Ecohydrology: A hydrologic perspective of climate-soil-vegetation dynamics

I. Rodriguez-Iturbe

Department of Civil and Environmental Engineering and Center for Energy and Environmental Studies Princeton University, Princeton, New Jersey

Abstract. The hydrologic mechanisms underlying the climate-soil-vegetation dynamics and thus controlling the most basic ecologic patterns and processes are described as one very exciting research frontier for the years to come. In this personal opinion I have concentrated on those processes where soil moisture is the key link between climate fluctuations and vegetation dynamics in space and time. The soil moisture balance equation at a site is shown to be the keystone of numerous fundamental questions which may be instrumental in the quantitative linkage between hydrologic dynamics and ecological patterns and processes. Some of those questions are outlined here, and possible avenues of attack are suggested. The space-time links between climate, soil, and vegetation are also explored from the hydrologic perspective, and some exciting research perspectives are outlined.

It is a great thing for us to carry on the tradition of holding nature up to examination, of asking again and again why it is the way it is.

[Weinberg, 1994, p. 275]

Imagination is more important than knowledge.

[Einstein, 1996, p. 223]

1. Introduction

To write about the future of hydrologic research is a challenge that makes one think beyond short-term issues related to funding and popularity. It is obviously impossible to be very specific when guessing where the excitement is going to be. However, to talk only of generalities applicable to any area of the field or even outside hydrology is useless in a piece such as this.

Rather than trying to describe a number of problems in different areas which are interesting and waiting to be tackled, I believe that the objective of this opinion will be better served by addressing a whole area which I feel does not occupy, yet, the central role it should have in hydrologic research. I am referring to what I will call ecohydrology, where I believe we will see major breakthroughs and intensive activity in the next decade. In my opinion much of the research in hydrology has been unconnected to the particular ecological characteristics which make regions different from one

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another. The interplay between climate, soil, and vegetation cannot be one of general and universal characteristics. The dynamics of the interactions is crucially influenced by the scale at which the phenomena are studied as well as by the physiological characteristics of vegetation, the pedology of the soil, and the type of climate. This obvious fact is, nevertheless, one that is seldom made explicit in hydrologic research. Moreover, not only the temporal aspects but also the spatial aspects of the dynamics are crucially dependent on the above factors. Thus the climate-soil-vegetation dynamics, the core of hydrology itself, is fundamentally different between, say, forests, savannas, and grasslands. Unfortunately, we seldom emphasize those characteristics that make a biome what it is, and even less frequently do we relate hydrologic dynamics to such specific aspects which, in fact, control the space-time response and evolution of the region. I believe that the spatiotemporal linkage between the hydrologic and ecologic dynamics will be one of the most exciting frontiers of the future. It is full of challenging and unexplored questions which go to the heart of hydrology and which are of fundamental importance for understanding the environment in which we live and the state in which it will be inherited by future generations. Ecohydrology may be defined as the science which seeks to describe the hydrologic mechanisms that underlie ecologic patterns and processes. I do not intend to provide a full review of the extraordinarily wide range of challenges existing in

ecohydrology; instead, I will concentrate on the climate-soil-vegetation interaction in regions where water is a controlling factor.

2. Hydrology's Most Basic Equation: Questions and Challenges

The fundamental equation in hydrology is likely to be the soil moisture balance equation which in absence of pronounced topographical effects can be written at a point as

$$nZ_r \frac{ds}{dt} = I(s, t) - E(s, t) - L(s, t),$$
(1)

where n is the soil porosity, Z_r is the depth of the soil, s is the relative soil moisture content, I(s,t) is the infiltration into the soil, E(s,t) is the evapotranspiration, and L(s,t) is the leakage or deep infiltration. Although apparently simple, (1), nevertheless, presents serious challenges when the terms in the right-hand side are considered dependent on the state s. Indeed, how much infiltrates, evapotranspires, and leaks depends on the soil moisture present in the soil both when precipitation occurs and between storm periods.

