwise.

- [5] In our view, the merger of ecology and hydrology into a science of "ecohydrology" is aimed at understanding environmental systems in a more integrated or comprehensive way. For example, we advocate a science that better melds our understanding of hydrology within problems of a biological nature, and vice versa. In other words, ecologists and hydrologists should develop a perspective of approaching complex environmental problems from an ecohydrological (or interdisciplinary) viewpoint, and be willing to build strong cross collaborations that overcome or transcend traditional differences in disciplinary emphasis areas and approaches. It seems reasonable to expect that applying an ecohydrological approach that integrates concepts and tools from numerous disciplines (geology, biogeochemistry, plant physiology, soil science, and atmospheric science to name just a few) will allow us to significantly advance our understanding of vegetation-water-nutrient interactions. For example, topography and geologic landforms control solar irradiance, a primary biological driving force in dry regions, via differences in aspect and slope. Plant physiology contributes knowledge regarding the regulation of water acquisition, transport and loss. Soil texture regulates infiltration, percolation, and water and nutrient availability to plants. Atmospheric conditions regulate timing, intensity, and amount of precipitation, as well as vapor pressure deficits and wind conditions (the driving forces for evaporation and transpiration). Traditional investigations with a single disciplinary focus will likely miss key behaviors and may inadvertently neglect key mechanisms operating at finer spatial/ temporal scales or fail to predict how mechanisms will be manifested at coarser spatial/temporal scales.
- [6] Such a perspective will certainly broaden the individual disciplines of hydrology and ecology, but in so doing, a more general or "universal" understanding about how environmental systems work is likely to emerge. The benefits of this linkage is akin to the merger of physics and ecology into the now widely recognized realm of "environmental physics" [Monteith, 1975] and "biophysical ecology" [Gates, 1980]; and the integration of physiology and ecology into the hybrid discipline of "ecophysiology" [Billings, 1985]. Such collaborations promote development of novel, innovative research tools and approaches for studying environmental problems as integrated, hierarchical systems of interacting components and processes. While we recognize that ecology and hydrology have been linked to some extent previously in their respective disciplines, we argue that more explicitly focusing on improved linkages between ecology and hydrology is more likely to yield important new insights into system dynamics.
- [7] An additional aspect of our perspective is that ecohydrology should synthesize Newtonian and Darwinian approaches to science [e.g., *Harte*, 2002]. In other words, combining Newtonian principles of simplification, ideal systems, and predictive understanding (often, but not solely embraced by hydrologists) with Darwinian principles of complexity, contingency, and interdependence (often, but not solely embraced by ecologists) offers the potential for

profound and more rapid advances in our understanding of environmental processes. *Harte* [2002] identifies three "ingredients" for how such a synthesis can be realized: (1) development of simple, falsifiable models, (2) identification of patterns and laws (e.g., scaling laws), and (3) embracing the science of place. These ideas are relevant to the rest of the discussion in this paper, and our perspectives on ecohydrology are particularly germane to water-limited environments.

2. Water-Limited Environments: Background

- [8] Water-limited environments include arid, semiarid, and subhumid regions (sometimes collectively called drylands), and occupy approximately 50% of the global land area [Parsons and Abrahams, 1994]. These environments are considered water limited because annual precipitation (P) is typically less than annual potential evapotranspiration (E_p) , such that the ratio of P to E_p ranges from about 0.03 to 0.75, and because extreme temporal variability results in extended periods with little to no precipitation [Parsons and Abrahams, 1994; Guswa et al., 2004]. Although variable with respect to physiography, geology, soils and vegetation, these environments are often sensitive and prone to change because of limitations in water and/or nutrients, which dictate fluxes and transport in the critical zone. Examples of environmental changes that have occurred over vast areas in water-limited environments include desertification, woody plant encroachment, groundwater depletion, salinization, and soil erosion [De Fries et al., 2004]. These phenomena continue to transform water-limited environments, meaning that problems inherent to these landscapes (low and highly variable precipitation, sensitivity to environmental change, and the potential for catastrophic change) will increasingly affect human societies [Schlesinger et al., 1990; Bonan, 2002]. Already, water-limited environments contain some of the fastest growing urban and exurban centers in the world [Brown et al., 2005]. What happens in these regions is likely to have a growing influence on global biogeochemical cycles, even affecting areas geographically far removed [Schlesinger et al., 1990]. Effective management of environmental problems in the critical zone of water-limited environments will not be possible without the interdisciplinary, collaborative approach that ecohydrology provides.
- [9] In addition to the goal of explaining our perspectives on ecohydrology, we also want to highlight some of the key ecohydrological problems and issues in water-limited environments. We begin by presenting two examples from the southwest United States (hereafter referred to as the Southwest): one examining the current problem of widespread drought-induced tree mortality, the other focusing on the invasion of riparian corridors by nonnative vegetation. We then discuss some of the fundamental challenges and problems that require an integration of ideas and perspectives between the hydrological and ecological communities. Finally, we conclude by discussing strategies and potential benefits of our ecohydrological perspective.

2.1. Example 1: Regional-Scale Drought-Induced Mortality of Trees

[10] Water-limited ecosystems are typically characterized by a patchy distribution of vegetation. The proportions and types of woody plants (shrubs and trees) vary according to

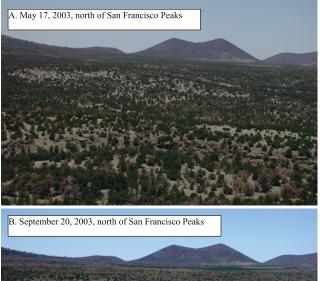




Figure 1. Massive die-off of piñon pine (*Pinus edulis*) near San Francisco Peaks, Arizona, caused by a combination of drought and infestation by bark beetles, between (a) May 2003 and (b) September 2003. Green trees in Figure 1b are mostly juniper (*Juniperous monosperma*). Photos courtesy of N. Cobb.

ecosystem type (grassland, shrubland, savanna, woodland, forest [House et al., 2003]), and these variations dictate the local environment beneath and near plant canopies, up to the ecosystem or watershed scale [Martens et al., 2000]. In water-limited landscapes, the type and pattern of woody plant cover affects (1) streamflow and groundwater recharge [Wilcox, 2002; Huxman et al., 2005], (2) biophysical interactions between land surfaces and the atmosphere [Graetz, 1991; Bonan, 1997; Hoffmann and Jackson, 2000], (3) carbon source-sink relationships [Pacala et al., 2001; Jackson et al., 2002; Houghton, 2003], and (4) tropospheric chemistry, via emissions of NO_x and volatile organic compounds [Guenther et al., 1999; Isebrands et al., 1999; Martin et al., 2003].

[11] Further, the nature and extent of woody vegetation cover are important determinants of biodiversity, wildlife habitat, livestock-grazing capacity, soil erosion potential, aesthetics, and real estate values [House et al., 2003]. Changes in the abundance of woody plants, consequently, have a wide range of ecological, hydrological, and societal implications. Under certain circumstances, such as regional-scale drought, these changes can occur rapidly. For example, the 1950s drought in the Southwest shifted the ecotone between forest and woodland >2 km along an elevational gradient in New Mexico [Allen and Breshears, 1998] and

triggered shrub encroachment in southern Great Plains grasslands [Archer, 1995].

[12] A current multistate drought (1999–2006 as of this writing) has again effected rapid changes in vegetation cover in piñon-juniper woodlands across the Southwest (Figure 1) [Breshears et al., 2005]. Development of effective policies and management plans for lands subject to infrequent but recurring catastrophic changes of this kind requires a framework that integrates ecology and hydrology. Neither discipline on its own can answer such critical questions as: What hydrological and ecological factors determine the level of plant-available water that triggers tree mortality? How will extensive changes in woody plant abundance modify erosion, surface runoff, and groundwater recharge? How will nitrogen deposition, atmospheric CO₂ enrichment, climate variability, and climate change influence the postdrought dynamics of vegetation cover?

2.2. Example 2: Invasion of Riparian Corridors by Nonnative Vegetation

[13] Riparian corridors represent a distinct ecotone between rivers and uplands in water-limited landscapes. They are of tremendous ecological importance, being home to novel organisms and pivotal ecological and hydrological processes. Commonly, riparian ecosystems are heavily invaded by exotic species of plants and animals, for which they serve as dispersal channels [Prieur-Richard and Lavorel, 2000; Tickner et al., 2001].

[14] Huge swaths of riparian terrain in the Southwest have been radically transformed by human alteration of water flows [Johnson, 1994] and by the introduction of invasive nonnative shrubs, primarily Russian olive (Elaeagnus angustifolia) and salt cedar (Tamarix spp.) (Figure 2). Salt cedar has colonized about 1 million hectares of riparian habitat in the western United States [Brock, 1994], and Russian olive is widely distributed in 17 western states, reaching densities of >1000 trees per ha [Katz and Shafroth, 2003]. These transformations have potentially enormous ecological and hydrological consequences and for this reason have caught the attention of policy makers and land managers. The U.S. Federal Government and many state governments are investing considerable resources in efforts to control these invasive species with the stated goals of enhancing water supply, improving water quality, providing flood protection, and restoring native habitats.

[15] Unfortunately, there is a problem. There is considerable misinformation and little scientific data documenting that such goals can be attained through control of these invasive species. For example, it is commonly stated in the agricultural extension and popular literature that an individual salt cedar uses up to 750 L day⁻¹ of water, an amount that is physiologically impossible. More likely the upward amount is around 50 L day⁻¹ [Glenn and Nagler, 2005].

[16] We know in a general sense that the water budgets of riparian zones are strongly influenced by the vegetation found in them [Dahm et al., 2002], but we know relatively little about the ecological-hydrological interactions between invasive plants and their new environments. For example, how does water use by nonnative plants compare with that of the displaced native plants? Do exotic plants significantly alter evapotranspiration and influence streamflow and groundwater recharge? If so, does their removal lead to an





Figure 2. (a) Riparian salt cedar along the Pecos River in Texas receiving herbicide application by helicopter (photo courtesy Charles R. Hart). (b) Russian olive along the Rio Chama, New Mexico (photo courtesy Johnny Salazar). Note the high-density, monoculture habit of both nonnative plant types.

increase in streamflow and groundwater recharge; and under what conditions? How might hydrological factors control the pattern and rate of spread of nonnative species, their interactions with native species, and their ultimate geographical range? How do riparian communities dominated by exotics respond to drought? How do they affect fundamental ecosystem processes, such as primary production, decomposition, and nutrient cycling? Does the establishment of exotic plants alter disturbance regimes (e.g., pest outbreaks, fire) in ways that will modify local hydrology? Such questions can be answered only through coupled studies of the hydrology and ecology of riparian corridors. Indeed, the growing field of ecohydrology could make a lasting and socioeconomically vital contribution to the health of these environments by undertaking studies that focus on nonnative riparian plants.

3. Challenges

[17] Below we discuss six scientific challenges deemed central to a better understanding of the ecohydrology of water-limited environments. The delineation of these challenges is not intended to be comprehensive, but rather to

illustrate how interdisciplinary science can address difficult issues in water- and nutrient-limited environments.

