Ecohydrology—a challenging multidisciplinary research perspective

AMILCARE PORPORATO
Department of Hydraulics, Transport and Civil Infrastructures, Polytechnic of Turin, Corso Duca degli Abruzzi 24, I-10129 Turin, Italy
porporato@polito.it

IGNACIO RODRIGUEZ-ITURBE
Department of Civil and Environmental Engineering and Princeton Environmental Institute, Princeton University, Princeton, New Jersey 08544, USA

Abstract Ecohydrology is the science that studies the mutual interaction between the hydrological cycle and ecosystems. Such an interaction is especially intense in water-controlled ecosystems, where water may be a limiting factor, not only because of its scarcity, but also because of its intermittent and unpredictable appearance. Soil moisture is the key variable modulating the complex dynamics of the climate–soil–vegetation system and controlling the spatial and temporal patterns of vegetation. In this note the authors' perspective to the field is discussed and some open questions are outlined.

Key words ecohydrology; climate–soil–vegetation; ecosystems; system dynamics; disturbances; scale problems

Ecohydrologie: une perspective stimulante de recherche multidisciplinaire

Résumé L'écohydrologie est la science qui étudie l'interaction mutuelle entre le cycle hydrologique et les écosystèmes. Cette interaction est particulièrement intense dans les écosystèmes contrôlés par l'eau, où l'eau peut être un facteur limitant, non seulement en raison de sa rareté mais aussi à cause de sa disponibilité intermittente et imprévisible. L'humidité du sol est la variable clef dans la modulation des dynamiques complexes du système climat–sol–végétation et dans le contrôle des répartitions spatiales et temporelles de la végétation. Les auteurs discutent dans cet article de leurs perspectives dans le domaine et abordent quelques questions ouvertes.

Mots clefs écohydrologie; climat–sol–végétation; écosystèmes; dynamiques systémiques; perturbations; problèmes d'échelle

INTRODUCTION

Ecohydrology is the science that studies the mutual interaction between the hydrological cycle and ecosystems. It is a fast-growing science that is expected to explain important problems related to natural processes and provide engineering solutions with reduced environmental impact. In particular, the understanding of the basic processes of ecohydrology will, it is hoped, lead to the development of the necessary tools for a sustainable use of the water resources.

The area of interest of ecohydrology is so vast and manifold (e.g. Kundzewicz, 2002, and references therein), that the initial approach must necessarily focus on the most important components of the system. In this perspective, soil moisture and plants are undoubtedly the two main subjects of ecohydrology, the former being at the heart of the hydrological cycle and the latter representing the main component of terrestrial eco-

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systems. The interaction between the hydrological cycle and ecosystems is most intense (and interesting) when water is present intermittently, be it abundant, as in wetlands, or scarce, as in arid and semiarid regions. In either case, the fluctuating nature of the hydrological cycle, together with the network of dynamic links within the climate–soil–vegetation system, considerably complicates the analysis of the processes involved.

The interaction between water balance and plants, which is at the core of ecohydrology, is responsible for some of the fundamental differences among various biomes (e.g. forests, grasslands, savannas) and for the developments of their space–time patterns. Thus, the first objective of ecohydrology is to understand the intertwined characteristics of climate, soil, and vegetation that make a biome what it is and to relate hydrological dynamics to the space–time response of vegetation in a region (Rodriguez-Iturbe, 2000).

The present approach to ecohydrology has focused on water-controlled (or water-stressed) ecosystems, where water is a limiting factor, not only because of its scarcity, but also because of its intermittent and unpredictable appearance. Analytical tools have been developed to describe the various mechanisms responsible for the dynamics of soil moisture, from the most basic ones at a point to more complete ones involving different spatial and temporal scales (e.g. Rodriguez-Iturbe *et al.*, 1999a,b; Laio *et al.*, 2001a,b; Porporato *et al.*, 2001; Rodriguez-Iturbe *et al.*, 2001a,b; Fernandez-Illescas *et al.*, 2001; Porporato *et al.*, 2002; D'Odorico *et al.*, 2002; Fernandez-Illescas & Rodriguez-Iturbe, 2002a,b). In the following, the philosophy of this approach is reviewed and some open problems discussed.