Precipitation, rainfall in this paper, is the driving factor of the dynamics, and its basic random nature makes (1) a stochastic differential equation. How one describes the different terms in the balance depends on the timescale under consideration. When the interest lies in

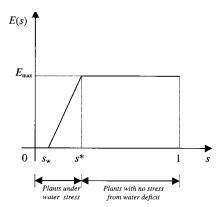


Figure 1. Schematic representation of the dependence of evapotranspiration on relative soil moisture.

the dynamic interaction between climate, soil, and vegetation, the intermittency of rainfall and its most relevant features need to be incorporated into the mechanisms which produce I(s, t). Thus climate, most crucially during the growing season, needs to be described in terms of the frequency and characteristics of the storm events whose stochastic character may itself vary from year to year. These tasks embody extensive data analyses as well as probabilistic modeling yet to be performed. Moreover, we need to do it for a number of climatic regions occupied by different biomes. The infiltration term, I(s, t), in (1) depends on s because even assuming that surface runoff occurs only because of saturation from below, the amount of infiltration from a particular storm cannot exceed the available void volume in the soil. This dependence of I(s, t) both on the stochastic characteristics of the rainfall input and on the soil moisture state adds considerable richness to the dynamics.

The evapotranspiration term has the general form shown in Figure 1. For soilplant-climate interaction it is crucial to realize the full dependence of that graph on the vegetation and soil characteristics. Thus the wilting point and the soil moisture below which the plant transpires at less than its maximum value depend on the type of vegetation at the site. This is also true for the maximum unstressed value of evapotranspiration. Under the same climatic conditions and even under similar soil environments, Figure 1 may be quite different, say, for woody and for herbaceous vegetation. These differences play a key role in the stress the plant undergoes because of water limitations and have a direct impact on the spatial interaction between

vegetation at neighboring sites. The leakage is commonly modeled as $K_s s^c$, where K_s is the saturated hydraulic conductivity and the exponent c depends on the type of soil.

The final product from (1) is the probabilistic description of soil moisture at a point as a function of climate, soil, and vegetation. The description involves both the probability distribution of s as well as its correlation structure in time. We cannot expect to attempt space-time modeling of soil moisture if we still lack a comprehensive description for the dynamics at a point. Considerable progress has certainly been accomplished on this topic, but there still remains much to be done both in modeling and in data collection and analysis. These two efforts should proceed in parallel to avoid on the one hand that modeling schemes get either unrealistically oversimplified or so enormously complex that they shed little light on a unifying picture and to assure, on the other hand, that there is an effective feedback between observations and theory.

It is only very recently [Rodriguez-Iturbe et al., 1999] that the steady state probability density function of soil moisture at a point described by (1) has been obtained for rainfall of random and intermittent characteristics when both the infiltration as well as the losses depend on the state of the system in a nonlinear manner. The crucially interesting case incorporating moisture flow due to gravity effects from higher neighboring points is still unsolved. Its solution will provide the probability distribution of soil moisture integrated vertically at a given point on a hillslope under realistic conditions of rainfall input and evapotranspiration losses. One could then foresee viable attempts to link the spatial structure of the soil moisture field and its inherent temporal fluctuations with the organization and scaling that has been found and has been, indeed, successfully modeled in the interlocked system of hillslopes and channels which make up the river basin. This approach will blend in a natural manner the temporal and spatial dynamics of the process, accounting at the same time for the stochastic fluctuations in precipitation and for the statistical geometry of the basin. The transient probability density function for soil moisture is not available under the framework described before. This function will allow the study of the probabilistic evolution of soil moisture throughout the growing season as a function of

time and initial soil water content. The different impacts of wet and cold versus warm and dry winters on the structure and patterns of vegetation could then be attempted under a quantitative hydrologic framework.

A preliminary attempt to uncover the effects of climate fluctuations on the probabilistic structure of soil moisture will naturally follow from the solution of (1). Thus rather than considering as constant the parameters controlling the precipitation process, for example, rate of arrivals of storms, mean storm depth, etc., one may see them as random variables which change throughout time, say, from year to year and whose own fluctuations dramatically impact the soil moisture structure through their effect on the infiltration term. Thus even in the most simple case of the dynamics of soil moisture at a point, the probability distribution of the moisture content may undergo changes not only of quantitative character but may also become qualitatively affected, for example, changing from unimodal to bimodal, because of parameter fluctuations in the rainfall input. These drastic shifts in the behavior of the process at a site due to climate fluctuations may have very important implications for the existing vegetation which will increase or decrease the rate of some physiological processes (e.g., growth or photosynthesis) depending on the fluctuations of soil moisture.