3.1. Challenge 1: Partitioning of Evaporation and Transpiration

[18] The amount of biologically available water is arguably the central driver of many plant and microbial processes in water-limited environments (e.g., water lost through evaporation from the soil is no longer biologically available). The amount of biologically available water is determined by the spatial and temporal distribution and amount of precipitation, but also by how precipitation is redistributed via processes such as interception, stemflow, infiltration, percolation, evaporation, and runoff. Most hydrological studies have estimated water budgets by lumping canopy interception, soil evaporation (E), and transpiration (T) into a single term, evapotranspiration (ET) [Loik et al., 2004; *Huxman et al.*, 2005] (but see *Reynolds et al.* [2000] and Yepez et al. [2003]). Although combining E and T is expedient for some applications (e.g., runoff assessment), it "black boxes" biological processes, which play a significant role in regulating the hydrological cycle, whether directly or indirectly at short (hourly, daily) or long (seasonal, interannual) timescales. Interception, soil evaporation, and transpiration all depend on vegetation cover, but in different ways. Therefore we need to examine these processes separately to better understand how they are affected by cover and their influence on ecohydrological dynamics. Notably, failure to partition E and T limits understanding of biological water demand, thereby constraining our ability to quantitatively represent biological feedbacks on the hydrologic cycle. That E and T typically account for >95% of the water budget in water-limited ecosystems [Wilcox et al., 2003a] is prima facie evidence of the importance of partitioning E from T. Few studies have attempted to quantify this partitioning, and those differ in methodology, ecosystem type, and temporal scale [Reynolds et al., 2000; Unsworth et al., 2004; Huxman et al., 2005; Scanlon et al., 2005a]. Consequently, we cannot yet make robust generalizations or predictions about E and T and how their relative importance varies among sites, through time, or in response to land management, and climate change/variability. Untangling these relationships will require explicit consideration of root patterns and physiology, including the complicating process of hydraulic redistribution [e.g., Zou et al., 2005]. Another critical factor is the role played by the stochastic nature of precipitation forcing on the partitioning of E and T. The spatial and temporal stochasticity of precipitation in water-limited environments results in highly dynamic, context-dependent patterns of soil water distribution, vegetation performance, and nutrient availability [e.g., Porporato et al., 2002; Knapp et al., 2002; Rodríguez-*Iturbe and Porporato*, 2004]. Assessments of controls on E and T must be made in this context and cannot be derived or inferred from simple, coarse estimates of mean seasonal or annual amounts of precipitation.

3.2. Challenge 2: Water and Nutrient Interactions

[19] Water has typically been regarded as the limiting resource in communities subject to low precipitation rates. However, nutrient availability, which usually is inextricably linked with water availability, may exert a strong or even codominant influence. For example, availability of nutrients

can limit the responses of vegetation to precipitation and soil moisture; and soil moisture availability drives the fixation of N₂ by microbial symbionts of plants as well as microbial mineralization of soil organic matter [Noy-Meir, 1973; Austin et al., 2004; Schwinning and Sala, 2004; Belnap et al., 2005]. Therefore building a better understanding of water and nutrient interactions is important for improving environmental forecasts involving such issues as changes in community structure and functioning, eutrophication, and water quality.

[20] It is generally assumed that in temperate regions having relatively low annual precipitation, water is the main constraint on aboveground net primary productivity, whereas in regions having relatively high annual precipitation, it is nitrogen. To test this assumption, Hooper and Johnson [1999] synthesized results from fertilization experiments in arid, semiarid, and subhumid rangelands. Across this wide geographic rainfall gradient, they found no strong evidence of a shift from water to nitrogen as primary limiter. In fact, they found that even in dry locations and during years of below-average rainfall, productivity typically increased when nitrogen was added. These results suggest a tight coupling between water and nitrogen and that they act to colimit productivity [Chapin et al., 1987; Chapin, 1991a, 1991b]. This notion is supported by findings from modeling studies that incorporate the nitrogen cycle along with the hydrological and carbon cycles [Schimel et al., 1997]. In addition, because the three cycles operate at different timescales, inclusion of nitrogen cycling into ecosystem models adds behavior at longer timescales than those represented in purely biophysical models. Furthermore, models coupling the nitrogen and carbon cycles with vegetation dynamics and water availability have shown that the variable and stochastic nature of rainfall forcing results in a rich set of ecohydrological and biogeochemical responses [Rodríguez-Iturbe and Porporato, 2004]. The observance of close correlations between nitrogen fluxes and ET suggests that both changes in nitrogen input (e.g., fertilization or N deposition) and changes in climate will have large and long-lived effects on primary production and, by extension, the hydrological cycle.

[21] The importance of water-nutrient interactions in water-limited environments is not restricted to the root or soil zone. In the Southwest, thick subsoil vadose zones can contain large inventories of nitrate that are not accessible to roots. Although significant uncertainties remain, it appears that nitrogen inventories in warm deserts and shrublands worldwide could be anywhere from 14 to 71% higher than previously thought [Walvoord et al., 2003]. Residence times (based on chloride mass balance) indicate that in many Southwestern areas, vadose zones have acted as nitrate sinks for $10^3 - 10^4$ years. This begs the question, why have these nitrate inventories developed in ecosystems where nitrogen is one of the chief limitations to primary production? Are hydrological processes in these regions somehow preventing more efficient use of nitrogen in the soil zone? In addition, stores of nitrate are large enough in some areas that groundwater degradation could occur if changes in climate or land use result in flushing of the vadose zone [Walvoord et al., 2003; Scanlon et al., 2005b].

[22] Another important consideration is that temperate and tropical biomes currently receive more nitrogen via wet

and dry atmospheric deposition than during preindustrial times (e.g., temperate ecosystems in the northern hemisphere receive on average over four times their preindustrial levels [Holland et al., 1999]). It is thus becoming increasingly urgent to understand how water and nitrogen influence ecosystem processes, both independently and interactively [Burke et al., 1991; Vitousek et al., 1997a, 1997b]. For example, if increased inputs of nitrogen reduce or alleviate nitrogen limitations [e.g., Schimel et al., 1997], a shift in the composition of plant species is likely, which may render primary production more responsive to increases in atmospheric CO₂ and more sensitive to temporal variations in rainfall. How will such changes affect hydrology, ecosystem management, restoration, and remediation? Our ability to answer that question may well depend on the extent to which our understanding of ecosystem dynamics is constrained by our focus on water rather than, or in isolation from, nutrient availability.

3.3. Challenge 3: Vegetation and Streamflow

[23] Understanding the influence of vegetation on streamflow is part of the foundational basis of ecohydrology. Much of the early and classic work in watershed management of water-limited landscapes centered on this topic (summarized by *Hibbert* [1983]) and it remains a topic of interest and importance today, especially as water supplies become increasingly taxed.

[24] The role of vegetation in the dynamics of soil moisture, runoff, and streamflow in water-limited environments has been studied through (1) point- and hillslope-scale observations [e.g., Wilcox et al., 1997, 2003b; Newman et al., 1998, 2004; Neave and Abrahams, 2002], (2) mathematical modeling along hillslope transects and over a spatial domain [e.g., Porporato et al., 2002; Ridolfi et al., 2003; Fernández-Illescas and Rodríguez-Iturbe, 2004], and (3) remote sensing [e.g., Cayrol et al., 2000; Kerkhoff et al., 2004b].

[25] Overland flow is clearly a major contributor to streamflow in water-limited environments and can often be the only contributor. Thus it is important to understand how overland flow is affected by spatial patterns of vegetation and topography [e.g., *Wilcox et al.*, 2003b]. The high density of drainages in water-limited environments appears to be the consequence of the sparseness of vegetation canopies and infrequent, high-intensity storms. These factors result in large amounts of overland flow over short time periods despite low annual precipitation, and ultimately result in erosion and formation of channel networks [*Abrahams*, 1984]. Studies quantifying relationships between the type and pattern of vegetation and overland flow are thus a critical step in developing an ecohydrological approach to resource management and environmental change.

[26] Given the tight coupling between vegetation and water in water-limited environments, it would be reasonable to expect that water supplies might be augmented by reducing vegetation cover. Riparian corridors, where woody plants are directly accessing groundwater, would be the most likely to respond to reductions in plant cover [Huxman et al., 2005]. In some parts of the United States it has become an article of faith that if shrubs are removed, river flow will increase; and both public and political support for using tax dollars to this end is strong. For example, in Texas

about \$40 million has been spent or allocated for cost sharing shrub control [Texas State Soil and Water Conservation Board, 2002]; and at the federal level, the 108th U. S. Congress is considering a bill to provide \$20 million a year for control of salt cedar as a means of increasing water availability. Both endeavors, unfortunately, are examples of policy and politics getting ahead of science. There is still considerable uncertainty as to whether water yields can be augmented through vegetation management, especially on a large scale [Wilcox, 2002]. However, the reality for many water-limited landscapes is that there is little potential for success. Even in areas where vegetation may be affecting water yield, (e.g., floodplains and riparian zones dominated by salt cedar), the relationship has yet to be conclusively demonstrated.

[27] Which environments have the potential for increasing water yield through manipulation of vegetation? In many water-limited environments, Hortonian (infiltration excess) runoff can be an important contributor to streamflow [Wilcox, 2002]. Thus, in these settings, the connection between surface and subsurface hydrological processes along streams is much weaker than in more humid climates. Because the lateral water fluxes that characterize these regions are, by definition, short-lived and limited in spatial extent, increases in streamflow from vegetation manipulation may be less than some expect. Where streams have a perennial or intermittent base flow component (for example areas with karst geology or predominantly winter precipitation) the potential for augmenting streamflow and recharge through vegetation manipulation may be higher (though this has yet to be demonstrated at larger scales). Areas with a Mediterranean climate where streamflow is derived mostly from winter precipitation or melting snow have been shown to respond to vegetation manipulation [Hibbert, 1983; Baker, 1984; Williamson et al., 2004] and therefore may also be favorable landscapes for vegetation management.

3.4. Challenge 4: Vegetation and Groundwater Recharge

[28] Differences in recharge beneath vegetated and nonvegetated lysimeters demonstrate that plants substantively influence groundwater recharge [Gee et al., 1994; Scanlon et al., 2005a]. The important link between vegetation and recharge has been dramatically shown in eucalypt woodlands in Australia, where large-scale tree removal increased recharge rates up to two orders of magnitude [Allison et al., 1990]. Such examples underscore the importance of linking vegetation dynamics, soil water storage, and precipitation in predictive models of recharge. The coupling is two-way: soil water storage varies with rainfall, which influences vegetation productivity; and vegetation productivity, in turn, influences percolation, soil water storage, and recharge. For example, elevated El Niño winter precipitation in the Southwest would be expected to increase groundwater recharge; however, increases in infiltration triggers vegetation growth which extracts the additional water before it becomes recharge [Smith et al., 2000; Scanlon et al., 2005a]. The Pleistocene-Holocene climate change (~10,000-15,000 years ago) is another example: the resultant shift in vegetation from mesic to xeric altered interfluvial basin hydrology throughout the Southwest, from recharging (net downward water movement) to discharging (net upward

water movement) [Walvoord et al., 2002; Scanlon et al., 2003; Seyfried et al., 2005].

