# Integrated Ecohydrologic Research and Hydro-Informatics

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The purpose of this paper is to offer our view of where ecohydrologic research will be going in the next 20 years and suggest how enabling technologies from hydro-informatics will support this research. Two decades ago Klemeš (1986) suggested that the hydrologist's "efforts expended on the fitting of flood and drought frequency curves would be better spent in acquiring deeper knowledge of climatology, meteorology, geology, and ecology." Klemeš was of course calling for interdisciplinary hydrology. Recently, a number of community reports have proposed a more interdisciplinary approach to hydrology, including the development of community infrastructure such as large scale hydrologic observatories with integrated, multi-scale monitoring and advanced informatics tools to enable this research (Band et al. 2002, Gupta et al. 1999, Hornberger et al. 2000, Maidment 2008). Specific calls were included to integrate the more physically or statistically oriented approaches in hydrology with ecosystem sciences including biogeochemical cycling and population ecology.

The emergence of ecohydrologic research is one example of how hydrologic science has begun to move in this direction. Ecohydrologic research seeks to understand how hydrological processes affect biological communities, and in turn how such communities affect water cycling (Newman et al. 2006, Rodriguez-Iturbe 2000). With this marriage of ecology and hydrology new avenues of research are opening up, and with these come new scientific and technical challenges. Some of the scientific challenges relate to the long-term memory in biological and geomorphic systems, complex feedbacks on water cycling, and the continuum of such interactions across space. Technical challenges include building more sophisticated simulation models to deal with such spatial dynamics, acquiring and managing the data needed to support these models, improving geo-visualization of spatial predictions and errors, and quantifying uncertainty associated with model structure and parameterization. Another interdisciplinary subfield of hydrology, hydroinformatics, emphasizes the development of information technology to help meet these challenges.

Newman et al. (2006) identified a number of research challenges for ecohydrologic research in semi-arid regions, including dealing with spatial and temporal heterogeneity, scaling up to regional and global extent, improving understanding of subsurface processes, and addressing long-term processes. They argue for a greater emphasis on place-based research where long-term data sets are being compiled. Efforts aimed at addressing these problems are underway, albeit with a focus on vegetation in semi-arid environments, equilibrium models with stochastic inputs, and knowledge obtained in traditional plots or stands. We suggest that for ecohydrologic research to be globally relevant it must embrace the full spectrum of environments, including non-water limited regions and wetland-rich regions. Over the next two decades, ecohydrologic research will explore more deeply the nature of transient system evolution and elucidate characteristic timescales of processes, such as those associated with ecosystem aggradation and degradation. It will move toward developing predictive capability that builds from an understanding of processes along spatial gradients, including adaptations of nutrient cycling and plant hydraulics at wetland-upland transitions. Moreover, as cyber-infrastructure improves these activities will transcend individual study sites by utilizing combinations of data sets

not traditionally included in hydrologic analysis, including networks of flux towers, component ground-based measurements, multiple process models, phenology networks, and remotely sensed information. We elaborate on these ideas below and offer suggestions for how advances in hydroinformatics will help sustain these activities over the next 20 years. To help focus the discussion we use a running example, canopy transpiration, which is a process that straddles the ecological and hydrological divide.

#### **Challenge: Ecohydrology Beyond Water Scarce Environments**

The emergence of ecohydrologic research is for hydrology the recognition that biological processes play a large role in the cycling of water (Eagleson 1982, 2002, Newman et al. 2006). The soil-vegetation-atmosphere continuum in turn is an important component in climate. By tapping into sub-surface water sources, plant roots help to maintain a flow of water from the soil to the atmosphere well after surface soil moisture levels have drained or dried to the point that they are too low to sustain evaporation. The global relevance of such processes is clear. In humid regions, evapotranspiration  $(E_{T})$  typically consumes half the annual precipitation; this proportion is much higher in semi-arid regions. Plant canopy transpiration  $(E_c)$  amounts to about half of annual  $E_{T}$ , but generally represents a much higher proportion during periods when plants are most active, during dry inter-storm periods, or in water-scarce environments. Thus, future research on land surface water-energy interactions and hydroclimatic research will continue to depend on insights into vegetative responses to environmental drivers. However, such insights will not come from a focus on just water scarce environments, since plants are adapted to and exert influence on environments across a full spectrum of available soil water. For instance, feedbacks between ecosystem and hydrological processes in wetlandrich environments are poorly represented in current climate models, which lack specific mechanisms for ground water dynamics and anaerobic processes. In urban and other human managed ecosystems, significant subsidy of water and nutrients, and built