It is a challenge for hydrologists to explain the effects of low water availability under naturally varying random conditions on the productivity of natural ecosystems. Although water is by no means the only controlling resource, it is, indeed, one that plays a crucial role because of its major impact on all physiological processes and because of the relatively large quantities of water required for the proper functioning of plants. Even the effects of temperature are partly exerted through processes related to water because of the dependence of evapotranspiration on temperature [Lambers et al., 1998]. It is not sufficient to perform the analyses under annually or seasonally averaged climatic conditions; the effect of environmental fluctuations both within the year and between different years is of fundamental importance in the quantitative description of vegetation dynamics. Much research needs to be carried out on the soil moisture dynamics at a site with realistic descriptions of the stochastic nature of the precipitation process, the infiltration dynamics, and the dependence of evapotranspiration losses on the vegetation being considered.

The spatial structure of soil moisture and its evolution in time is also cause and consequence of the regional vegetation. It is important for hydrologists to be heavily involved in research concerning the use of water by different kinds of vegetation and its relation to soil and climatic factors. Thus, for example, it has been frequently argued that trees and grasses have preferential use of different kinds of moisture in the soil, trees being able to extract water from deep soil layers and grasses being effective in the use of shallow soil moisture. This so-called Walter hypothesis is used then as a general mechanism to explain the presence and coexistence of woody and herbaceous plants. There is little doubt that the differential water use implied by the Walter hypothesis exists in regions which, as an example, have relatively cold winter seasons with abundant precipitation. In this case, water will be able to infiltrate to deeper layers where it will be available for use during the warm growing season. Nevertheless, many savannas of the world are characterized by a hot, wet, growing season followed by a dry and warm winter, and thus there is no opportunity for water to infiltrate into deep layers [Scholes and Walker, 1993]. In these cases, plants compete for the same resource, usually the moisture in the shallow layers of the soil. Thus the Walter hypothesis cannot be invoked as a general mechanism for the explanation of the coexistence of trees and grasses. A fact that has been experimentally verified through the root zone coverage of these plants in many savannas [Scholes and Walker, 1993].

The above example clearly shows the commanding role of space-time hydrological dynamics in the establishment of many ecological patterns. This dynamics is also intimately linked to the competitive aspects of plant reproduction. Thus, for example, large interannual fluctuations in rainfall frequently driving the level of soil moisture below the wilting point of the existing vegetation will tend to favor the existence of grasses which reproduce faster than woody plants. Trees, although more resistant to drought conditions, once they die need to undergo a much longer period before they are competitive in reproductive terms. During this period the seedlings are highly vulnerable to both climate fluctuations and competition from other

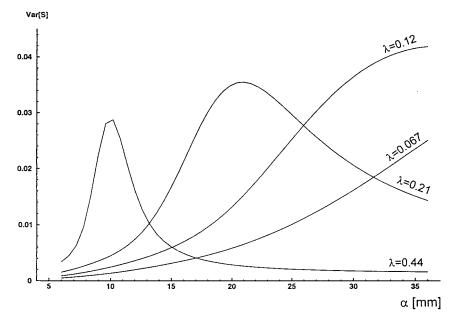


Figure 2. Variance of soil moisture shown as function of the rate of arrivals of storms (per day) and average storm depth (millimeters) for the following parameters corresponding to soil and vegetation: $K_s = 800 \text{ mm d}^{-1}$, $s^* = 0.35$, nZr = 40 cm, $E_{\text{max}} = 4.5 \text{ mm d}^{-1}$ [from *Rodriguez-Iturbe et al.*, 1999].

plants. All these dynamics need to be quantitatively described and linked to the driving hydrologic processes. An example of this is the insight that can be derived from the variance of the soil moisture process as described by (1).