SOIL MOISTURE AND PLANT DYNAMICS

Water-controlled ecosystems are complex evolving structures whose characteristics and dynamic properties depend on many interrelated links between climate, soil, and vegetation. On the one hand, climate and soil control vegetation dynamics; on the other, vegetation exerts important control on the entire water balance and is responsible for many feedbacks to the atmosphere.

Soil moisture is the key variable modulating the action of climate, soil, and vegetation on the water balance and the dynamic impact of the latter on plants (e.g. Rodriguez-Iturbe *et al.*, 2001a; Laio *et al.*, 2001a; Porporato *et al.*, 2001). If rainfall, at a first analysis, may be regarded as a gross surrogate of soil moisture in determining plant ecosystem structure at the continental scale (see Fig. 1), the actual assessment of plant conditions depends on the specific soil moisture dynamics at a site. This is clear in the example of Fig. 2, which shows how the recruitment of *Bouteloua gracilis*, a small dominant grass in the Colorado steppe, is strongly linked to soil water availability (Laurenroth *et al.*, 1996).

The idea that soil moisture dynamics is at the core of water-controlled ecosystems is not new. It permeated some of the pioneering works in the field, such as those by Gardner (1960), Cowan (1965), Noy-Meir (1973), Eagleson (1978, 1982), and Federer (1979), among others. As stated by Noy-Meir (1973), the soil is the store and regulator in the water flow system of ecosystems, both as a temporary store for the precipitation input, allowing its use by organisms, and as a regulator controlling the partition of this input between the major outflows: runoff, evapotranspiration redistribution, and the flow between the different organisms.

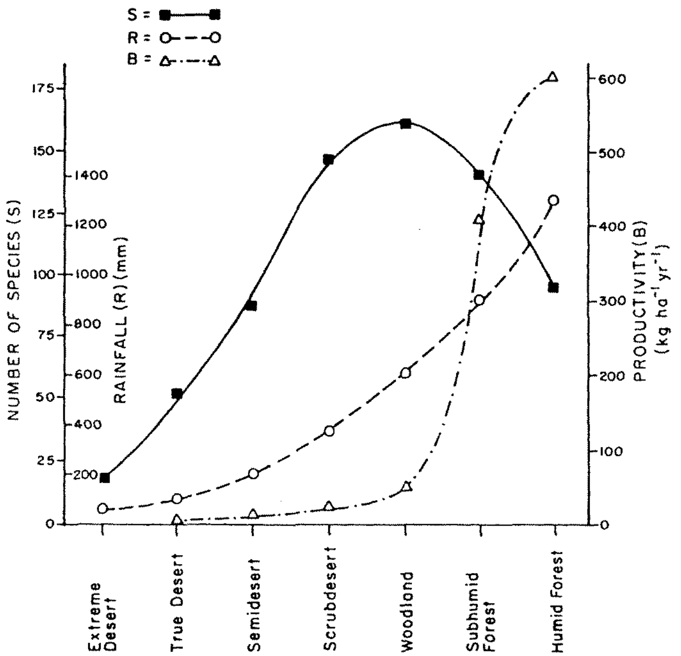

Fig. 1 General link between precipitation (*R*), biomass (*B*), and biodiversity (number of species, *S*) in water-controlled ecosystems. After Shmida & Burgess (1982).

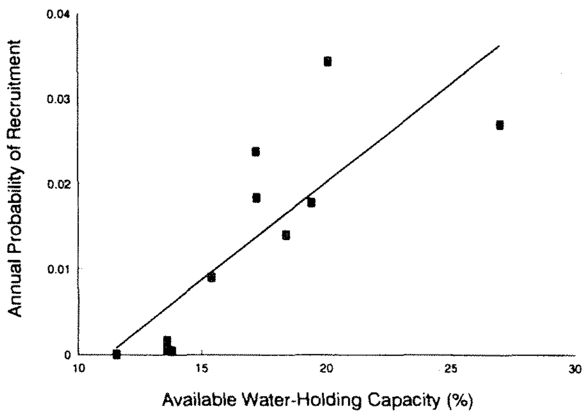

Fig. 2 Soil-moisture dependence of recruitment of new plants of *Bouteloua gracilis* for a site in Colorado. After Laurenroth *et al.* (1994).