[29] If specific correlations among recharge, hydraulic factors, extent and type of vegetation, and biomass could be defined, through coordinated measurement and monitoring in diverse biomes, a database could be generated that could enable vegetation to be used as a proxy for recharge [e.g., Walvoord and Phillips, 2004; Kwicklis et al., 2005]. Vegetation mapping, readily conducted via ground-based, aerial, or satellite approaches, could then be used to predict subsurface flow and recharge in lieu of subsurface sampling and analyses. Such methods should improve local, regional, and continental estimates of recharge.

[30] Specific parameters needed for a predictive database would likely include climatic variables (e.g., precipitation characteristics, vapor pressure deficit, and temperature); vegetation parameters (e.g., functional group or species composition, leaf area index, net aboveground primary production, transpiration, stomatal conductance, plant water potential, normalized difference vegetation index, temporal variation in depth of soil water access); geological variables (e.g., soil depth and texture, bedrock lithology, and structure); and hydrologic parameters (e.g., soil water content and storage, hydraulic conductivity). A well-constructed database should accommodate identification of critical climate thresholds at which, under a given set of vegetation conditions, episodic recharge would occur. A study comparing water movement in a ponderosa pine forest with that in a piñon-juniper woodland in New Mexico [Newman et al., 1997] illustrates the importance of multifaceted measurement and characterization. In the ponderosa pine forest, downward fluxes were about 0.2 mm yr⁻¹. In contrast, the piñon-juniper woodland fluxes were higher at about 2 mm yr⁻¹ even though the woodland receives around 40 mm less precipitation annually than the ponderosa pine forest. This counterintuitive result is explained in part by hydraulic properties: a low-hydraulic-conductivity layer in the ponderosa pine soil inhibits downward water movement below the root zone and allows more removal of water by ET, producing an outcome contrary to that expected solely on the basis of vegetation type and precipitation amount.

[31] Hydrologic processes in the thick vadose zones of water-limited environments unfold over longer timescales than those in surface and near-surface soils. Characterizing these would require additional deep vertical profiles of water content and water potential (to ascertain if gradients favored upward versus downward water movement), along with chloride profiles (to quantify recharge by the chloride mass balance method). Fortunately, changes in recharge brought about by changes in vegetation (triggered by climate variability, land use, fire, and/or disease) can be predicted through a substitution of space for time. Thick vadose zones take hundreds to many thousands of years to fully equilibrate with current surface conditions; and changes at greater depths lag behind those nearer the surface. Patterns in shallow depths thus indicate how recharge has changed in response to the vegetation change, whereas patterns at greater depths in a vertical profile indicate recharge patterns in place prior to the vegetation change. For example, the upper portions of chloride profiles in the Southwest frequently reflect Holocene climate and vegetation, while the deeper portions reflect Pleistocene climate and

vegetation [*Phillips*, 1994; *Walvoord et al.*, 2002; *Scanlon et al.*, 2003]. Ideally, space-for-time monitoring should be complemented by experimental manipulations (e.g., of vegetation) that are followed through time, as each approach provides unique perspectives with offsetting weaknesses.

3.5. Challenge 5: Hydrological Change and Vegetation

[32] In general, the distribution, growth, and mortality of vegetation is more sensitive to the hydrologic cycle than to any other factor, including nutrients and sunlight [Weltzin and Tissue, 2003]: the greater the total annual precipitation, the greater the growth and biomass accumulation of vegetation [Knapp and Smith, 2001; Waring and Running, 1998]. Seasonality of precipitation also has dramatic effects on vegetation type [Schwinning and Ehleringer, 2001; Fernández-Illescas and Rodríguez, 2004], diversity [Chesson et al., 2004], sensitivity to invasion [Weltzin et al., 2003], and productivity [Smith et al., 1997; Huxman et al., 2004]. In the Southwest, the season of highest precipitation is typically midsummer because of the North American monsoon. However, relatively hot weather is also typical of this season, so that if drought occurs, plants can experience temperature stress, cavitation, and even mortality. The current drought in the Southwest has already brought about such effects (see example 1). Vegetation along riparian corridors (example 2), which depends on flooding as a source of nutrients and water, is also vulnerable because irrigation diversion and damming to control river flows have reduced flooding and produced profound changes in ecosystem properties [e.g., Johnson, 1994].

[33] To predict how hydrological changes will affect vegetation, models must be based on first principles of plant carbon-water balance [Running and Coughlan, 1988; Williams et al., 1996; Landsberg and Waring, 1997], because plant productivity and survival are dependent on carbon gain (photosynthesis). The fields of plant physiological ecology [Lambers et al., 1998; Larcher, 2003] and ecosystem ecology [Aber and Melillo, 1991; Waring and Running, 1998] have valuable concepts and tools to offer both the water and carbon aspects of ecohydrology. Recent advances in modeling the dependence of plant carbon assimilation on soil moisture are described by Rodríguez-Iturbe and Porporato [2004].

[34] We briefly discuss below some of the recent studies demonstrating that significant advances are being made in our understanding of how water is utilized by plants, how water moves through various parts of the plant, and how plants are affected by other ecosystem components. This discussion also highlights the breadth of measurements and techniques required to improve our current conceptual and quantitative understanding of how hydrologic changes impact vegetation. Vast improvements in our understanding of whole-plant transpiration have occurred in the last few decades [e.g., Granier, 1987]. These advances reflect technological advances enabling continuous sapflow measurements; branch-level conductivity measurements; leaf level measurements of stomatal regulation of transpiration [Cowan, 1977; Jarvis and Morison, 1981; Bond and Kavanaugh, 1999; Oren et al., 1999], and quantification of xylem cavitation thresholds [Tyree and Sperry, 1988; Holbrook and Zwieniecki, 1999; Sperry et al., 2002]. Relatively new molecular and biophysical approaches are enhancing our ability to predict plant rooting depth and water uptake

[Jackson et al., 2000] to better address how vegetation contributes to hydraulic redistribution (the movement of water from wetter to drier regions of the soil profile via roots) [Dawson, 1993; Burgess et al., 1998; Caldwell et al., 1998; Brooks et al., 2002; Zou et al., 2005]. In addition, comparisons of stable isotope composition of C, O, and H in plants, soils and precipitation enable short- and long-term quantification of when and where plants are obtaining soil moisture and how primary production and water use efficiency is affected by environmental conditions [Leavitt, 1993, 1994; McNulty and Swank, 1995; Livingston and Spittlehouse, 1996; Lin et al., 1996; Boutton et al., 1999; Williams and Ehleringer, 2000; Roden and Ehleringer, 2000].

[35] Modeling root water uptake is a particularly challenging area, but is especially critical because of the tight linkage with spatial and temporal variations in soil water content [Hopmans and Bristow, 2002; Feddes and Raats, 2004; Wang and Smith, 2004]. In fact, root water uptake has significant implications for all six of the challenges presented here. Most models of root water uptake are based on either a minimum of a demand and soil water supply function, a derivative of Ohm's law that calculates water effects on canopy resistance, or use a direct function based on soil water availability (see discussions by Jackson et al. [2000], Sperry et al. [2002], Feddes and Raats [2004], Wang and Smith [2004], and Simunek et al. [2005]). Such models provide tools to understand how uptake is affected by combinations of root properties and behaviors, soil textures, and hydraulic potentials; and are keys to linking root water uptake with larger-scale (e.g., basin-regional scale) models. Some of the major difficulties with current root water uptake models include a lack of available data for model parameterization [Hopmans and Bristow, 2002; Feddes and Raats, 2004] and the effects of spatial and temporal resolution of field data on modeling results [e.g., Guswa et al., 2004]. In addition, processes and controls such as hydraulic redistribution, different uptake behaviors/ limits between large and small roots, xylem hydraulics, and salinity effects are either not incorporated in models or require improvements in the way they are represented [Jackson et al., 2000; Pagès et al., 2000; Hopmans and Bristow, 2002; Sperry et al., 2003; Feddes and Raats, 2004]. Another important consideration is that two- and three-dimensional approaches may sometimes be needed to properly represent spatial variation in root water uptake and drainage rates [Vrugt et al., 2001].

[36] Although significant progress has been made on elucidating fundamental mechanisms by which plants regulate water uptake, translocation, and loss, methods relating carbon gain to hydrologic regime are in earlier stages of development. Stable carbon isotope ratios of plant organic matter have demonstrated species adaptation to water availability over the lifespan of plants [Ehleringer et al., 1993]. Eddy covariance measurements of ecosystem carbon exchange provide insights to elucidate how plants respond to water pulses on daily to annual timescales [Huxman et al., 2004] and chamber-based approaches provide robust estimates of seasonal and annual carbon fluxes [Ryan, 1991]. Ecosystem-scale stable isotope measurements are now showing regional and temporal response of ecosystem water use efficiency to water availability [Bowling et al., 2002] and canopy conductance [McDowell et al., 2004].

[37] Incorporating these tools and data from plant physiological ecology and ecosystem ecology into a framework that addresses key coupled processes within the critical zone [e.g., Schimel et al., 1997] will be useful for predicting both the response of vegetation to changes in water inputs and the effects of vegetation on water fluxes and storage. At larger scales, changes in vegetation abundance and species composition resulting from climatic fluctuation and disturbance must be taken into account [Neilson and Marks, 1994; Neilson, 1995]. Although measurements at large scales are the least advanced of all, new technologies, such as enhanced satellite remote sensing capabilities [Ustin, 2004] and trace gas measurements from tall towers [e.g., Bakwin et al., 1998], promise to improve our ability to quantify biogeographic responses to changes in the hydrologic cycle, and eventually to predict terrestrial carbon sequestration under various climate change scenarios [Intergovernmental Panel on Climate Change, 2001]. Combining these concepts and techniques with hydrological techniques (listed elsewhere in this paper) will yield new insights on ecohydrologic processes.

3.6. Challenge 6: Landscape Interactions in the Paleodominated and Human-Dominated Ages

[38] Human activity has been a primary factor in modification of the ecohydrological system, through agricultural, industrial, transportation, and communications development [Vitousek, 1994; Vitousek et al., 1997b; De Fries et al., 2004]. In the coming decades, the science of hydrology will be dealing more and more with human-caused global-scale environmental changes and attempting to predict their effects on ecohydrological systems. These changes will stimulate feedbacks that will determine how the primary characteristics of drainage basins (e.g., vegetation type and distribution, soils, water tables, drainage networks) evolve. Currently, our ability to model such complex feedback responses is unproven. One of the best ways to develop and evaluate models is to base their design on simulations of past events and the documented responses to those events.

[39] Hydrological models have been constructed on the basis of generalized paleoclimate considerations [Plummer, 2002]. However, few, if any, attempts have been made to link detailed contemporary hydrological investigations and models with the geological record of environmental change. Such an endeavor would utilize a basin for which a detailed and integrated hydrologic/vegetation/geomorphic model has already been constructed. Available paleoenvironmental studies of the area would then be synthesized to build a comprehensive reconstruction of the climatic, hydrological, vegetational, and geomorphic history of the basin; additional studies would be conducted to fill in gaps and extend the modern record into the prehistoric period. With these reconstructions as a basis, the model would then be forced through the use of external (mainly climate) records. Model predictions of vegetation dynamics, runoff, recharge, geomorphic change would then be compared with those from the geological record and subsequently refined to better reflect the actual processes and outcomes. This iterative, holistic, and process-oriented approach would lay a solid foundation for predicting the effects of future environmental changes.