Figure 2 shows Var[s] as function of the rate of arrival and the mean depth of storms, λ and α , respectively, for soil and vegetation characteristics corresponding to the plants of southern Texas. Notice the drastic changes affecting Var[s] in its functional dependence on climate. There are many combinations of λ and α for which Var[s] shows a pronounced peak, implying significant fluctuations of the soil moisture for relatively small changes in the rainfall regime. As discussed above, this has serious and varied implications for the adaptability of different species of plants.

The incorporation of the effect of climatic fluctuations on the temporal and spatial dynamics of vegetation needs to account for the physiologic characteristics of the existing plants and needs also to be connected with the soil properties of the region. Even if one deals with a homogeneous region from the rainfall perspective at a seasonal timescale, soil and vegetation, nevertheless, involve random fields of parameters which make attacking the problem both challenging and fascinating.

3. Space-Time Links Between Climate, Soil, and Vegetation

Satellite measurements, as well as a variety of other remote sensing data, are providing us with a wealth of information about the spatiotemporal evolution of vegetation at different scales and under different climatic conditions. Thus satellite-based measurements of reflectance in the near-infrared and in the visible spectra are being used in the estimation of the normalized difference vegetation index, which is, in turn, a good predictor of the net primary productivity (net biomass gain by vegetation by unit time, g C m⁻² yr⁻¹). It is my belief that in order to effectively orient the collection and processing of the large spatial data sets generated through the above techniques much research needs to be carried out in the development of models which effectively represent the space-time dynamic interaction between climate, soil, and vegetation. In regions where water is the controlling factor, the above interaction necessarily passes through the space-time dynamics of soil moisture. At regional scales it is necessary that we represent the competition or interaction between a typical site and its neighbors. A site is thus understood to have a size approximately equal to the space occupied by a typical woody plant (e.g., a few meters of characteristic length). Thus, in most general terms one

could think that in many regions a site may be occupied by a woody plant, by grass, or by bare soil.

At regional scales of sizes as described above, I believe that a promising approach is to tackle the modeling through cellular automata type of schemes. It is necessary to represent the variability in soil conditions from site to site as well as the stochastic character of the precipitation input. Moreover, different plant types will experience different stress conditions and use different rates of the resource for their transpiration needs. All of the above coupled with the need to represent the competition for soil moisture among neighboring sites which may have such different characteristics makes any modeling attempt a challenging task. Cellular automata appear especially attractive for the representation of this dynamics. The probabilistic characterization of the soil moisture at a single site with given soil and vegetation conditions may be used as the starting description from where competition among neighbors then proceeds. The temporal evolution may be represented by the random climatic conditions which characterize the growing seasons of consecutive years. In this manner, time and space are naturally linked in the evolutionary dynamics of the climate-soil-vegetation interaction at the regional scale.

Ecologists have developed a variety of models for the evolution of competing vegetation which incorporate spatial dynamics. Nevertheless, most, if not all, of those models operate based on a set of probabilities controlling birth, death, and colonization which have no objective modelistic linkage with the characteristics of soil and climate fluctuations. Hydrology has an exciting and little explored frontier in this topic. Thus one could think that the birth, death, and reproduction of plants could be made explicitly dependent on the climate-soilvegetation relationship. As an example, consider the evolution of soil moisture as function of time at a specific site. The crossing characteristics of this process could be studied under a simplified framework appropriate for a daily timescale. Considering a homogeneous growing season, rainfall could be modeled as a marked Poisson process whose parameters change from year to year. The evolution of soil moisture is then described by (1). The crossing aspects of two particular levels are of special relevance: (1) those related to the wilting point s_w of vegetation at the site and (2) those cor-

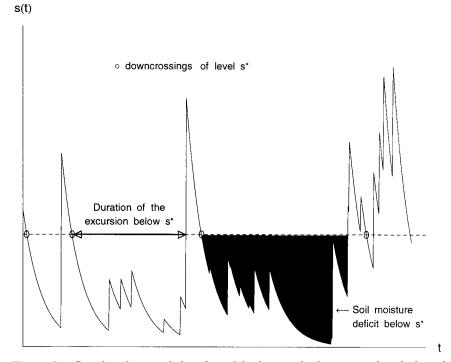


Figure 3. Crossing characteristics of special relevance in the temporal evolution of soil moisture content.