Due to lack of soil moisture, many ecosystems of tropical and subtropical latitudes suffer from water stress (e.g. Porporato *et al.*, 2001). Although other sources of stress (fire, grazing, nutrient availability, etc.) are certainly also present, in many of the world ecosystems soil moisture is the most important resource affecting vegetation and its dynamics is also linked to the other sources of stress. Plants play a special role in the system dynamics, having an active role in water use that heavily influences the water balance of the system and at the same time being impacted by the arid conditions they contribute to produce (Porporato *et al.*, 2001; Rodriguez-Iturbe *et al.*, 2001b).

LEVELS OF ANALYSIS AND SIMPLIFICATIONS

There are two characteristics which make especially daunting the quantitative analysis of the problem (Rodriguez-Iturbe *et al.*, 2001a): (a) the very large number of different processes and phenomena which make up the dynamics, and (b) the extremely large degree of variability in time and space that the phenomena present.

The first of the above characteristics obviously calls for simplifying assumptions in the modelling scheme, while still preserving the most important features of the dynamics, whilst the second one calls for a stochastic description of some of the processes controlling the overall dynamics.

In the attempt to capture the essential dynamics of ecosystems, plants responding in a similar way to a syndrome of environmental factors are often grouped together referring to plant functional types (Gitay & Noble, 1997). However, when the analysis is focused on a particular biome (e.g. forest, grassland, or savanna), the mechanisms of special adaptation to water stress and intra-/inter-species interactions (e.g. competition for water and reproduction) become essential. As shown in Fig. 3, the control of soil moisture on water stress may be quite different among species (as well as for each individual) and this, in turn, may drive the emergence of specific temporal niches of soil water and nutrient availability and patterns of coexistence (e.g. Porporato *et al.*, 2001; Fernandez-Illescas *et al.*, 2001). As noted by Tilman (1996), biodiversity seems to stabilize ecosystem properties. While inter-species competition magnifies the effect of a perturbation on the abundances of individual species, the competitive release

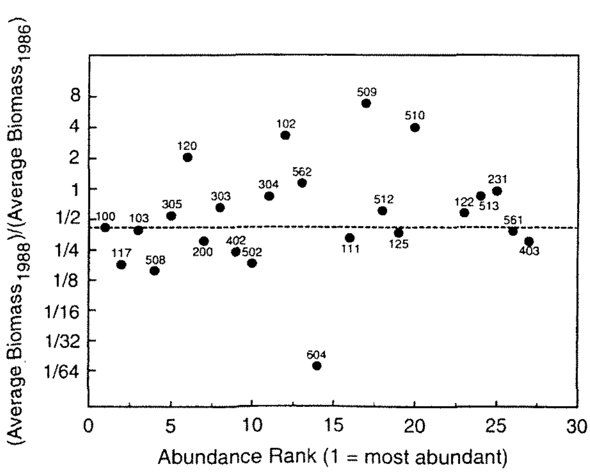

Fig. 3 Change in the average biomass of 24 abundant species, from before the drought (1986) to the peak of the drought (1988) in a long-term study of 207 grassland plots in Minnesota, graphed against their ranked abundance. The dashed line shows the response of community biomass with each dot representing a species identified by the number. Notice the quite diversified response to drought and how many species performed better during drought than did plant community biomass. After Tilman (1996).

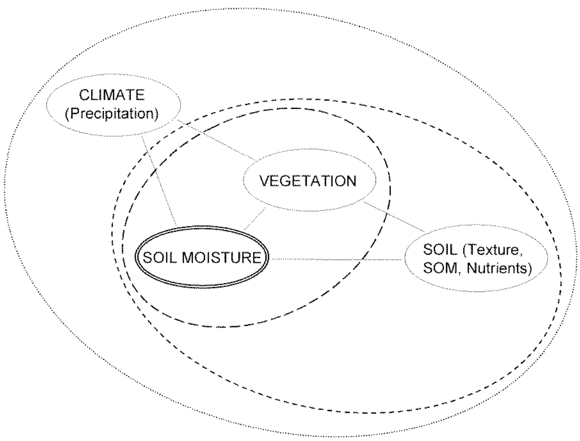

Fig. 4 Levels of description of the soil–plant–atmosphere system having at the centre soil moisture. (SOM: soil organic matter).

experienced by disturbance-resistant species acts to stabilize total biomass in species-rich communities.