[40] Drainage basins in water-limited landscapes are particularly well suited for studying environmental feedbacks and responses because they contain long and relatively complete records of past environmental change, in part because of the exceptional preservation of organic matter in dry environments. One of the most important records is tree rings, which provide a detailed archive of growth and stable isotope composition that can be related to climate variation and vegetation response over annual to millennial timescales [e.g., Roden et al., 2005]. In arid regions of the United States, tree ring records may extend back several thousand years [Scuderi, 1993; Grissino-Mayer, 1995], and in a few cases up to 8,000 years [Feng and Epstein, 1994]. The availability of data with annual resolution covering such long timescales enables statistical analysis of important hydroclimatic phenomena, such as ENSO-related variability and decadal-scale climate oscillations (e.g., North Atlantic Oscillation, Pacific Decadal Oscillation) [e.g., Swetnam and Betancourt, 1998]. Likewise, such records can be used to interpret vegetation response to management scenarios designed to reduce water stress during drought such as restoration thinning [McDowell et al., 2006].

[41] Another natural archive of vegetation response to long-term climate forcing is preserved in fossil packrat middens [Betancourt et al., 1990]. Midden records may extend as far back as 40,000 years, but more commonly they cover the past 10,000 to 20,000 years, an interval that includes the end of the last glaciation, which is the most recent major climatic/hydrologic event on the continent [Phillips et al., 2004]. Tree ring and packrat midden records can be supplemented by other independent paleoclimatic and paleohydrological archives. One of the most important of these is speleothems (calcium carbonate precipitates in caves), which can provide a time series going back hundreds of thousands of years [Burns et al., 2001]; and under favorable circumstances, can also yield records with annual resolution [Polyak and Asmerom, 2001]. Other sources of data are aquifers, which serve as paleoenvironmental repositories of information on temperature, groundwater isotopic composition, and groundwater recharge rates dating back tens of thousands of years [Fontes et al., 1993]; and lacustrine sediments and shoreline deposits from closed basin lakes, which record fluctuations in water balance [Street-Perrott and Harrison, 1985].

[42] Changes in the physical hydrology of the landscape, produced over long periods by changes in temperature, precipitation, and vegetation, and manifested as landscape incision, degradation, and alluviation [Tucker and Slingerland, 1997; Bull, 1991; Molnar, 2001], are well preserved in the arid landscape. Many of these records have been extensively studied and dated [McFadden and McAuliffe, 1997; Waters and Haynes, 2001] and provide clues about the conditions under which they were created.

[43] Although many individual aspects of climatic and environmental change in water-limited landscapes have been reconstructed from paleorecords, the current challenge is first to weave them together into a history of forcings, processes, and linkages between the two and second to arrive at some predictive (and retrodictive) quantification. These complex relationships would seem to require a new and more integrated way of looking at our disciplinary

research, one that improves the likelihood that hidden or currently unmeasured variables and linkages will emerge.

[44] A remarkable example of the insight that understanding the earth history of arid regions can bring to bear on modern issues has recently been uncovered in Australia. During the mid 20th century, decreasing precipitation and increasing temperature were associated with lower streamflow and higher ET. Atmospheric scientists initially reasoned the changes in temperature were a greenhouse effect, and that changes in rainfall reflected large-scale reorganization of the atmospheric circulation. However, Pitman et al. [2004] argued that reduced tree cover and expanded grassland and agricultural crops in the 20th century explain the changes in precipitation and temperature, via feedback to the atmosphere. This hypothesis is paralleled by recent evidence regarding the massive extinction of large mammals in Australia about 45,000 years ago. Using stable isotopes in bone and eggshell, Miller et al. [2005] discovered that this extinction was probably caused by replacement of grassland by xeric shrub. This replacement may have been self-reinforcing because of meteorological feedbacks that weakened the monsoon. Miller et al. [2005] hypothesized that it was human activity, specifically the setting of intentional fires, that forced vegetation change. The evolution of ecohydrological systems is a fundamentally historical process and quantitative understanding of the past will bear fruit when applied to today's challenges.

4. Crosscutting Problems

[45] We now present three problems that represent major hurdles in addressing ecohydrological challenges. They are crosscutting because they apply to all six of the scientific challenges described here and to many others. They represent research areas that should be addressed within a place-based research framework, and have important ramifications in terms of our ability to forecast behaviors in the critical zone and how we manage environmental resources.

4.1. Crosscutting Problem 1: Spatial Complexity and Scaling

[46] The search for patterns and laws is one of the key ingredients identified by Harte [2002] for achieving a synthesis of Newtonian and Darwinian approaches to science (in this case the science of ecohydrology). Identification of scaling patterns and laws should lead to improved predictions of cross-scale interactions, a critical element for successful forecasting of catastrophic events [Peters et al., 2004]. Hydrologists have a long history of researching how spatial complexity, scaling, and vegetation patterns influence rainfall processes, runoff dynamics, river network structure, and geomorphic evolution [e.g., Wood et al., 1990; Bloschl and Sivapalan, 1995; Rodríguez-Iturbe and Rinaldo, 2001]. Recent evidence suggests that vegetation self-organizes in spatial patterns as an optimized response to climatic and landscape conditions [Van Wijk and Rodríguez-Iturbe, 2002; Caylor et al., 2004; Fernández-Illescas and Rodríguez-Iturbe, 2004; Wu and Archer, 2005]. While this realization advances our understanding of ecohydrological dynamics, the effects of scale and spatial complexity on water-vegetation interactions have yet to be fully elucidated [e.g., Kerkhoff et al., 2004a]. In water-limited environments, the temporal variability of meteorological conditions, the

spatial variability of geologic and topographic setting, and differences in the ways plants use water create particular challenges in translating model and field data from local to larger scales and vice versa.

[47] Progress in dealing with this crosscutting problem is impeded by the paucity of data at multiple scales and poor quantification of spatial interactions among traditional hydrologic elements (i.e., topography, soils, rainfall) and the dynamics of communities, ecosystems, and ecotone boundaries. Thus a premeditated coupling of process-oriented field experiments with long-term monitoring within a spatially nested design framework is needed [e.g., *Archer and Bowman*, 2002; *Wilcox et al.*, 2003b; *Peters et al.*, 2004]. It is imperative that the experiments and monitoring be designed to ensure collection of data specifically required for parameterizing and testing of models (i.e., the simple, falsifiable modeling approach discussed by *Harte* [2002]).

[48] A particularly useful conceptual framework for evaluating relationships between fine and broad-scale patterns was presented by *Peters et al.* [2004]. The framework identifies four sequential scales of processes that can progress to trigger rapid, nonlinear responses in a variety of environmental contexts: within patch initiation, within patch spread, between patch spread, and fine to broad-scale feedback at larger spatial scales. This framework may prove to be particularly useful for evaluating ecological and hydrological feedbacks at multiple scales.

4.2. Crosscutting Problem 2: Thresholds

[49] The conditions that lead to threshold behaviors, and the nonlinear responses that occur when thresholds are crossed are key aspects of forecasting and mitigating catastrophic events [Scheffer et al., 2001; Harte, 2002; Peters et al., 2004]. Identifying and quantifying thresholds are critical for assessing ecosystem stability and resilience, and the potential for shifts into and out of alternative stable states [Scheffer et al., 2001; Zalewski, 2002]. Threshold behavior is indicated by a response to a driver that is proportionally much larger, or of fundamentally different character, than previous responses to the same driver. Failure to understand and manage threshold responses leads to environmental surprises, missed opportunities, and potentially catastrophic consequences. One important example of threshold behavior in water-limited environments is the large shift in runoff that can occur from reduction of vegetation cover [Scheffer et al., 2001; Peters et al., 2004]. Bare patches (e.g., around a few m²) are common in water-limited landscapes and are typically associated with high runoff at the patch scale. However, if these patches are isolated, per unit area runoff at the larger hillslope scale is often lower because of limited bare patch connectivity [e.g., Wilcox et al., 2003b]. If vegetation cover is reduced to a sufficient point where bare patches become connected, highly nonlinear increases in runoff and erosion will occur [Davenport et al., 1998]. Other examples of threshold behavior include water content conditions required to trigger plant recruitment or mortality [Watson et al., 1996, 1997; Allen and Breshears, 1998; Villalba and Veblen, 1998; Bowers and Turner, 2001; Breshears et al., 2005]; and pulses of lateral subsurface flow and shifts in flow chemistry associated with changes in soil water content levels [Newman et al., 1998]. Multiparameter, observational data sets of ecohydrological processes and

manipulative field investigations coupled with modeling experiments would be a fruitful way of identifying new threshold behaviors and for quantifying conditions under which threshold behaviors occur.

4.3. Crosscutting Problem 3: Feedbacks and Interactions

[50] Biotic and hydrologic components of environmental systems exhibit numerous interactions and feedbacks, which can be positive (self-reinforcing) or negative (self-dampening). As an example, the hydrology of an environment controls ecological processes such as photosynthesis, which dictate the type, amount, and productivity of vegetation at a given locale [Waring and Running, 1998]. At the global scale, photosynthesis is controlled by soil water availability and atmospheric water content [Running et al., 2004]. During periods when moisture is abundant, photosynthesis and hence transpiration are high (open stomata, greater leaf areas). In contrast, during dry periods, plants limit transpirational water loss (stomatal closure, decreased leaf area), thus constraining photosynthesis. Variations in transpiration feed directly back on ecosystem hydrology: water that might otherwise percolate below the root zone and become groundwater recharge is consumed. Further, variations in canopy leaf area directly affect precipitation interception, stemflow, throughfall, and evaporation. For example, when leaf area increases, more water is intercepted; subsequently, the water may either be evaporated without reaching the soil surface or it may be funneled to the plant base via stemflow and concentrated where infiltration rates are high, thus increasing plant-available water. "Carryover" effects [Ewers et al., 1999], dynamic shifts in vegetation attributes (e.g., leaf area, root biomass) that modify the water balance, may also take place, enabling vegetation to mediate streamflow and groundwater recharge over multiannum periods. Unfortunately, our understanding of such feedbacks and interactions relies heavily on ecosystem process models [Running and Coughlan, 1988; Williams et al., 1996; Landsberg and Waring, 1997], and a lack of empirical data has limited the development and rigorous testing of these models. Long-term, place-based studies with directed collection of data to test (falsify) how well feedbacks are represented in models is yet another way that an ecohydrological approach can lead to improved forecasts of environmental change, including catastrophic behavior [Scheffer et al., 2001; Harte, 2002; Zalewski et al., 2002; Peters et al., 2004].