responding to the level $s = s^*$ in Figure 1, where s^* represents the soil moisture content below which the plant is under water-related stress. Three kinds of crossing-related random variables are important: (1) the number of crossings of levels $s = s_w$ and $s = s^*$ in a given interval of time; (2) the duration of the excursions below those levels, and (3) the volume of soil moisture deficit during those excursions. They are shown in Figure 3. The probabilistic characterization of those random variables is a challenging analytical problem, but it will shed important light on the soil-plantclimate relationship at a site as well as on the spatial dynamics of soil moisture and vegetation. Thus one may think of a spatially evolutionary model where vegetation at each site dies if the mean time it spends below wilting point conditions is higher than a critical value which varies with the type of plant (e.g., tree or grass). Similarly, colonization of empty neighboring spaces could be made dependent on these crossing properties. A cellular automata could thus be built which although still simple in its structure will, nevertheless, incorporate objective climate-soil-vegetation interactive characteristics which themselves evolve in time according to the climatic fluctuations and the evolution of vegetation in the spatial domain.

Hydrology is also a key factor in other processes which have crucial consequences in ecologic dynamics. A most important example is the frequency, intensity, and spread of fires. All these are related to the rainfall regime and its natural fluctuations in several complicated ways. Moreover, the reduction of fire frequency or intensity results in an increase of woody plants and their biomass relative to that of grasses. This by itself has a direct impact on the regional evapotranspiration and on the spacetime dynamics of the soil water content. Fire propagation depends on the spatial patterns of vegetation which are, in turn, related to hydrology-controlled variables and to the past occurrence of fires. Carbon and elements bound to it such as nitrogen and phosphorous, which are needed for the growth of vegetation, are released to the atmosphere during fires, and thus their space-time dynamics is also affected by fires [Scholes and Walker, 1993]. Extensive quantitative research and modeling needs to be carried out linking in space and time vegetation, soil moisture, climate fluctuations, and fire. There are cellular automata for forest fires which could be linked to fundamental ecological and hydrological processes. One could also imagine ecohydrologic models such as the ones

described in this paper including the occurrence and effects of fires.

It is my belief that the above represents an exciting research area for fruitful interaction between ecologists and hydrologists. These phenomena are at the core of my definition of ecohydrology where the patterns of ecological processes are fundamentally dependent on the hydrologic dynamics of the region. We are attempting to model an open, dissipative system with a large number of elements interacting locally through a highly nonlinear dynamics which is itself driven by noisy environmental processes. Is there an emergence of global properties out of this dynamics (e.g., does the system self-organize)? Does it tend to any equilibrium values, for example, a relatively stable proportion of trees and grasses for the case of savannas, or, on the contrary, is the system always undergoing change with scaling properties in the frequency and magnitude of the changes? Is there a spontaneous emergence of spatial vegetation patterns associated with the temporal dynamics of the climatic fluctuations? Can we reproduce some of the observed, strikingly visual, patterns? Is there hidden order in the space-time evolution which models could help to uncover? Does the system evolve naturally, for example, without being explicitly directed to do so, to states which minimize regional water stress or that maximize biomass production?

A similar set of questions could be asked about the drainage network and its associated vegetation. The drainage network plays a fundamental role as the pattern which connects the different regions of the basin with the outlet and among themselves. In the three-dimensional structure of a plant the amount of biomass supported by the tree above a randomly chosen point in its structure is itself a random variable with an approximate power law distribution whose exponent changes from species to species. Does the biomass upstream of a point in a river network follow a similar type of statistical arrangement? If so, is it different from the distribution of the area draining through a randomly chosen point which has been found to be remarkably stable through a range of very different river basins? How does the three-dimensional organization implicit in a river basin and about which we have learned so much in recent years connect with the vegetation existing in the basin?