As it is typical of complex systems, the dynamics of the climate–soil–vegetation system presents different levels of complexity according to the scale of interest: the importance of the various hydrological processes may be different whether one considers daily, seasonal, or interannual fluctuations, or point (i.e. plot), regional (i.e. hillslope to catchment), or continental scales. Such a distinction of scales is important, as it naturally suggests different levels of analysis and simplifications in which only the principal components may be retained (Fig. 4).

A first basic level of analysis of the climate–soil–vegetation system is at the spatial scale of a few metres and at the temporal scale of the growing season. At such scales, soil moisture dynamics directly impacts vegetation through plant water stress, while the rainfall input and the soil characteristics may be considered as external components (Fig. 5).

A second, and more complex, level of analysis involves the links between soil moisture, soil nutrient cycles, and the related evolution of soil properties. Such factors are all interrelated with vegetation dynamics and represent a relatively little studied area by both ecologists and hydrologists. This problem will be addressed later.

Finally, a more general level of description is introduced when the system is analysed at large spatial scales (e.g. continental). Large-scale patterns of vegetation types (and also water stress) induce corresponding patterns of albedo and transpiration characteristics that heavily influence the dynamics of the atmospheric boundary layer and the formation of convective precipitation. Thus the climatic/atmospheric component becomes influenced by the feedbacks induced by the soil–plant system. The climate component is no longer an external forcing component and becomes an essential part of the dynamics (e.g. Segal *et al.*, 1988; Eltahir, 1996; Sellers *et al.*, 1997; Pielke, 2001). Such a problem connects ecohydrology to hydrometeorology, another new discipline from the family of hydrological sciences. The implications of soil–plant–atmosphere interaction involve not only the exchange of water between the components of the system, but also CO_2 fluxes between ecosystems and the

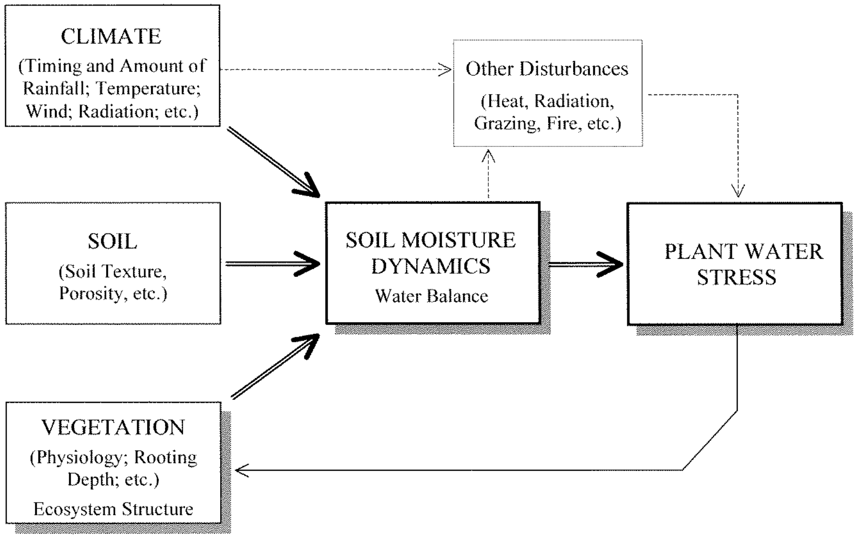

Fig. 5 First and basic level of description of the climate–soil–vegetation system. Climate and soil characteristics may be considered as external forcing components while soil moisture dynamics pivots the mutual links between the vegetation and water stress. Modified after Rodriguez-Iturbe *et al.* (2001a).

atmosphere and the many feedbacks on the nitrogen cycle (e.g. Siqueira *et al.*, 2000; Dickinson *et al.*, 2002).

TEMPORAL AND SPATIAL SCALES

Although plant physiologists generally work at small temporal scales (e.g. hourly), soil moisture fluctuations controlling ecological processes and patterns may be studied through suitable functional representations of the main processes at the daily time scale, avoiding the explicit modelling of the short-term variations in the different parameters (e.g. internal storm structure, diurnal cycles of evapotranspiration and photosynthesis, etc.).

Steady probabilistic solutions of soil moisture dynamics modelled at the daily time scale have been obtained by Rodriguez-Iturbe *et al.* (1999b) and Laio *et al.* (2001a) and then applied to the analysis of plant water stress and optimal plant conditions by Porporato *et al.* (2001), Laio *et al.* (2001b), and Fernandez-Illescas *et al.* (2001).