**Figure 1**. Conceptual response of vegetation processes to available soil water. Both water scarcity and excess water represent limiting conditions for plants. The solid line represents equilibrium responses based on short-term processes, while the gray zone represents a range of responses reflecting long-term transients and memory.

drainage systems provide dramatically altered ecohydrologic gradients in limiting resources, tending to alleviate water limitations in drier climates and potentially introduce water limitations in more humid environments.

Vegetative responses to available soil water are conceptualized in Figure 1. Plants adapt to conditions of water scarcity by growing deeper roots (e.g., Jackson et al. 1996), supporting lower leaf areas (e.g., Grier and Running 1977), and reducing the vulnerability of their water conducting xylem to damage caused by air entry (e.g., Sperry et al. 1998). While these patterns are more easily observed under water stressed conditions, the mechanisms responsible for these adaptations give plants competitive advantages in all environments. For instance, excessive soil water requires that plants adapt shallow and sometimes above ground roots for aeration, and nitrogen fixation for obtaining sufficient nitrogen in anaerobic environments. The implication for obligate wetland species of a drop in the water table is a reduced ability to acquire sufficient water to maintain  $E_c$  (Ewers et al. 2007). Stomatal closure, in particular, occurs at mid-day even in high levels of soil water because of limits in hydraulic transport from roots to leaves (Sperry et al. 1998, Tyree and Sperry 1989). Moreover, evidence of coordination between photosynthetic

activity and hydraulic conductance (Brodribb and Field 2000, Brodribb et al. 2002) provides a clear link between plant hydraulics and carbon uptake, which ultimately feeds into vegetation growth and long-term memory effects of biological processes on water cycling. Feedbacks between these biological responses to environmental drivers and water cycling across the full spectrum of available soil water has so far received little attention, but an understanding of such processes will provide a vital contribution to the problem of making hydrologic predictions in ungaged basins (Sivapalan et al. 2003).

Much uncertainty remains in the parameterization of stomatal conductance even in place-based research (Mackay et al. 2003, Samanta et al. 2007), and it currently cannot be conveniently estimated as a spatial variable in large-scale models. Indeed, in regional to global scale models it is accessed from lookup tables keyed to remotely sensed vegetation types (e.g., Dickenson et al. 1998, Loveland and Belward 1997, Running et al. 1995, Sellers et al. 1996). Recent studies have shown that stomatal closure is proportional to the rate of water loss for a wide variety of species (Addington et al. 2004, Ewers et al. 2001, Ewers et al. 2005, Ewers et al. 2007. Oren et al. 1999. Wullschleger et al. 2002). We believe such insights will lead to dynamic modeling of stomatal function at relevant scales by linking the physiological understanding with dynamic parameterization from satellites. Theoretical work towards this includes linking the complementary relationship between potential or actual evapotranspiration and stomatal conductance (e.g., Pettijohn and Salvucci 2006). Technical advances with thermal remote sensing are now exploiting the large-scale equilibrium between the lower atmospheric moisture content and evaporation rate (e.g., Hashimoto et al. 2008), and multi-temporal remote sensing to take advantage of soil thermal properties (e.g., Anderson et al. Furthermore, hyperspectral data from 2007). sensors such as Hyperion have shown potential for quantifying photosynthetic activity (Grace et al. 2007). These advances in technology coupled with the predictive power of physiology-based models will become common elements of watershed hydrology, hydroclimatology, and water resource sustainability research.