All of the above questions, and many

others, need to be tackled both theoretically and experimentally. As discussed earlier, theoretical modeling of the soil moisture dynamics can be immensely useful in pointing out directions of research, synthesis of results, discovery of hidden patterns, etc. Obviously, theoretical modeling has to go hand in hand with the analysis of real data which nowadays is becoming more and more available through different remote sensing techniques.

I do not want to finish this vision for the future without highlighting, in the context of the above discussion, the role of soil moisture as a crucial link between hydrological and biogeochemical processes. The complex interactions between chemical, biological, and hydrological processes occurring over any spatially extended region and most especially in river basins involve all kinds of possible dynamics operating on a wide range of temporal and spatial scales. Soil moisture is a key variable linking hydrologic and biogeochemical processes, and its study from this perspective offers new and exciting challenges to hydrologists. Figure 4 from Webb and Walling [1996] shows a simplified representation of these processes; I have added dashed lines to indicate the main interactions between the hydrologic and biogeochemical dynamics. Notice the key role of soil moisture in the weathering process involved in the release of solutes which are governed by the thermodynamics and kinetics of the reactions as well as by the residence time of water in the soil [Walling, 1980]. Moreover, the dynamics of nutrient uptake is also crucially controlled by chemical and biological processes where soil moisture plays a fundamental role. The incorporation of nutrients into biomass is intimately linked to the transpiration of the plant which is itself controlled by the soil water state. Thus water may be a controlling factor either because of its direct influence as in the metabolism of carbon through regulation of photosynthesis or because of indirect influence, for example, its dominant effect on nitrogen mineralization. In the latter case the rate of nitrogen mineralization increases as function of soil moisture until it reaches a maximum not unlike Figure 1 which describes the dependence of transpiration on soil moisture content. These types of dependence are so important that in biomes like savannas the linkage between rainfall and biomass production so widely observed probably operates

through the influence of soil moisture availability in the nitrogen and phosphorous cycles, which then constrain the carbon cycle [Scholes and Walker, 1993]. The key effect of the water being in this case is control of the available nitrogen rather than a direct effect on photosynthesis. The abundance of the nitrogen pool and other nutrients is itself spatially affected by the presence or absence of vegetation and by the type of plants. There is also a direct effect of surface runoff on the spatial dynamics of nutrients. Runoff may increase because of either more frequent and intense storms or because of loss of vegetation resulting from drought, fire, and grazing. As a consequence, the resulting locally increased runoff leads to the soil erosion and landscape incision with an increased transport of water, nitrogen, and other nutrients across different sites. The net effect of these fluxes is to increase the heterogeneity of the spatial distribution of soil moisture and nutrients through the region, leading to islands of fertility in otherwise arid regions [Schlesinger et al., 1990]. Again, one observes the crucial importance of hydrologic mechanisms in the above biogeochemical processes and the mutual feedbacks between the ecologic and the hydrologic dynamics. The space-time modeling of these interactions incorporating the most basic soil moisture balance dynamics under climate fluctuations, as described in section 2, is a frontier where major advances will be achieved during the next 5 years.

4. Final Comments

This paper is not a state of the art review nor a comprehensive and global perspective of the science of ecohydrology. That would be unfeasible here, and moreover, it would defeat the purpose of this "Vision for the Future." Thus, except for nitrogen mineralization, I have made almost no reference to processes involving animal dynamics, both aquatic and terrestrial, and their interaction with hydrologic mechanisms. This is not because they are not important, they are, but because in this vision paper I have preferred to concentrate on climate, soil, and vegetation. I have tried to give a personal perspective of some of the areas where I believe that major new and exciting discoveries will occur in the next 5 or 10 years. In some of these I have tried to point out research avenues that