Steady conditions are not always representative, especially at the beginning of the growing season. For example, the soil moisture initial condition is very different between the savannas of Nylvsley in South Africa and the forests of Oregon in the northwestern United States. At Nylvsley, the growing season from September to April contains 98% of the annual rainfall and is preceded by a warm and dry winter season, which makes initial soil moisture conditions at the start of the growing season practically irrelevant, while in the northwestern United States, a relatively dry growing season is preceded by a wet and cold winter season: these factors, combined with a deep active soil layer, make the initial value of soil moisture storage a commanding factor in water use by plants. As a consequence, the case of Nylvsley is likely to be well represented by the statistically steady state properties of the soil moisture process, while, for the forests of the northwestern United States, the statistically transient properties are crucial.

In other cases, seasonal components in transpiration and precipitation may have dramatic consequences for plants. For example, in many subtropical climates, rainfall and transpiration are in phase and have highest rates during the growing season, while in Mediterranean climates, rainfall, being mostly concentrated during the winter season, is in counterphase with the growing-season transpiration. This results in very different seasonal patterns of soil water availability and thus, even if the total annual precipitation and average temperature are the same, in completely different vegetation structures. Figure 6 reports the typical vegetation catenae (from an arboreal temperate formation to a contracted desert) for Mediterranean and subtropical climates: in the region between 400 and 250 mm of annual rainfall, for instance, one may find steppe forests and open shrublands in Mediterranean climates, or open savannas and drought deciduous shrublands in ecosystems with subtropical climates.

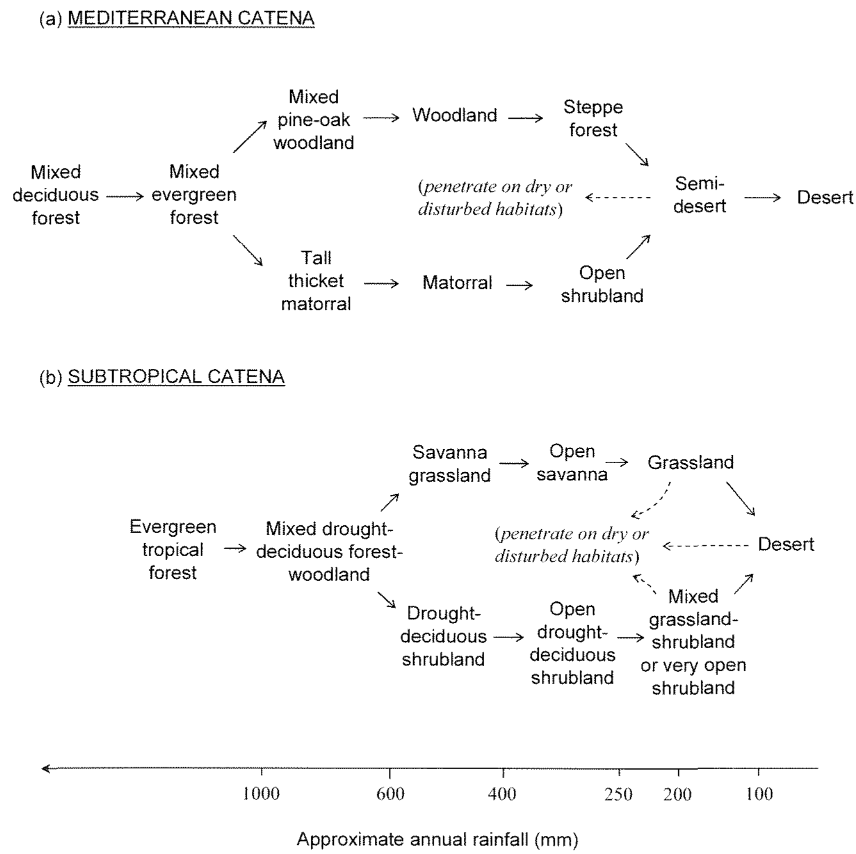

Fig. 6 Different vegetation catenae from an arboreal temperate formation to a contracted desert as an example of specific ecosystem structures resulting from different seasonal patterns of water availability. Modified after Shmida & Burgess (1988).

At longer time scales, interannual fluctuations also become important, superimposing themselves onto the daily and seasonal components. Rodriguez-Iturbe *et al.* (1999a), D'Odorico *et al.* (2000), and Fernandez-Illescas & Rodriguez-Iturbe (2002a,b) have analysed the impact of interannual rainfall fluctuations on the ecosystem structure.