## **Research Challenge: Modeling Transience**

The characteristic timescales of ecosystem processes are affected by ground water dynamics, ecosystem aggradation and degradation, soil development, and climatic cycles. Short-term processes include the diurnal adjustments of stomatal conductance discussed above, daily or longer-term adjustments to available soil water, seasonal adjustments in plant growth, inter-annual plant responses to disturbance and competition for available resources, decadal adjustments to soil carbon and nitrogen, and much longer-term changes in soil or landform development. Characteristic time responses for different processes need to be understood if we are to make better predictions of global climate change effects on water resources. To address this problem Eagleson (1982, 2002) hypothesized short-term canopy density adjustments to minimize soil water stress, medium-term preference for species that minimize consumption of scarce soil water, and long-term adjustments in soil properties that maximize the optimal canopy density. In this view, plants were seen to optimize their environment. Such an optimization view lends itself to equilibrium modeling of which there are many examples (e.g., Arris and Eagleson 1994, Collins and Bras 2007, Eagleson 1982, Kergoat 1998, Nemani and Running 1989, Rodriguez-Iturbe et al. 1999, van Wijk and Bouten 2001, Zea-Cabrera et al. 2006). Optimization models are appealing because they generally require only a small amount of data, can be developed with mathematical elegance, and can often generate patterns that fit an intuitive understanding of ecohydrologic systems. However, they generally lack feedbacks between water, carbon, and nutrient cycles such that, for instance, root growth is enabled to sustain  $E_{\rm c}$  without concomitant carbon and nutrients "costs" to the plant. One promising development in the equilibrium approach is that of D'Odorico et al. (2003) who incorporated below ground nutrient responses to soil water. However, their approach still did not couple below and above ground processes, which would tend to impart memory effects of the soil biogeochemistry on the vegetation while at same time adjusting over the long-term to the development of vegetation

Global climate change dictates that an understanding of coupled hydrologic and ecological processes requires long-term memory effects involving transient system evolution in a broad range of climates and biomes. Ecohydrologic research on this front has been slower to develop. primarily because of a lack of data. A few models that feature long-term memory with planthydrology feedbacks (e.g., Running and Gower 1991) have been incorporated into global (e.g., Foley et al. 1996, Running and Hunt 1993) and watershed models (e.g., Band and Tague 2004, Mackay and Band 1997, Vertessy et al. 1996) to understand biogeographic responses of vegetation to climatic and topographic controls (Kim and Eltahir 2004) and to deal with vegetation succession (Bond-Lamberty et al. 2005). A fundamental problem with simulating transience is the paucity of observational records that are sufficiently long to show, for example, inter-annual anomalies. Some long-term data sets do exist, such as the Long-Term Ecological Research Station network, flux tower networks, remote sensing records, and phenology networks. However, with the exception of remote sensing, most long-term observations are limited in terms of spatial extent, such as single stands (Dunn et al. 2007), and so their relevance to regional or global scale is uncertain. Over the next 20 years, with sufficient funding, some of the shortterm data sets may become multi-decadal, which should help. However, multi-site data will need to be assimilated in future ecohydrologic studies at regional and larger scales, and this is going to require greater reliance on cyber-infrastructure to more seamlessly integrate diverse data sets. While "eco-hydro-informatics" is not necessarily unique in its need for improved data and model infrastructure, it does span types of data not typically employed in hydrologic research, such as below ground carbon and nutrient accounting. As such, new enabling technologies are needed that build in the intelligence to deal with "knowledge" that extends beyond the traditional sphere of hydrology. Moreover, maximum benefits will be gained from this knowledge only once we are able to explicitly deal with spatial continua of biological and hydrological interactions.

Finally, much of the structure and function of

ecosystems is based on disturbance regime, and the transient recovery from disturbances of varying magnitudes. The effect of fire, harvest and numerous other disturbance sources on watershed hydrology are not adequately handled by ecohydrologic analysis and models based on equilibrium concepts. Direct coupling of disturbance regimes into ecohydrologic analysis is critical.