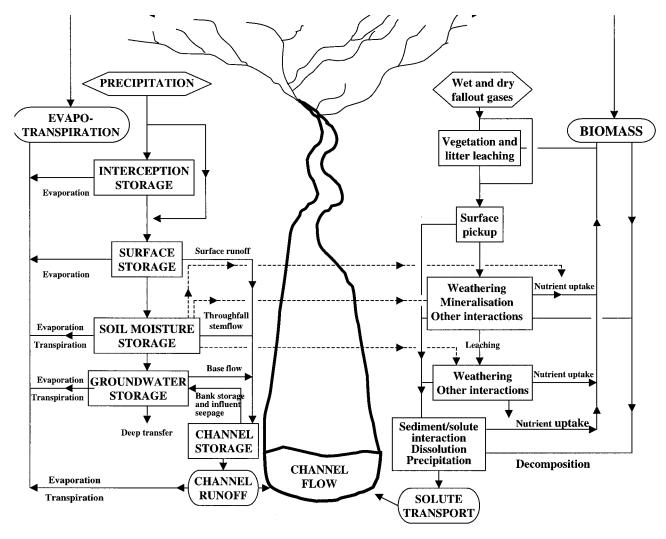


Figure 4. Simplified representation of the interaction of hydrological and biochemical processes operating in a drainage basin [from *Webb and Walling*, 1996].

may be useful for tackling the problems. If I find a unifying theme in the different research challenges I have presented here, it would be the necessity to gain a predictive understanding based on solid and quantitative scientific grounds of the responses of different biomes to a changing global environment. In many cases these responses are controlled by the underlying hydrologic dynamics or at least are crucially influenced by this dynamics. A common thread throughout has also been the need to account for the stochastic character of the climatic fluctuations which influence different vegetation in very different ways. The integrated spatiotemporal character of the climatesoil-vegetation system with interannual and intraannual fluctuations in precipitation depends on the scale at which the analysis is performed. Nevertheless, most valuable information may be assimilated from one scale to another, and

even results from the dynamics at a site or point can be extremely valuable for modeling at larger scales. Hydrologically oriented research has, indeed, much to contribute toward the understanding of some of the most challenging and important problems related to biodiversity and ecosystem function.

In a more personal note regarding the future of hydrology, I am extremely optimistic with respect to the years ahead. The field has a truly outstanding crop of young researchers much more worried about understanding nature than about applications to solve specific problems. Not that the latter is irrelevant, but we should not fall into the temptation to neglect the study of what is important because of the pressures of the urgent. I encourage this outstanding group to pursue their own dreams, to follow their instincts, and to set their own agenda. Part of the duties of their more senior col-

leagues is to facilitate this possibility. In doing so, hydrology will surely become one of the most exciting sciences of the 21st century.

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References

- Einstein, A., *The Quotable Einstein*, edited by A. Calaprice, Princeton Univ. Press, Princeton, N. J., 1996.
- Lambers, H., F. S. Chapin, and T. L. Pons, *Plant Physiological Ecology*, Springer-Verlag, New York, 1998.
- Rodrìguez-Iturbe, I., A. Porporato, L. Ridolfi, V. Isham, and D. R. Cox, Probabilistic modelling of water balance at a point: The role of climate, soil and vegetation, *Proc. R. Soc. London, Ser. A.*, 455, 3789–3805, 1999. Schlesinger, W. H., J. F. Reynolds, G. L. Cun-
- ningham, L. F. Huenneke, and W. M. Jarrell, R. A. Virginia, and W. G. Whitford, Biological feedbacks in global desertification, *Science*, 247, 1043–1048, 1990.
- Scholes, R. J., and B. H. Walker, An African Savanna, Cambridge Univ. Press, New York, 1993.
- Walling, D. E., Water catchment ecosystems, in *Water Quality in Catchment Ecosystems*, pp. 2–47, John Wiley, New York, 1980.
- Webb, B. W., and D. E. Walling, Water quality, II, Chemical characteristics, in *River Flows and Channel Forms*, edited by G.
- Petts and P. Calow, chap. 6, pp. 102–129, Blackwell Sci., Cambridge, Mass., 1996. Weinberg, S., *Dreams of a Final Theory*, Vintage, New York, 1994.
- I. Rodriguez-Iturbe, Department of Civil and Environmental Engineering, Princeton University, E-220 Engineering Quad, Princeton, NJ 08544. (irodrigu@princeton.edu)

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