Spatial scales are extremely important too in the analysis of the climate–soil–vegetation system. At the local scale, differences in the active soil depth produce a variety of different responses to the rainfall input, with clear implications for plant water stress (Noy-Meir, 1973; Porporato *et al.*, 2001). Wherever relevant topographic features are present, the lateral fluxes may be an important factor for the spatial distribution of soil moisture and its temporal evolution; slope and aspect also control the local net radiation input and, consequently, soil moisture dynamics. Unfortunately, due to the spatial components, the mathematical analysis is considerably more difficult and analytical solutions are often replaced by numerical analyses (e.g. Ridolfi *et al.*, 2002). Brought to the entire catchment scale, this line of research will hopefully blend in a natural manner the interaction among the statistical fluctuations in precipitation and soil moisture, the statistical geometry of the river basins, and the structure of vegetation. Finally, as mentioned above, at even larger spatial scales (e.g. continental) the ecohydrological analysis requires the involvement of the whole climate–soil–vegetation system at the most general level (see Fig. 4).

SOIL MOISTURE AND THE CYCLES OF SOIL NUTRIENTS

In many regions of the world, soil moisture dynamics is the key factor determining the duration of the periods in which primary production and nutrient mineralization can occur. The production of plant residues is directly dependent on the growth of vegetation through its photosynthetic capacity, which in turn depends on water availability.

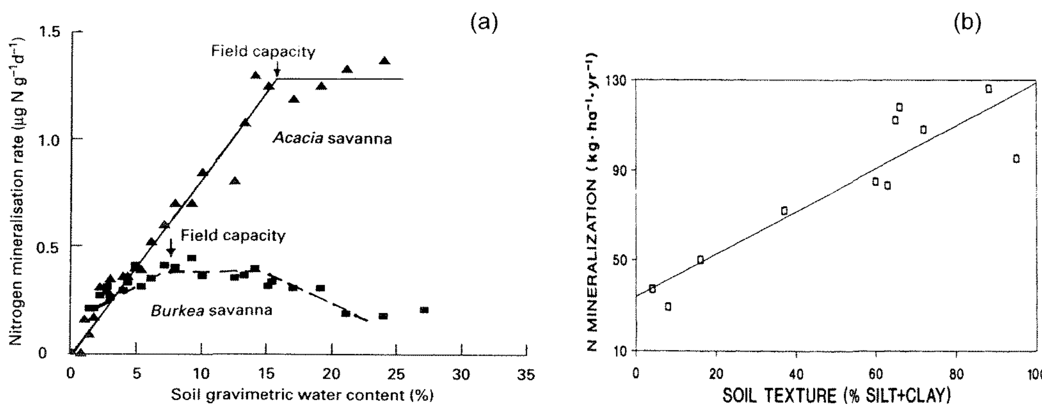

Fig. 7 (a) Nitrogen mineralization rate in soils as a function of soil water content in the broad-leafed and fine-leafed savanna at Nylsvley (South Africa). After Scholes & Walker (1993); (b) measured nitrogen mineralization rates for several stands in Wisconsin in relation to soil texture, which is one of the main controlling factors of average soil water availability. Modified after Aber *et al.* (1991).

Soil moisture is also a controlling factor of mineralization and uptake. Figure 7 shows how the equilibrium nitrogen cycling rate for a site is directly related to its water availability. To study this dynamics, Porporato *et al.* (2002) and D'Odorico *et al.* (2002) have recently developed a model for carbon and nitrogen dynamics in soils driven by soil moisture fluctuations. Their results show the paramount importance of soil moisture control on the different components of the nitrogen cycle at a wide range of time scales, from the high frequency variability of leaching and uptake, to the low frequency temporal dynamics of the soil organic matter pools. An example of a sudden flush of nitrate, following a prolonged wet period after a drought, is shown in Fig. 8. In these conditions, first the dry soil hinders decomposition and favours the accumulation of soil organic matter, then the subsequent wet period elicits microbial biomass growth and enhances mineralization. Such episodic changes in nitrate levels greatly influence plant growth, and are thus of considerable importance for natural ecosystems.