### **Research Challenge: Spatial Heterogeneity**

Hydrological models incorporate parameterized vegetation (e.g., Entekhabi and Eagleson 1989, Wood et al. 1992), assume potential vegetation (e.g., Dickinson 1984, Foley 1996, Pielke and Avissar 1990, Sellers 1986), or model vegetation dynamics (e.g., Foley et al. 2000, Mackay and Band 1997, Vertessy et al. 1996). However, these models rely on measurements made in stands. Indeed, the traditional stand/gap approach to both measuring and modeling fluxes in vegetative communities has been to identify centers of relatively homogeneous ecosystem types, make flux measurements, and then apply mechanisms learned in these plots to whole landscapes or larger scales (e.g., Mackay et al. 2002). This unnecessary simplification ignores changes in vegetation function along gradients, promotes classification of vegetation in terms of potential vegetation, and ignores important feedbacks between the terrestrial biosphere and climate, and between adjacent vegetation patches connected along hydrologic flow paths. Given present-day and future climate and land use changes, it is conceptually appealing to think of all terrestrial ecosystems as transitional in space. There is also a growing recognition that spatial variation of water storage and fluxes (e.g., Grayson et al. 1997, 2002, Seyfried and Wilcox 1995, Tromp-van Meerveld and McDonnell 2006) is critical to understanding hydrologic path ways. Future ecohydrologic research must embrace spatial variability and move beyond the use of unrealistic vegetative boundaries. Recently, Adelman et al. (2008) for a lodgepole pine-covered slope in southern Wyoming, and Loranty et al. (2008) for an aspen-wetland gradient in northern Wisconsin, have shown that spatial variability of tree transpiration changes with environmental



**Figure 2**. Relativized variograms of tree transpiration from among 120 trees in an aspen-wetland transition. Based on a figure in Loranty et al. (2008).

drivers. Figure 2 illustrates the increase in spatial heterogeneity as transpiration increases, a response attributable to spatial variability in biological responses. Such feedbacks between plants and water flux rates suggest non-linearities that are lost in the homogenization that occurs with traditional center-of-stand methodology.

The patch-based approaches to ecohydrologic systems also do not allow the investigation of spatial dependency in the form of soil-vegetation catenae along hydrologic flow paths. In more humid environments, where lateral redistribution of soil and ground water are significant, the behavior of hill slope and catchment ecosystems may not be generalized as the sum of discrete ecosystem patch behavior because one-dimensional mass balance approaches cannot capture emergent patterns in ecosystem form and function, or in runoff production. Lateral redistribution of soil water creates heterogeneity in biogeochemical and soil water effects on canopy physiology, and generally tends to dampen temporal variability of ecohydrologic flux while maintaining spatial variability (e.g., Band et al. 1993). Future work will incorporate and develop methods of estimating the effects of heterogeneity through spatially explicit simulation, as has already been done, and by developing statistical-dynamic methods for estimating growth and decay of hydrologic heterogeneity (e.g., Albertson and Montaldo 2003).

This spatially explicit measurement and modeling

approach needs to be employed in a variety of ecosystems, and over longer time periods than are possible with single projects. While such efforts are laborious, new developments in automated sensor networks using wireless technology should make spatially explicit ecohydrologic measurements feasible. Moreover, a true move to a mechanistic understanding of ecohydrologic processes will in the next few years embrace spatially explicit genetics. With the sequencing of genetic code for tree species (e.g., populous) and identification of genes specifically responsible for controlling plant water use (e.g., Cao et al. 2007) the next 20 years of ecohydrologic research will definitely be dominated by molecular biological research and will almost certainly require a genetic component.

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#### References

- Addington, R. N., R. J. Mitchell, R. Oren, and L. A. Donovan. 2004. Stomatal sensitivity to vapor pressure deficit and its relationship to hydraulic conductance in *Pinus palustris*. *Tree Physiology* 24: 561-569.
- Adelman, J. D., B. E. Ewers, and D. S. Mackay. 2008. Using temporal patterns in vapor pressure deficit to explain spatial autocorrelation dynamics in tree transpiration. *Tree Physiology* 28: 647-658.