5. Strategy and Expected Benefits

[51] One strategy for addressing the scientific challenges identified for water-limited environments and for developing an integrated ecohydrological perspective is to build a framework that fosters proactive collaboration of ecologists and hydrologists. Such a strategy has been identified by Newman et al. [2003] and Hannah et al. [2004] as essential for realizing the full potential of ecohydrology. As discussed earlier, our vision also includes a synthesis of contrasting scientific philosophies. Harte [2002] suggests that physical scientists (e.g., hydrologists) tend toward a reductionist, Newtonian view, which attaches great value to simplification, ideal systems, a search for laws, and predictive understanding; whereas ecological scientists, whose roots

are in biology, have a Darwinian tradition of research emphasizing the complexity, contingency, and the interdependence of system components, all of which limit prospects for prediction. Although this view is somewhat overgeneralized (e.g., physiological and ecosystem ecologists commonly use reductionist approaches [see *Aber and Melillo*, 1991; *Waring and Running*, 1998]), Harte points out that combining reductionist and holistic systems approaches will likely have tremendous benefits to science. Hierarchy theory, which balances the search for mechanisms with an assessment of their significance at various spatial/temporal scales, is one way of bridging these two approaches [*Allen and Starr*, 1982; *O'Neill et al.*, 1986].

[52] In contrast to reductionism, hierarchy theory permits evaluation of a complex system without reducing it to a series of simple, disconnected subsystems. No single level in the hierarchy of an ecological system is considered fundamental; understanding a system at one level of organization (e.g., leaf, plant, plant-soil, plant community, landscape, etc.) requires knowledge of the levels above and below. As a result, interpreting behavior of a system at one level of organization without consideration of adjacent levels may generate misleading results. Holistic (systems) and reductionist approaches, although diametrically opposed, should not be viewed as mutually exclusive. Each provides something the other cannot. The reductionist approach provides explanation for phenomena, but cannot interpret significance unless placed within the context of higher levels of organization. In contrast, the holistic approach describes and recognizes significant phenomena, but often without providing explanation [Passioura, 1979]. The search for mechanisms should therefore be balanced by concern for their significance. New discoveries or insights at a given level in a hierarchy often result from examining adjacent levels [Allen et al., 1984; Lidicker, 1988]. This hierarchical perspective is widely applied in ecological studies and would be integral to an ecohydrological perspective.

[53] Place-based research would be an effective way of promoting collaboration and focusing efforts on the integration of reductionist and holistic approaches (for example, basin-scale monitoring networks or hydrological observatories with an explicit focus on ecohydrology). This recommendation is consistent with Zalewski [2002] who describes the basin scale as a logical framework for developing the principles of ecohydrology. An ideal starting point would be a monitoring network situated in a water-limited (e.g., arid or semiarid) basin, because such areas are (1) geographically extensive and contain a significant and growing proportion of the human population, (2) extremely sensitive to ecohydrological processes, and (3) composed of welldefined and broad elevational gradients, with numerous, closely spaced ecotonal and hydrological transition zones ideal for comparative studies. Such features are advantageous for understanding linkages among water, vegetation, and nutrients and the effects of management and land use on the processes that govern their interactions. A monitoring network in a water-limited region would provide a research infrastructure that would facilitate collaboration between ecologists and hydrologists, from the experimental design phase through interpretation and modeling. To date, a marriage of the two disciplines has yet to occur on any significant scale; thus the full benefit of integrated interdis-

- ciplinary ecohydrological research has yet to be realized [Harte, 2002; Zalewski, 2002; Newman et al., 2003; Hannah et al., 2004].
- [54] The place-based approach would require special technological elements to make the conceptual elements of an ecohydrology vision a reality. Improvements in information systems, necessary for effective data management and distribution, would underpin interdisciplinary and cross-scale interactions and lay a foundation for future comparative analyses with more humid regions. The latter will be critical for determining the extent to which robust generalizations and noteworthy exceptions can be elucidated. Technological constraints often limit our ability to effectively monitor and characterize ecohydrological processes (e.g., partitioning E from T) and new technologies (e.g., instrumentation, wireless network capabilities, etc.) will play a vital role in overcoming these constraints and provide new perspectives on old problems.
- [55] Implementation of our ecohydrological vision will promote synergistic growth and the development of new perspectives with a high potential for generating novel and more powerful approaches to environmental problem solving. Ecohydrological approaches will expedite scientific progress and enhance the role of science in the policy arena. However, the specifics of these benefits and when they will accrue are difficult to determine a priori [Harte, 2002]. In essence, our ecohydrological vision is a wager (and we think it is a good one) on the potential for synthesis to be a catalyst for significant advances relative to critical, but highly complex environmental issues. The potential payoff includes broad social and economic benefits, addressing serious issues related to water supply and quality as well as ecosystem health and diversity in water-limited environments.
- [56] One final benefit is that place-based research with an ecohydrology focus will facilitate training of a new generation of scientists with essential cross-disciplinary experience and perspectives. Such training fosters the development of science that is robust, comprehensive, and adaptable enough to address current, new, and as yet unforeseen environmental problems.
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References

- Aber, J., and J. Melillo (1991), *Terrestrial Ecosystems*, Saunders Coll. Publ., Philadelphia, Pa.
- Abrahams, A. D. (1984), Channel networks: A geomorphological perspective, Water Resour. Res., 20, 161–188.
- Allen, C. D., and D. D. Breshears (1998), Drought-induced shift of a forest-woodland ecotone: Rapid landscape response to climatic variation, *Proc. Natl. Acad. Sci. U. S. A.*, 95, 14,839–14,842.
- Allen, T. F. H., and T. B. Starr (1982), Hierarchy: Perspectives for Ecological Complexity, Univ. of Chicago Press, Chicago, Ill.
- Allen, T. F. H., R. V. O'Neill, and T. W. Hoekstra (1984), Interlevel relations in ecological research and management: Some working principles from hierarchy theory, *Gen. Tech. Rep. RM*–110, Rocky Mtn. Range and Forest Exp. Stn., Fort Collins, Colo.

- Allison, G. B., P. G. Cook, S. R. Barnett, G. R. Walker, I. D. Jolly, and M. W. Hughes (1990), Land clearance and river salinisation in the western Murray Basin, Australia, J. Hydrol., 119, 1–20.
- Austin, A. T., L. Yahdjian, J. M. Stark, J. Belnap, A. Porporato, U. Norton, D. A. Ravetta, and S. M. Schaeffer (2004), Water pulses and biogeochemical cycles in arid and semiarid ecosystems, *Oecologia*, 141, 221– 235, doi:10.1007/s00442-004-1519-1.
- Archer, S. (1995), Tree-grass dynamics in a *Prosopis*-thornscrub savanna parkland: Reconstructing the past and predicting the future, *Ecoscience*, 2, 83–99.
- Archer, S., and A. Bowman (2002), Understanding and managing rangeland plant communities, in *Global Rangelands: Progress and Prospects*, edited by A. C. Grice and K. C. Hodgkinson, pp. 63–80, CAB Int., Wallingford, U. K.
- Baird, A. J., and R. L. Wilby (Eds.) (1999), Ecohydrology: Plants and Water in Terrestrial and Aquatic Environments, Routledge, Boca Raton, Fla
- Baker, M. B. (1984), Changes in streamflow in an herbicide-treated pinyonjuniper watershed in Arizona, Water Resour. Res., 20, 1639–1642.
- Bakwin, P. S., R. J. Andres, J. W. C. White, and P. P. Tans (1998), Determination of the isotope (C¹³/C¹²) discrimination by terrestrial biology from a global network of observations, *Global Biogeochem. Cycles*, 12, 555–562
- Belnap, J., J. R. Welter, N. B. Grimm, N. Barger, and J. A. Ludwig (2005), Linkages between microbial and hydrologic processes in arid and semiarid watersheds, *Ecology*, 86, 298–307.
- Betancourt, J. L., T. P. Van Devender, and P. S. Martin (1990), Packrat Middens: The Last 40,000 Years of Biotic Change, Univ. of Ariz. Press, Tucson.
- Billings, W. (1985), The historical development of physiological plant ecology, in *Physiological Ecology of North American Plant Commu*nities, edited by B. Chabot and H. Mooney, pp. 1–15, CRC Press, Boca Raton, Fla.
- Bloschl, G., and M. Sivapalan (1995), Scale issues in hydrological modeling: A review, *Hydrol. Processes*, 9, 251–290.
- Bonan, G. B. (1997), Effects of land use on the climate of the United States, Clim. Change, 37, 449–486.
- Bonan, G. B. (2002), Ecological Climatology, Cambridge Univ. Press, New York.
- Bond, B. (2003), Hydrology and ecology meet and the meeting is good, *Hydrol. Processes*, 17, 2087–2089.
- Bond, B. J., and K. L. Kavanaugh (1999), Stomatal behavior of four woody species in relation to leaf-specific hydraulic conductance and threshold water potential, *Tree Physiol.*, 19, 503–510.
- Bonell, M. (2002), Ecohydrology: A completely new idea? Discussion, Hydrol. Sci. J., 47, 809–810.
- Boutton, T. W., S. R. Archer, and A. J. Midwood (1999), Stable isotopes in ecosystem science: Structure, function and dynamics of a subtropical savanna, *Rapid Commun. Mass Spectrom.*, 13, 1263–1277.
- Bowers, J. E., and R. M. Turner (2001), Dieback and episodic mortality of *Cercidium microphyllum* (foothill paloverde), a dominant Sonoran Desert tree, *J. Torrey Bot. Soc.*, *128*, 28–140.
- Bowling, D. R., N. G. McDowell, B. J. Bond, B. E. Law, and J. R. Ehleringer (2002), ¹³C content of ecosystem respiration is linked to precipitation and vapor pressure deficit, *Oecologia*, *131*, 113–124.
- Breshears, D. D. (2005), An ecologist's perspective of ecohydrology, *Bull. Ecol. Soc. Am.*, *86*, 296–300.
- Breshears, D. D., et al. (2005), Regional vegetation die-off in response to global-change-type drought, *Proc. Natl. Acad. Sci. U. S. A.*, 102, 15,144–15,148.
- Brock, J. H. (1994), *Tamarix* spp. (salt cedar), an invasive exotic woody plant in arid and semi-arid riparian habitats of western USA, in *Ecology* and *Management of Invasive Riverside Plants*, edited by L. C. de Waal et al., pp. 27–44, John Wiley, Hoboken, N. J.
- Brooks, J. R., F. C. Meinzer, R. Coulombe, and J. Gregg (2002), Hydraulic redistribution of soil water during summer drought in two contrasting Pacific Northwest coniferous forests, *Tree Physiol.*, 22, 1107–1117.
- Brown, D. G., K. M. Johnson, T. R. Loveland, and D. M. Theobald (2005), Rural land-use trends in the conterminous United States, 1950–2000, *Ecol. Appl.*, 15, 1851–1863.
- Bull, W. B. (1991), Geomorphic Response to Climate Change, Oxford Univ. Press, New York.
- Burgess, S. S. O., M. A. Adams, N. C. Turner, and C. K. Ong (1998), The redistribution of soil water by tree root systems, *Oecologia*, 115, 306–311.
- Burke, I. C., T. G. F. Kittel, W. K. Lauenroth, P. Snook, C. M. Yonker, and W. J. Parton (1991), Regional analysis of the Central Great Plains: Sensitivity to climate variability, *BioScience*, 41, 685–692.