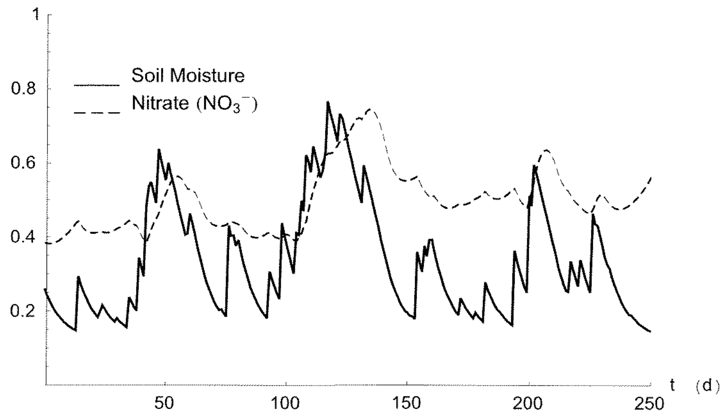

Fig. 8 Example of nitrate flush after persistent rainfall following a period of drought (relative soil moisture is dimensionless, while nitrate is in g m^{-3}). After D'Odorico *et al.*, 2002.

SOIL MOISTURE DYNAMICS AND ECOSYSTEM STRUCTURE

The influence of soil moisture on water stress and soil nutrient dynamics drives the growth, reproduction, and competition abilities of plants. Since the different species (as well as each individual) have a specific response to soil moisture dynamics, the hydrological fluctuations continually (and randomly) shift the habitat preference in favour of different species and plant functional types.

The spatial components due to changes in soil characteristics and plant competition further complicate the picture (e.g. Rodriguez-Iturbe *et al.*, 1999a; Fernandez-Illescas *et al.*, 2001; Fernandez-Illescas & Rodriguez-Iturbe, 2002a,b). Temporal and spatial dynamics are thus highly intertwined and give rise to regular and irregular spatial patterns in continuous evolution. Figure 9 is an example of a savanna in southern Texas, where the complex spatial and temporal patterns of tree–grass coexistence are driven by interannual rainfall fluctuations (Archer *et al.*, 1988). The understanding of such dynamics requires the combination of hydrological models with suitable quantitative

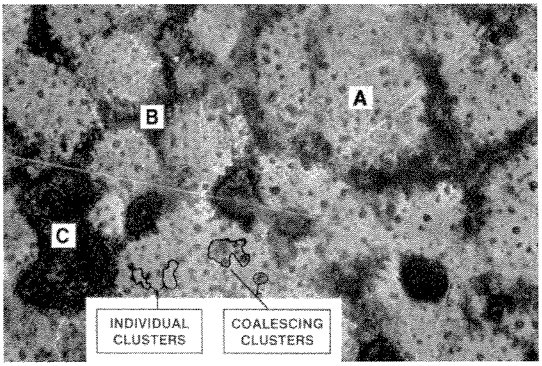

Fig. 9 Aerial view of the savanna of La Copita (southern Texas, USA). The two-phase patterns of discrete clumps of woody vegetation, are scattered throughout a grassy matrix (A). Bordering the two-phase portions of the landscape are monophasic woodlands associated with more mesic drainages (B) and low-centres polygons of playas (C). The clusters, organized about mesquite (*Prosopis glandulosa*), represent chrono-sequences whose species compositions at latter stages of development are similar to that of the closed canopy woodlands in region B. The largest clusters in the two-phase zone represent a mosaic of coalesced clusters. After Archer *et al.* (1988).

description of growth and death of plants as well as their competition and colonization properties (Fernandez-Illescas & Rodriguez-Iturbe, 2002a,b).

In some extreme cases, the interaction of vegetation with the site water balance and nutrient cycles may even lead to dramatic changes in the equilibrium conditions of ecosystems of entire regions. This is the case of some arid grasslands in New Mexico, which have gradually been converted into shrublands with extensive patches of bare soil.

CONCLUSIONS

Ecohydrology of water-controlled ecosystems is developing new theories and models to explain the complex interaction between hydrological processes and plant ecosystems in arid and semiarid regions. At this stage of development, it is particularly important that theoretical models are supported by specifically-planned experiments in the field. In this way, the phenomenological explanations of the processes related to natural ecosystems will hopefully be replaced by physically sound analytical models (typically spatially-explicit dynamical systems forced by stochastic hydrological fluctuations) amenable to quantitative analyses.

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