- Albertson, J. D. and N. Montaldo. 2003. Temporal Dynamics of Soil Moisture Variability: 1. Theoretical Basis, *Water Resources Research* 39 (10): 1274, doi:10.1029/2002WR001616.
- Anderson, M. C., W. P. Kustas, and J. M. Norman. 2007. Upscaling flux observations from local to continental scales using thermal remote sensing. *Agronomy Journal* 99: 240-254.
- Arris, L. L. and P. S. Eagleson. 1994. A water use model for locating the boreal/deciduous forest ecotone in eastern North America. *Water Resources Research* 30(1): 1-9.
- Band, L.E., P. Patterson, R.R. Nemani and S.W. Running, 1993. Forest ecosystem processes at the watershed scale: 2. Adding hillslope hydrology. *Agricultural* and Forest Meteorology 63: 93-126.
- Band, Lawrence E. and C. Tague. 2004. Feedbacks and coupling between water, carbon and nutrient cycling at the hillslope scale. Pages 269-279 in Axel Bronstert, J. Carrera, P. Kabat, and S. Lütkemeier (eds.) *Coupled Models for the Hydrological Cycle -Integrating Atmosphere, Biosphere, and Pedosphere.* Springer-Verlag, 2004.
- Band, L. E., F. Ogden, J. Butler, D. Goodrich, R. Hooper, D. Kane, D. McKnight, N. Miller, M. Williams, K. Potter, B. Scanlon, R. Pielke, and K. Reckhow. 2002. *Hydrologic Observatories*, CUAHSI Technical Report Number 4, August 2002, Washington D.C.
- Bond-Lamberty, B., S. T. Gower, D. E. Ahl, and P. Thornton. 2005. Reimplementation of the Biome-BGC model to simulate successional change. *Tree Physiology* 25(4): 413-424.
- Brodribb T. J. and T. S. Field. 2000. Stem hydraulic supply is linked to leaf photosynthetic capacity: Evidence from new caledonian and tasmanian rainforests. *Plant Cell & Environment* 23: 1381-1388.
- Brodribb T. J., N. M. Holbrook, and M. V. Gutierrez. 2002. Hydraulic and photosynthetic co-ordination in seasonally dry tropical forest trees. *Plant Cell & Environment* 25: 1435-1444.
- Cao, H.-X., Z.-B. Zhang, P. Xu, L.-Y. Chu, H.-B. Shao, Z.-H. Lu, and J.-H. Liu. 2007. Mutual physiological genetic mechanism of plant high water use efficiency and nutrition use efficiency. *Colloids and Surfaces B: Biointerfaces* 57: 1-7.
- Collins, D. B. G. and R. L. Bras. 2007. Plant rooting

strategies in water-limited ecosystems. *Water Resources Research* 43: W06407, doi:10.1029/2006WR005541.

- Dickinson, Robert E. 1984. Modeling evapotranspiration for three-dimensional climate models. Pages 58-72 in J.E. Hanson and T. Takahashi (eds.) *Climate Processes and Climate Sensitivity*. Geophysical Monographs Series 29, American Geophysical Union: Washington D.C.
- Dickinson, R. E., M. Shaikh, R. Bryant, and L. Graumlich. 1998. Interactive canopies in a climate model. *Journal of Climate* 11: 2823-2836.
- D'Odorico, P., F. Laio, A. Porporato, and I. Rodriguez-Iturbe. 2003. Hydrologic controls on soil carbon and nitrogen cycles. II. A case study. *Advances in Water Resources* 26: 59-70.
- Dunn, A. L., C. C. Barford, S. C. Wofsy, M. L. Goulden, B. C. Daube. 2007. A long-term record of carbon exchange in a boreal black spruce forest: means, responses to interannual variability, and decadal trends. *Global Change Biology* 13(3): 577–590, doi:10.1111/j.1365-2486.2006.01221.x.
- Eagleson, P. S. 1982. Ecological optimality in waterlimited natural soil-vegetation systems. 1. Theory and hypothesis. *Water Resources Research* 18: 325-340.
- Eagleson, P. S. 2002. *Ecohydrology: Darwinian Expression of Vegetation Form and Function*. Cambridge University Press: Cambridge, UK.
- Ehtekhabi, D. and P. Eagleson. 1989. Landsurface hydrology parameterization for atmospheric circulation models including subgrid variability. *Journal of Climate* 2: 579-589.
- Ewers, B. E., S. T. Gower, B. Bond-Lamberty, and C. Wang. 2005. Effects of stand age and tree species composition on transpiration and canopy conductance of boreal forest stands. *Plant Cell & Environment* 28: 660-678.
- Ewers, B. E., D. S. Mackay, and S. Samanta. 2007. Interannual consistency in canopy stomatal conductance control of leaf water potential across seven tree species. *Tree Physiology* 27: 11-24.
- Ewers, B. E., R. Oren, N. Phillips, M. Stromgren, and S. Linder. 2001. Mean canopy stomatal conductance responses to water and nutrient availabilities in *Picea abies* and *Pinus taeda*. *Tree Physiology* 21: 841-850.