- Burns, S. J., D. Fleitmann, A. Matter, U. Neff, and A. Mangini (2001), Speleothem evidence from Oman for continental pluvial events during interglacial periods, *Geology*, 29, 623–626.
- Caldwell, M. M., T. E. Dawson, and J. H. Richards (1998), Hydraulic lift: Consequences of water efflux from the roots of plants, *Oecologia*, *113*, 151–161.
- Caylor, K. K., T. M. Scanlon, and I. Rodríguez-Iturbe (2004), Feasible optimality of vegetation patterns in river basins, *Geophys. Res. Lett.*, 31, L13502, doi:10.1029/2004GL020260.
- Cayrol, P., L. Kergoat, S. Moulin, G. Dedieu, and A. Chehbouni (2000), Calibrating a coupled SVAT-vegetation growth model with remotely sensed reflectance and surface temperature—A case study for the HAPEX-Sahel grassland sites, J. Appl. Meteorol., 39, 2452–2472.
- Chapin, F. S., III (1991a), Effects of multiple environmental stresses on nutrient availability and use by plants, in *Response of Plants to Multiple Stresses*, edited by H. A. Mooney, W. E. Winner, and E. J. Pell, pp. 67–88, Elsevier, New York.
- Chapin, F. S., III (1991b), Integrated responses of plants to stress: A centralized system of physiological responses, *BioScience*, 41, 29–36.
- Chapin, F. S., III, A. J. Bloom, C. B. Field, and R. H. Waring (1987), Plant responses to multiple environmental factors, *BioScience*, 37, 49–57.
- Chesson, P., R. L. Gebauer, S. Schwinning, N. Huntly, K. Wiegand, M. S. K. Ernest, A. Sher, A. Novoplansky, and J. F. Weltzin (2004), Resource pulses, species interactions and diversity maintenance in arid and semi-arid environments, *Oecologia*, 141, 236–253, doi:10.1007/s00442-004-1551-1.
- Clark, J., et al. (2001), Ecological forecasting: An emerging imperative, Science, 293, 657–660.
- Cowan, I. (1977), Stomatal behaviour and environment, *Adv. Bot. Res.*, 4, 117–228.
- Dahm, C. N., J. R. Cleverly, J. E. A. Coonrod, J. R. Thibault, D. E. McDonnell, and D. F. Gilroy (2002), Evapotranspiration at the land/water interface in a semi-arid drainage basin, *Freshwater Biol.*, 47, 831–843
- Davenport, D. W., D. D. Breshears, B. P. Wilcox, and C. D. Allen (1998), Viewpoint: Sustainability of piñon-juniper ecosystems: A unifying perspective of soil erosion thresholds, *J. Range Manage.*, 51, 231–240.
- Dawson, T. E. (1993), Hydraulic lift and water use by plants: Implications for water balance, performance and plant-plant interactions, *Oecologia*, 95, 565-574.
- De Fries, R., G. P. Asner, and R. Houghton (Eds.) (2004), *Ecosystems and Land Use Change, Geophys. Monogr. Ser.*, vol. 153, 308 pp., AGU, Washington, D. C.
- Eagleson, P. S. (2002), Ecohydrology: Darwinian Expression of Vegetation Form and Function, 496 pp., Cambridge Univ. Press, New York.
- Ehleringer, J. R., A. E. Hall, and G. D. Farquhar (1993), Stable Isotopes and Plant Carbon-Water Relations, Elsevier, New York.
- Ewers, B. E., R. Oren, T. J. Albaugh, and P. M. Dougherty (1999), Carry-over effects of water and nutrient supply on water use of *Pinus taeda*, *Ecol. Appl.*, 9, 513–525.
- Feddes, R. A., and P. A. C. Raats (2004), Parameterizing the soil-waterplant root system, in *Unsaturated Zone Modeling: Progress, Challenges, and Applications*, edited by R. A. Feddes et al., pp. 95–141, Springer, New York.
- Feng, X., and S. Epstein (1994), Climatic implications of an 8000-year hydrogen isotope time series from bristlecone pine trees, *Science*, 265, 1079–1081.
- Fernández-Illescas, C. P., and I. Rodríguez-Iturbe (2004), The impact of interannual rainfall variability on the spatial and temporal patterns of vegetation in a water-limited ecosystem, *Adv. Water Resour.*, 27, 83–95
- Fontes, J. C., M. Stute, P. Schlosser, and W. S. Broecker (1993), Aquifers as archives of paleoclimate, Eos Trans. AGU, 74, 21–22.
- Gates, D. M. (1980), Biophysical Ecology, Springer, New York.
- Gee, G. W., P. J. Wierenga, B. J. Andraski, M. H. Young, M. J. Fayer, and M. L. Rockhold (1994), Variations in water balance and recharge potential at three western desert sites, *Soil Sci. Soc. Am. J.*, 58, 63–71.
- Glenn, E. P., and P. L. Nagler (2005), Comparative ecophysiology of *Tamarix ramosissima* and native trees in western US riparian zones, *J. Arid Environ.*, 61, 419–446.
- Granier, A. (1987), Evaluation of transpiration in a Douglas-fir stand by means of sap flow measurements, *Tree Physiol.*, 3, 309–320.
- Graetz, R. D. (1991), The nature and significance of the feedback of changes in terrestrial vegetation on global atmospheric and climatic change, *Clim. Change*, 18, 147–174.
- Grissino-Mayer, H. D. (1995), The climate and fire history of El Malpais National Monument, New Mexico, Ph.D. thesis, Univ. of Ariz., Tucson.

- Guenther, A., S. Archer, J. Greenberg, P. Harley, D. Helmig, L. Klinger, L. Vierling, M. Wildermuth, P. Zimmerman, and S. Zitzer (1999), Biogenic hydrocarbon emissions and landcover/climate change in a subtropical savanna, *Phys. Chem. Earth B*, 24, 659–667.
- Guswa, A. J., M. A. Celia, and I. Rodriguez-Iturbe (2004), Effect of vertical resolution on predictions of transpiration in water-limited ecosystems, *Adv. Water Resour.*, 27, 467–480, doi:10.1016/j.advwatres.2004.03.001.
- Hannah, D. M., P. J. Wood, and J. P. Sadler (2004), Ecohydrology and hydroecology: A "new paradigm"?, Hydrol. Processes, 18, 3439–3445.
- Harte, J. (2002), Toward a synthesis of the Newtonian and Darwinian worldviews, *Phys. Today*, 55, 29-43.
- Hibbert, A. R. (1983), Water yield improvement potential by vegetation management on western rangelands, Water Resour. Bull., 19, 375–381.
- Hoffmann, W. A., and R. B. Jackson (2000), Vegetation-climate feedbacks in the conversion of tropical savanna to grassland, *J. Clim.*, 13, 1593– 1602.
- Holbrook, N. M., and M. A. Zwieniecki (1999), Embolism repair and xylem tension: Do we need a miracle?, *Plant Physiol.*, 120, 7–10.
- Holland, E. A., F. J. Dentener, B. H. Braswell, and J. M. Sulzman (1999), Contemporary and pre-industrial global reactive nitrogen budgets, *Bio-geochemistry*, 46, 7–43.
- Hooper, D. U., and L. Johnson (1999), Nitrogen limitation in dryland ecosystems: Responses to geographical and temporal variation in precipitation, *Biogeochemistry*, 46, 247–293.
- Hopmans, J. W., and K. L. Bristow (2002), Current capabilities and future needs of root water and nutrient uptake modeling, Adv. Agron., 77, 103– 183
- Houghton, R. A. (2003), Revised estimates of the annual net flux of carbon to the atmosphere from changes in land use and land management 1850–2000, *Tellus, Ser. B*, 55, 378–390.
- House, J., S. Archer, D. D. Breshears, R. J. Scholes, and the NCEAS Treegrass Interactions Participants (2003), Conundrums in mixed woodyherbaceous plant systems, *J. Biogeogr.*, 30, 1763–1777.
- Hunt, R. J., and D. A. Wilcox (2003), Ecohydrology: Why Hydrologists Should Care, Ground Water, 41, 289.
- Huxman, T., K. Snyder, D. Tissue, A. Leffler, K. Ogle, W. Pockman, D. Sandquist, D. Potts, and S. Schwinning (2004), Precipitation pulses and carbon fluxes in semiarid and arid ecosystems, *Oecologia*, 141, 254–268.
- Huxman, T. E., B. P. Wilcox, R. Scott, K. Snyder, D. D. Breshears, E. Small, K. Hultine, W. T. Pockman, and R. B. Jackson (2005), Ecohydrological implications of woody plant encroachment, *Ecology*, 86, 308–319.
- Infrastructure for Biology at Regional to Continental Scales Working Group (2003), Rationale, blueprint, and expectations for the National Ecological Observatory Network, report, Am. Inst. for Biol. Sci., Washington, D. C. (Available at http://ibrcs.aibs.org/reports/pdf/IBRCSWhitePaper_NEON.pdf)
- Intergovernmental Panel on Climate Change (2001), The Scientific Basis.

 Contribution of Working Group 1 to the Third Assessment Report of the Intergovernmental Panel on Climate Change, 881 pp., Cambridge Univ. Press. New York.
- Isebrands, J. G., A. B. Guenther, P. Hartley, D. Helmig, L. Klinger, L. Vierling, P. Zimmerman, and C. Geron (1999), Volatile organic compound emission rates from mixed deciduous and coniferous forests in northern Wisconsin, USA, Atmos. Environ., 33, 2527–2536.
- Jackson, R. B., J. S. Sperry, and T. E. Dawson (2000), Root water uptake and transport: Using physiological processes in global predictions, *Trends Plant Sci.*, 5, 482–488.
- Jackson, R. B., J. L. Banner, E. G. Jobbagy, W. T. Pockman, and D. H. Wall (2002), Ecosystem carbon loss with woody plant invasion, *Nature*, 418, 623-626.
- Jarvis, P., and J. Morison (1981), The control of transpiration and photosynthesis by the stomata, Soc. Exp. Biol. Seminar Ser., 8, 248–279.
- Johnson, W. C. (1994), Woodland expansion in the Platte River, Nebraska: Patterns and causes, Ecol Monogr., 64, 45–84.
- Katz, G. L., and P. B. Shafroth (2003), Biology, ecology and management of *Elaeagnus angustifolia L*. (Russian olive) in western North America, *Wetlands*, 23, 763–777.
- Kerkhoff, A. J., S. N. Martens, and B. T. Milne (2004a), An ecological evaluation of Eagleson's optimality hypothesis, *Funct. Ecol.*, 18, 404– 413.
- Kerkhoff, A. J., S. N. Martens, G. A. Shore, and B. T. Milne (2004b), Contingent effects of water balance variation on tree cover density in semiarid woodlands, *Global Ecol. Biogeogr.*, 13, 237–246.
- Knapp, A. K., and M. D. Smith (2001), Variation among biomes in temporal dynamics of aboveground primary production, *Science*, 291, 481–484.