- Foley, J. A., S. Levis, M. H. Costa, W. Cramer, and D. Pollard. 2000. Incorporating dynamic vegetation cover within global climate models. *Ecological Applications* 10(6): 1620-1632.
- Foley, J. A., I. C. Prentice, N. Ramankutty, S. Levis, D. Pollard, S. Sitch, and A. Haxeltine. 1996. An integrated biosphere model of land surface processes, terrestrial carbon balance, and vegetation dynamics. *Global Biogeochemical Cycles* 10(4): 603-628.
- Grace, J., C. Nichol, M. Disney, P. Lewis, T. Quaife, and P. Bowyer. 2007. Can we measure terrestrial photosynthesis from space directly, using spectral reflectance and fluorescence? *Global Change Biology* 13(7): 1484-1497.
- Grayson, R. B., G. Bloschl, A. W. Western, and T. A. McMahon. 2002. Advances in the use of observed spatial patterns of catchment hydrological response. *Advances in Water Resources 25*(8-12): 1313-1334.
- Grayson, R. B., A.W. Western, and F. H. S. Chiew. 1997. Preferred states in spatial soil moisture patterns: Local and nonlocal controls. *Water Resources Research* 33(12): 2897-2908.
- Grier, C. C. and S. W. Running. 1977. Leaf area of mature northwestern coniferous forests: Relation to site water balance. *Ecology* 58: 893-899.
- Gupta, H. V., S. Sorooshian, and P. O. Yapo. 1999. Status of automated calibration for hydrologic models: Comparison with multilevel expert calibration. *ASCE Journal of Hydrologic Engineering* 4(2): 135-143.
- Hashimoto, H., J. L. Dungan, M. A. White, F. Yang, A. B. Michaelis, S. W. Running, and R. R. Nemani. 2008. Satellite-based estimation of surface vapor pressure deficits using MODIS land surface temperature data. *Remote Sensing of Environment* 112(1): 142-155.
- Hornberger, G. M., J. D. Aber, J. Bahr, R. C. Bales, K. Beven, E. Foufoula-Georgiou, G. Katul, J. L. Kinter III, R. D. Koster, D. P. Lettenmaier, D. McKnight, K. Miller, K. Mitchell, J.O. Roads, B.R. Scanlon, and E. Smith. 2001. A Plan for a New Science Initiative on the Global Water Cycle, U.S. Global Change Research Program, Washington, D.C. 118 pages.
- Jackson, R. B., J. Canadell, E. R. Ehleringer, H. A. Mooney, O. E. Sala, and E. D. Schulze. 1996. A global analysis of root distributions for terrestrial biomes. *Oecologia* 108: 398-411.
- Kergoat, L. 1998. A model for hydrological equilibrium of leaf area index on a global scale, *Journal of*

Hydrology 212/213: 268-286.

- Kim, Y. and E. A. B. Eltahir. 2004. Role of topography in facilitating coexistence of trees and grasses within savannas. *Water Resources Research* 40: W07505, doi:10.1029/2003WR002578.
- Klemeš, V. 1986. Dilettantism in hydrology: Transition or destiny? *Water Resources Research* 22(9S): 177S-188S.
- Loranty, M. M., D. S. Mackay, B. E. Ewers, J. D. Adelman, and E. L. Kruger. 2008. Environmental drivers of spatial variation in whole-tree canopy transpiration and canopy average stomatal conductance in an aspen-to-wetland forest gradient. *Water Resources Research* 44: W02441, doi:10.1029/ 2007WR006272.
- Loveland, T. R. and A. S. Belward. 1997. The IGBP-DIS global 1-km land cover data set, DISCover: First results. *International Journal of Remote Sensing* 18: 3289-3295.
- Mackay, D. S. 2001. Evaluation of hydrological equilibrium in a mountainous watershed: incorporating forest canopy spatial adjustment to soil biogeochemical processes. *Advances in Water Resources* 24: 1211-1227.
- Mackay, D. S., D. E. Ahl, B. E. Ewers, S. T. Gower, S. N. Burrows, S. Samanta, and K. J. Davis. 2002. Effects of aggregated classifications of forest composition of estimates of evapotranspiration in a northern Wisconsin forest. *Global Change Biology* 8(12): 1253-1265.
- Mackay D. S., D. E. Ahl, B. E. Ewers, S. Samanta, S. T. Gower, and S. N. Burrows. 2003. Physiological tradeoffs in the parameterization of a model of canopy transpiration. *Advances in Water Resources* 26: 179-194.
- Mackay, D. S. and L. E. Band. 1997. Forest ecosystem processes at the watershed scale: Dynamic coupling of distributed hydrology and canopy growth. *Hydrological Processes* 11: 1197-1217.
- Maidment, D. R. 2008. Bringing water data together. Journal of Water Resources Planning and Management 134(2): 95-96.
- Nemani, R. R. and S.W. Running. 1989. Estimation of regional surface resistance to evapotranspiration from NDVI and thermal-IR AVHRR data. *Journal of Applied Meteorology* 28(4): 276-284.

Newman, B. D., B. P. Wilcox, S. R. Archer, D. D.

Breshears, C. N. Dahm, C. J. Duffy, N. G. McDowell, F. M. Phillips, B. R. Scanlon, and E. R. Vivoni. 2006. Ecohydrology of water-limited environments: A scientific vision. *Water Resources Research* 42, W06302, doi:10.1029/2005WR004141.

- Oren, R., J. S. Sperry, G. G. Katul, D. E. Pataki, B. E. Ewers, N. Phillips, and K.V. R. Schäfer. 1999. Survey and synthesis of intra- and interspecific variation in stomatal sensitivity to vapour pressure deficit. *Plant, Cell and Environment* 22: 1515-1526.
- Pettijohn, J. C. and G. D. Salvucci. 2006. Impact of an unstressed canopy conductance on the Bouchet-Morton complementary relationship. *Water Resources Research* 42: W09418, doi:10.1029/ 2005WR004385.
- Pielke, R. A. and R. Avissar. 1990. Influence of landscape structure on local and regional climate. *Landscape Ecology* 4(2/3): 133-155.
- Rodriguez-Itube, I. 2000. Ecohydrology: A hydrologic perspective of climate-soil-vegetation dynamics. *Water Resources Research* 36: 3-9.
- Rodríguez-Iturbe, I., P. D'Odorico, A. Porporato, and L. Ridolfi. 1999. Tree-grass coexistence in savannas: The role of spatial dynamics and climate fluctuations *Geophysical Research Letters* 26(2): 247-250.
- Running, S. W. and S. T. Gower. 1991. FOREST-BGC, a general model of forest ecosystem processes for regional applications II. Dynamic carbon allocation and nitrogen budgets. *Tree Physiology* 9: 147-160.
- Running, Steven. W. and E. R. Hunt, Jr. 1993. Generalization of a forest ecosystem process model for other biomes, BIOME-BGC, and an application for global scale models. Pages 141-158 in James R. Ehleringer and C.B. Field (eds.) *Scaling Physiological Processes: Leaf to Globe*, Academic Press: San Diego, CA.
- Running, S. W., T. R. Loveland, L. L. Pierce, R. R. Nemani, and E. R. Hunt, Jr. 1995. A remote sensing based vegetation classification for global land cover analysis. *Remote Sensing of Environment*, 51: 39-48.
- Samanta, S., D. S. Mackay, M. Clayton, E. L. Kruger, and B. E. Ewers. 2007. Bayesian analysis for uncertainty estimation of a canopy transpiration model. *Water Resources Research* 43: W04424, doi:10.1029/2006WR005028.
- Sellers P. J., S. O. Los, C. J. Tucker, C. O. Justice, D.