- Knapp, A. K., P. A. Fay, J. M. Blair, S. L. Collins, J. D. Carlisle, C. W. Harper, M. D. Smith, B. T. Danner, M. S. Lett, and J. K. McCarron (2002), Rainfall variability, carbon cycling and plant species diversity in a mesic grassland, *Science*, 298, 2202–2205.
- Kundzewicz, Z. W. (2002), Ecohydrology-seeking consensus on interpretation of the notion, *Hydrol. Sci. J.*, 47, 799–804.
- Kwicklis, E., M. Witkowski, K. Birdsell, B. Newman, and D. Walther (2005), Development of an infiltration map for the Los Alamos Area, New Mexico, *Vadose Zone J.*, 4, 672–693, doi:10.2136/vzj2004.0176.
- Lambers, H., F. S. Chapin, and T. L. Pons (1998), Plant Physiological Ecology, 356 pp., Springer, New York.
- Landsberg, J. J., and R. H. Waring (1997), A generalized model of forest productivity using simplified concepts of radiation-use efficiency, carbon balance and partitioning, For. Ecol. Manage., 95, 209–228.
- Larcher, W. (2003), Physiological Plant Ecology, 506 pp., Springer, New York.
 Leavitt, S. W. (1993), Environmental information from ¹³C/¹²C ratios of wood, in Climate Change in Continental Isotopic Records, Geophys. Monogr. Ser., vol. 78, edited by P. K. Swart et al., pp. 325–331, AGU, Washington, D. C.
- Leavitt, S. W. (1994), Major wet interval in white mountains medieval warm period evidenced in δ¹³C of bristlecone pine tree rings, *Clim. Change*, 26, 299–307.
- Lidicker, W. Z. (1988), The synergistic effects of reductionist and holistic approaches in animal ecology, Oikos, 53, 279–280.
- Lin, G. H., S. L. Phillips, and J. R. Ehleringer (1996), Monsoonal precipitation responses of shrubs in a cold desert community on the Colorado Plateau, *Oecologia*, 106, 8–17.
- Livingston, N. J., and D. L. Spittlehouse (1996), Carbon isotope fractionation in tree ring early and late wood in relation to intra-growing season water balance, *Plant Cell Environ.*, 19, 768–774.
- Loik, M. E., D. D. Breshears, W. K. Lauenroth, and J. Belnap (2004), A multiscale perspective on water pulses in dryland ecosystems: Climatology and ecohydrology of the western USA, *Oecologia*, 141, 269–281.
- Martens, S. N., D. D. Breshears, and C. W. Meyer (2000), Spatial distributions of understory light along the grassland/forest continuum: Effects of cover, height, and spatial pattern of tree canopies, *Ecol. Modell.*, 126, 79–93.
- Martin, R. E., G. P. Asner, R. J. Ansley, and A. R. Mosier (2003), Effects of woody vegetation encroachment on soil nitrogen oxide emissions in a temperate savanna, *Ecol. Appl.*, 13, 897–910.
- McDowell, N. G., D. R. Bowling, A. Schauer, B. J. Bond, J. Irvine, B. E. Law, and J. R. Ehleringer (2004), Associations between the carbon isotope content of ecosystem respiration, water availability, and canopy conductance, *Global Change Biol.*, 10, 1767–1784.
- McDowell, N. G., H. A. Adams, J. D. Bailey, M. Hess, and T. E. Kolb (2006), Homeostatic maintenance of gas exchange in ponderosa pine: A 40-year restoration thinning experiment, *Ecol. Appl.*, in press.
- McFadden, L. D., and J. R. McAuliffe (1997), Lithologically influenced geomorphic responses to Holocene climate changes in the southern Colorado Plateau, Arizona: A soil-geomorphic and ecologic perspective, *Geomorphology*, 19, 303–332.
- McNulty, S. G., and W. T. Swank (1995), Wood δC-13 as a measure of annual basal area growth and soil-water stress in a *Pinus strobus* forest, *Ecology*, 76, 1581–1586.
- Miller, G. H., M. L. Fogel, J. W. Magee, M. K. Gagan, S. J. Clarke, and B. J. Johnson (2005), Ecosystem collapse in Pleistocene Australia and a human role in megafaunal extinction, *Science*, 309, 287–290.
- Molnar, P. (2001), Climate change, flooding in arid environments, and erosion rates, *Geology*, 29, 1071–1074.
- Monteith, J. (1975), Principles of Environmental Physics, Edward Arnold, London.
- National Research Council (2001a), Envisioning the Agenda for Water Resources Research in the Twenty-First Century, Natl. Acad. Press, Washington, D. C.
- National Research Council (2001b), Basic Research Opportunities in Earth Science, Natl. Acad. Press, Washington, D. C.
- Neave, M., and A. D. Abrahams (2002), Vegetation influences on water yields from grasslands and shrubland ecosystems in the Chihuahuan Desert, Earth Surf. Processes Landforms, 27, 1011–1020.
- Neilson, R. P. (1995), A model for predicting continental-scale vegetation distribution and water balance, Ecol. Appl., 5, 362–385.
- Neilson, R., and D. Marks (1994), A global perspective of regional vegetation and hydrologic sensitivities from climate change, *J. Veg. Sci.*, 5, 715–730.
- Newman, B. D., A. R. Campbell, and B. P. Wilcox (1997), Tracer-based studies of soil water movement in semi-arid forests of New Mexico, J. Hydrol., 196, 251–270.

- Newman, B. D., A. R. Campbell, and B. P. Wilcox (1998), Lateral subsurface flow pathways in a semiarid ponderosa pine hillslope, *Water Resour. Res.*, 34, 3485–3496.
- Newman, B. D., O. Sala, and B. P. Wilcox (2003), Conference promotes study of ecohydrology of semi-arid landscapes, *Eos Trans. AGU*, *84*, 13–17.
- Newman, B. D., B. P. Wilcox, and R. C. Graham (2004), Snowmelt driven macropore flow and soil saturation in a semiarid forest, *Hydrol. Pro*cesses, 18, 1035–1042.
- Noy-Meir, I. (1973), Desert ecosystems: Environment and producers, Annu. Rev. Ecol. Syst., 4, 25–51.
- Nuttle, W. K. (2002), Eco-hydrology's past and future in focus, *Eos Trans. AGU.*, 83, 205–212.
- O'Neill, R. V., D. L. DeAngelis, T. F. H. Allen, and J. B. Waide (1986), A Hierarchical Concept of Ecosystems, Princeton Univ. Press, Princeton, N. J.
- Oren, R., J. S. Sperry, G. G. Katul, D. E. Pataki, B. E. Ewers, N. Phillips, and K. V. R. Schafer (1999), Survey and synthesis of intra- and interspecific variation in stomatal sensitivity to vapour pressure deficit, *Plant Cell Environ.*, 22, 1515–1526.
- Pacala, S. W., et al. (2001), Consistent land and atmosphere-based US carbon sink estimates, *Science*, 292, 2316–2320.
- Pagès, L., C. Doussan, and G. Vercambre (2000), An introduction on below-ground environment and resource acquisition, with special reference to trees: Simulation models should include plant structure and function, Ann. For. Sci., 57, 513–520.
- Parsons, A. J., and A. D. Abrahams (1994), Geomorphology of desert environments, in *Geomorphology of Desert Environments*, edited by A. D. Abrahams and A. J. Parsons, pp. 1–12, CRC Press, Boca Raton, Fla.
- Passioura, J. B. (1979), Accountability, philosophy and plant physiology, Search, 10, 347–350.
- Peters, D. P. C., S. R. Pielke, B. Bestelmeyer, C. D. Allen, S. Munson-McGee, and K. M. Havstad (2004), Cross-scale interactions, nonlinearities, and forecasting catastrophic events, *Proc. Natl. Acad. Sci. U. S. A.*, 101, 15.130–15.135.
- Phillips, F. M. (1994), Environmental tracers for water movement in desert soils of the American southwest, Soil Sci. Soc. Am. J., 58, 15–24.
- Phillips, F. M., M. A. Walvoord, and E. E. Small (2004), Effects of environmental change on groundwater recharge in the desert Southwest, in Groundwater Recharge in a Desert Environment: The Southwestern United States, Water Sci. Appl. Ser., vol. 9, edited by J. F. Hogan, F. M. Phillips, and B. R. Scanlon, pp. 273–294, AGU, Washington, D. C.
- Pitman, A., G. T. Narisma, R. A. Pielke, and N. J. Holbrook (2004), The impact of land cover change on the climate of southwest Western Australia, J. Geophys. Res., 109, D18109, doi:10.1029/2003JD004347.
- Plummer, M. A. (2002), Paleoclimatic conditions during the last deglaciation inferred from combined analysis of pluvial and glacial records, Ph.D. dissertation, N. M. Inst. of Min. and Technol., Socorro.
- Polyak, V. J., and Y. Asmerom (2001), Late Holocene climate and cultural changes in the southwest United States, *Science*, 294, 148–151.
- Porporato, A., and I. Rodriguez-Iturbe (2002), Ecohydrology—A challenging multidisciplinary research perspective, Hydrol. Sci. J., 47, 811–821.
- Porporato, A., P. D'Odorico, F. Laio, L. Ridolfi, and I. Rodríguez-Iturbe (2002), Ecohydrology of water-controlled ecosystems, Adv. Water Resour., 25, 1335–1348.
- Prieur-Richard, A.-H., and S. Lavorel (2000), Invasions: Perspective of diverse plant communities, Aust. Ecol., 25, 1-7.
- Reynolds, J. F., P. R. Kemp, and J. D. Tenhunen (2000), Effects of long-term rainfall variability on evapotranspiration and soil water distribution in the Chihuahuan Desert: A modeling analysis, *Plant Ecol.*, *150*, 145–159
- Ridolfi, L., P. D'Odorico, A. Porporato, and I. Rodríguez-Iturbe (2003), Stochastic soil moisture dynamics along a hillslope, *J. Hydrol.*, 272, 264–275.
- Roden, J. S., and J. R. Ehleringer (2000), Hydrogen and oxygen isotope ratios of tree ring cellulose for field-grown riparian trees, *Oecologia*, 123, 481–489
- Roden, J., D. Bowling, N. McDowell, B. Bond, and J. Ehleringer (2005), Carbon and oxygen isotope ratios of tree ring cellulose along a precipitation transect in Oregon, United States, *J. Geophys. Res.*, 110, G02003, doi:10.1029/2005JG000033.
- Rodriguez-Iturbe, I. (2000), Ecohydrology: A hydrologic perspective of climate-soil-vegetation dynamics, Water Resour. Res., 36, 3–9.
- Rodríguez-Iturbe, I., and A. Porporato (2004), Ecohydrology of Water-Controlled Ecosystems: Soil Moisture and Plant Dynamics, 442 pp., Cambridge Univ. Press, New York.
- Rodríguez-Iturbe, I., and A. Rinaldo (2001), Fractal River Basins: Chance and Self-Organization, 546 pp., Cambridge Univ. Press, New York.