A. Dazlich, G. J. Collatz, and D. A. Randall. 1996. A revised land surface parameterization (SiB2) for atmospheric GCMs. Part II: The generation of global fields of terrestrial biophysical parameters from satellite data. *Journal of Climate* 9: 676-705.

- Sellers, P. J., Y. Mintz, Y. C. Sud, and A. Dalcher. 1986. A simple biosphere model (SiB) for use within general circulation models. *Journal of Atmospheric Science* 43: 505-531.
- Seyfried, M. S. and B. P. Wilcox. 1995. Scale and the nature of spatial variability: Field examples having implications for hydrologic modeling. *Water Resources Research* 31(1): 173-184.
- Sivapalan, M., K. Takeuchi, S. W. Franks, V. K. Gupta, H. Karambiri, V. Lakshmi, X. Liang, J. J. McDonnell, E. M. Mendiondo, P. E. O'Connell, T. Oki, J. W. Pomeroy, D. Schertzer, S. Uhlenbrook, and E. Zehe. 2003. IAHS decade on prediction in ungauged basins (PUB), 2003-2012: Shaping an exciting future for the hydrological sciences. *Hydrological Sciences Journal* 48(6): 857-880.
- Sperry, J. S., F. R. Adler, G. S. Campbell, and J. P. Comstock. 1998. Limitation of plant water use by rhizosphere and xylem conductance: Results from a model. *Plant Cell & Environment* 21: 347-359.
- Tromp-van Meerveld, H. J. and J. J. McDonnell. 2006. On the interrelations between topography, soil depth, soil moisture, transpiration rates and species distribution at the hill slope scale. *Advances in Water Resources* 29(2): 293-310.
- Tyree, M. T. and J. S. Sperry. 1989. Vulnerability of xylem cavitation and embolism. *Annual Reviews of Plant Physiology and Plant Molecular Biology* 40: 19-38.
- van Wijk, M. T. and W. Bouten. 2001. Towards understanding tree root profiles: Simulating hydrologically optimal strategies for root distribution. *Hydrology and Earth Systems Sciences* 5(4): 629-644.
- Vertessy, R. A., T. J. Hatton, R. G. Behyon, and W. R. Dawes. 1996. Long-term growth and water balance predictions for a mountain ash (*Eucalyptus regnans*) for catchments subject to clear-felling and regeneration. *Tree Physiology* 16: 221-232.
- Wood, E. F., D. P. Lettenmaier, and V. Zartarian. 1992. A land surface hydrology parameterization with sub-grid variability for general circulation models. *Journal of Geophysical Research* 97(D3): 2717-2728.

- Wullschleger, S. D., C. A. Gunderson, P. J. Hanson, K. B. Wilson, and R. J. Norby. 2002. Sensitivity of stomatal and canopy conductance to elevated CO<sub>2</sub> concentration-interacting variables and perspectives of scale. *New Phytologist* 153: 485-496.
- Zea-Cabrera, E., Y. Iwasa, S. Levin, and I. Rodriguez-Iturbe. 2006. Tragedy of the commons in plant water use. *Water Resources Research* 42: W06D02, doi:10.1029/2005WR004514.