- Running, S. W., and J. C. Coughlan (1988), A general model of forest ecosystem processes for regional applications I. Hydrologic balance, canopy gas exchange and primary production processes, *Ecol. Modell.*, 42, 125–154.
- Running, S., R. Nemani, F. Heinsch, M. Zhao, M. Reeves, and H. Hashimoto (2004), A continuous satellite-derived measure of global terrestrial primary production, *Bioscience*, 54, 547–560.
- Ryan, M. G. (1991), A simple method for estimating gross carbon budgets for vegetation in forest ecosystems, *Tree Physiol.*, 9, 255–266.
- Scanlon, B. R., K. Keese, R. C. Reedy, J. Simunek, and B. J. Andraski (2003), Variations in flow and transport in thick desert vadose zones in response to paleoclimatic forcing (0 – 90 kyr): Field measurements, modeling, and uncertainties, *Water Resour. Res.*, 39(7), 1179, doi:10.1029/ 2002WR001604.
- Scanlon, B. R., D. G. Levitt, K. E. Keese, R. C. Reedy, and M. J. Sully (2005a), Ecological controls on water-cycle response to climate variability in deserts, *Proc. Natl. Acad. Sci. U. S. A.*, 102, 6033–6038.
- Scanlon, B. R., R. C. Reedy, D. A. Stonestrom, D. E. Prudic, and K. F. Dennehy (2005b), Impact of land use and land cover change on ground-water recharge and quality in the southwestern USA, *Global Change Biol.*, 11, 1577–1593.
- Scheffer, M., S. Carpenter, J. Foley, C. Folke, and B. Waker (2001), Stochastic events can trigger large state-shifts in ecosystems with reduced resilience, *Nature*, 413, 591–596.
- Schimel, D., B. Braswell, and W. Parton (1997), Equilibration of the terrestrial water, nitrogen and carbon cycles, *Proc. Natl. Acad. Sci. U. S. A.*, 94, 8280–8283.
- Schlesinger, W. H., J. F. Reynolds, G. L. Cunningham, L. F. Huenneke, W. M. Jarrell, R. A. Virginia, and W. G. Whitford (1990), Biological feedbacks in global desertification, *Science*, 247, 1043–1048.
- Schwinning, S., and J. R. Ehleringer (2001), Water-use trade-offs and optimal adaptations to pulse-driven arid ecosystems, J. Ecol., 89, 464–480.
- Schwinning, S., and O. E. Sala (2004), Hierarchy of responses to resource pulses in arid and semi-arid ecosystems, *Oecologia*, *141*, 211–220, doi:10.1007/s00442-004-1520-8.
- Scuderi, L. A. (1993), A 2000-year tree ring record of annual temperatures in the Sierra Nevada mountains, Science, 259, 1433-1436.
- Seyfried, M. S., S. Schwinning, M. A. Walvoord, W. T. Pockman, B. D. Newman, R. B. Jackson, and F. M. Phillips (2005), Ecohydrological control of deep drainage in arid and semiarid regions, *Ecology*, 86, 277–287.
- Šimůnek, J., M. T. van Genuchten, and M. Šenja (2005), The HYDRUS-1D software package for simulating the one-dimensional movement of water, heat, and multiple solutes in variably saturated media, version 3.0, *HY-DRUS Software Ser. 1*, Dep. of Environ. Sci., Univ. of Calif., Riverside.
- Smith, S. D., R. K. Monson, and J. E. Anderson (1997), Physiological Ecology of North American Desert Plants, Springer, New York.
- Smith, S. D., T. E. Huxman, S. F. Zitzer, T. N. Charlet, D. C. Housman, J. S. Coleman, L. K. Fenstermaker, J. R. Seemann, and R. S. Nowak (2000), Elevated CO₂ increases productivity and invasive species success in an arid ecosystem, *Nature*, 408, 79–82.
- Sperry, J. S., U. G. Hacke, R. Oren, and J. P. Comstock (2002), Water deficits and hydraulic limits to leaf water supply, *Plant Cell Environ.*, 25, 251–263.
- Sperry, J. S., V. Stiller, and U. Hacke (2003), Xylem hydraulics and the soil-plant-atmosphere continuum: Opportunities and unresolved issues, Agron. J., 95, 1362–1370.
- Street-Perrott, F. A., and S. P. Harrison (1985), Lake levels and climate reconstruction, in *Paleoclimate Analysis and Modeling*, edited by A. D. Hecht, pp. 291–340, John Wiley, Hoboken, N. J.
- Swetnam, T. W., and J. L. Betancourt (1998), Mesoscale disturbance and ecological response to decadal climatic variability in the American southwest, J. Clim., 11, 3128–3147.
- Texas State Soil and Water Conservation Board (2002), Texas State Soil and Water Conservation Brush Control Program 2002 annual report, Austin, Tex.
- Tickner, D. P., P. G. Angold, A. M. Gurnell, and J. O. Mountford (2001), Riparian plant invasions: Hydrogeomorphological control and ecological impacts, *Prog. Phys. Geogr.*, 25, 22–52.
- Tucker, G. E., and R. Slingerland (1997), Drainage basin responses to climate change, Water Resour. Res., 33, 2031–2047.
- Tyree, M. T., and J. S. Sperry (1988), Do woody plants operate near the point of catastrophic xylem dysfunction caused by dynamic water stress?, *Plant Physiol.*, *88*, 574–580.
- Unsworth, M. H., N. Phillips, T. Link, B. J. Bond, M. Falk, M. E. Harmon, T. M. Hinckley, D. Marks, and K. T. Paw U (2004), Components and controls of water flux in an old-growth Douglas-fir-western hemlock ecosystem, *Ecosystems*, 7, 468–481.

- Ustin, S. (Ed.) (2004), Remote Sensing for Natural Resources Management and Environmental Modeling, 3rd ed., 768 pp., John Wiley, Hoboken, N. J.
 Van Dijk, A. (2004), Ecohydrology: It's all in the game?, Hydrol. Processes, 18, 3683–3686.
- Van Wijk, M. T., and I. Rodríguez-Iturbe (2002), Tree-grass competition in space and time: Insights from a simple cellular automata model based on ecohydrological dynamics, *Water Resour. Res.*, 38(9), 1179, doi:10.1029/2001WR000768
- Villalba, R., and T. T. Veblen (1998), Influences of large-scale climatic variability on episodic tree mortality in northern Patagonia, *Ecology*, 79, 2624–2640.
- Vitousek, P. M. (1994), Beyond global warming: Ecology and global change, *Ecology*, 75, 1861–1876.
- Vitousek, P. M., J. D. Aber, R. W. Howarth, G. E. Likens, P. A. Matson, D. W. Schindler, W. H. Schlesinger, and D. G. Tilman (1997a), Human alteration of the global nitrogen cycle: Sources and consequences, *Ecol. Appl.*, 7, 737–750.
- Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo (1997b), Human domination of Earth's ecosystems, *Science*, 277, 494–499.
- Vrugt, J. A., M. T. van Wijk, J. W. Hopmans, and J. Simunek (2001), One-two-, and three-dimensional root uptake functions for transient modeling, *Water Res. Research*, 37, 2457–2470.
- Walvoord, M. A., and F. M. Phillips (2004), Identifying areas of basin-floor recharge in the Trans-Pecos region and the link to vegetation, *J. Hydrol.*, 292, 59–74.
- Walvoord, M. A., M. A. Plummer, F. M. Phillips, and A. V. Wolfsberg (2002), Deep arid system hydrodynamics: 1. Equilibrium states and response times in thick desert vadose zones, *Water Resour. Res.*, 38(12), 1308, doi:10.1029/2001WR000824.
- Walvoord, M. A., F. M. Phillips, D. A. Stonestrom, R. D. Evans, P. C. Hartsough, B. D. Newman, and R. G. Striegl (2003), A reservoir of nitrate beneath desert soils, *Science*, 302, 1021–1024.
- Wang, E., and C. J. Smith (2004), Modeling the growth and water uptake function of plant root systems: A review, *Aust. J. Agric. Res.*, 55, 501–523. Waring, R. H., and S. W. Running (1998), *Forest Ecosystems: Analysis at*

Multiple Scales, Elsevier, New York.

- Waters, M. R., and C. V. Haynes (2001), Late Quaternary arroyo formation and climate change in the American southwest, Geology, 29, 399-402.
- Watson, I. W., D. G. Burnside, and A. M. Holm (1996), Event-driven or continuous: Which is the better model for managers?, *Rangelands J.*, 18, 351–369.
- Watson, I. W., M. Westoby, and A. M. Holm (1997), Continuous and episodic components of demographic change in arid zone shrubs: Models of two *Eremophila* species from western Australia compared with published data on other species, *J. Ecol.*, 85, 833–846.
- Weltzin, J. F., and D. T. Tissue (2003), Resource pulses in arid environments—Patterns of rain, patterns of life, New Phytol., 157, 171–173.
- Weltzin, J. F., et al. (2003), Assessing the response of terrestrial ecosystems to potential changes in precipitation, *BioScience*, *53*, 941–952.
- Wilcox, B. P. (2002), Shrub control and streamflow on rangelands: A process-based viewpoint, J. Range Manage., 55, 318–326.
- Wilcox, B. P., B. D. Newman, D. Brandes, D. W. Davenport, and K. Reid (1997), Runoff from a semiarid ponderosa pine hillslope in New Mexico, *Water Resour. Res.*, 33, 2301–2314.
- Wilcox, B. P., M. S. Seyfried, and D. D. Breshears (2003a), The water balance on rangelands, in *Encyclopedia of Water Science*, edited by B. A. Stewart and T. A. Howell, pp. 791–794, Marcel Dekker, New York. Wilcox, B. P., D. D. Breshears, and C. D. Allen (2003b), Ecohydrology of a
- Wilcox, B. P., D. D. Breshears, and C. D. Allen (2003b), Ecohydrology of a resource-conserving semiarid woodland: Effects of scale and disturbance, *Ecol. Monogr.*, 73, 223–239.
- Williams, D. G., and J. R. Ehleringer (2000), Intra- and interspecific variation for summer precipitation use in pinyon juniper woodlands, *Ecol. Monogr.*, 70, 517–537.
- Williams, M., E. B. Rastetter, D. N. Fernandes, M. L. Goulden, S. C. Wofsy, G. R. Shaver, J. M. Melillo, J. W. Munger, S.-M. Fan, and K. J. Nadelhoffer (1996), Modelling the soil-plant-atmosphere continuum in a *Quercus-Acer* stand at Harvard Forest: The regulation of stomatal conductance by light, nitrogen and soil/plant hydraulic properties, *Plant Cell Environ.*, 19, 911–927.
- Williamson, T. N., B. D. Newman, R. C. Graham, and P. J. Shouse (2004), Regolith water in zero-order chaparral and perennial grass watersheds four decades after vegetation conversion, *Vadose Zone J.*, 3, 1007–1016.
- Wood, E. F., M. Sivapalan, and K. Beven (1990), Similarity and scale in catchment storm response, Rev. Geophys., 28, 1–18.
- Wu, X. B., and S. R. Archer (2005), Scale-dependent influence of topography-based hydrologic features on vegetation patterns in savanna landscapes, *Landscape Ecol.*, 20, 733–742.

- Yepez, E. A., D. G. Williams, R. L. Scott, and G. Lin (2003), Partitioning overstory and understory evapotranspiration in a semiarid savanna woodland from the isotopic composition of water vapor, *Agric. For. Meteorol.*, 119, 53–68.
- Zalewski, M. (2002), Ecohydrology—The use of ecological and hydrological processes for sustainable management of water resources, *Hydrol. Sci. J.*, 47, 823–831.
- Zou, C. B., P. W. Barnes, S. Archer, and C. McMurtry (2005), Soil moisture redistribution as a mechanism of facilitation in savanna tree-shrub clusters, *Oecologia*, *145*, 32–40, doi:10.1007/s00442-005-0110-8.
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