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Plants in water-controlled ecosystems: active role in hydrologic processes and response to water stress I. Scope and general outline

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Abstract

This series of four papers studies the complex dynamics of water-controlled ecosystems from the hydro-ecological point of view [e.g., I. Rodriguez-Iturbe, Water Resour. Res. 36 (1) (2000) 3–9]. After this general outline, the role of climate, soil, and vegetation is modeled in Part II [F. Laio, A. Porporato, L. Ridolfi, I. Rodriguez-Iturbe, Adv. Water Res. 24 (7) (2001) 707–723] to investigate the probabilistic structure of soil moisture dynamics and the water balance. Particular attention is given to the impact of timing and amount of rainfall, plant physiology, and soil properties. From the statistical characterization of the crossing properties of arbitrary levels of soil moisture, Part III develops an expression for vegetation water stress [A. Porporato, F. Laio, L. Ridolfi, I. Rodriguez-Iturbe, Adv. Water Res. 24 (7) (2001) 725–744]. This measure of stress is then employed to quantify the response of plants to soil moisture deficit as well as to infer plant suitability to given environmental conditions and understand some of the reasons for possible coexistence of different species. Detailed applications of these concepts are developed in Part IV [F. Laio, A. Porporato, C.P. Fernandez-Illescas, I. Rodriguez-Iturbe, Adv. Water Res. 24 (7) (2001) 745–762], where we investigate the dynamics of three different water-controlled ecosystems.

Keywords: Soil moisture; Vegetation; Ecohydrology; Stochastic processes; Hydrology; Water stress; Water balance; Savannas; Grasslands; Crossing analysis

1. Introduction

Water-controlled ecosystems are complex, evolving structures whose characteristics and dynamic properties depend on many interrelated links between climate, soil, and vegetation (Fig. 1). On the one hand, climate and soil control vegetation dynamics (e.g. [4,15,17,21,22]); on the other hand, vegetation exerts important control on the entire water balance and is responsible for many feedbacks to the atmosphere (e.g. [18,38,46]). Many important issues depend on the quantitative understanding of this dynamics, including environmental preservation and proper management of resources (e.g. [2,3,27,40,41]). In fact, ecohydrology itself may be defined as the science which seeks to describe the hydrologic mechanisms that underlie ecologic patterns and processes [36].

Soil moisture is the key variable which synthesizes the action of climate, soil, and vegetation on the water balance and the dynamic impact of the water balance on plants (e.g. [21,23,25,27,44,45]). Many ecosystems of tropical and subtropical latitudes suffer water stress, which is in turn controlled by the temporal fluctuations of soil moisture (e.g. [26,42]). 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 structure and organization.

Vegetation itself plays a special role in water-controlled ecosystems: plants have an active role in water use that heavily conditions the water balance of the system. At the same time plants are also impacted by the arid conditions and the water stress they produce. The connections between the role of plants in the water

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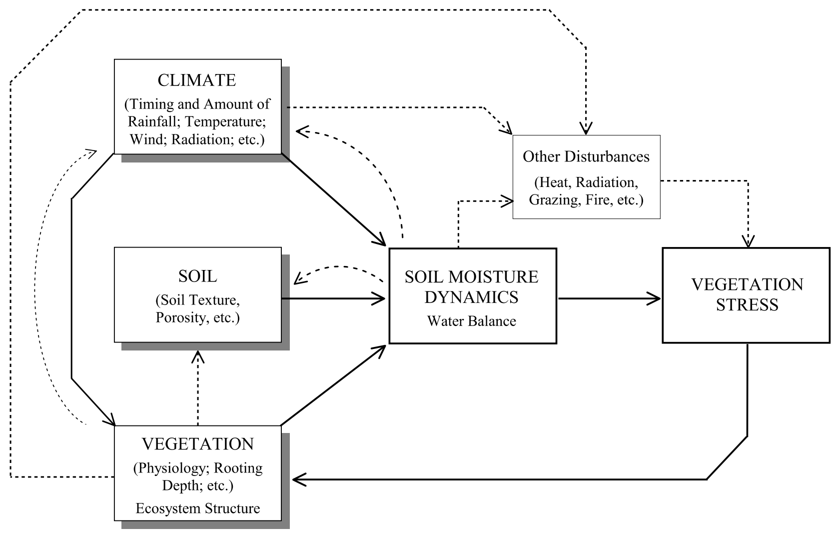

Fig. 1. Schematic representation of the climate, soil, and vegetation system. Solid arrows refer to the main dynamic links, dotted lines to secondary interactions not directly considered here.

balance and their water-stress response is a fascinating and in great part unexplored topic which lies at the heart of ecohydrology. Differences in soil moisture dynamics are among the principal reasons for the existence of particular functional vegetation types (e.g., grasslands, savannas, forests, etc.). Special adaptation to water stress and intra/inter-species interactions are likely connected to the dynamics of the climate–soil–vegetation system and, moreover, the coexistence of different functional vegetation types may be explained through the emergence of specific temporal niches of soil water availability [7,39]. The dynamics of the climate–soil–vegetation interactions are critically 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. Thus such dynamics are fundamentally different between, say, forests, savannas, and grasslands.

In terms of water availability, ecosystem response is controlled not only by rainfall scarcity, but also by its intermittent and unpredictable nature, by its coupling with the temperature changes throughout the year and by the soil characteristics, which control the infiltration process. The uncertainty of both the timing and amount of rainfall has induced vegetation to develop different strategies to respond to water stress and optimize reproduction and productivity (e.g. [27]). Any effort towards hydro-ecological modeling has to take into account the stochastic character of soil moisture dynamics, with fluctuation at different temporal and spatial scales. We concentrate here on a modeling scheme towards a quantitative description of the temporal dynamics of the climate–soil–vegetation system. Simplifying, yet realistic, assumptions will be made in order to keep analytical tractability and, at the same time, to be able to achieve results with general physical interpretation. This kind of approach stems from the conviction that only models with a framework of general characteristics can provide a valuable interface between the real changing environment and data obtained from specific experiments. In this respect the philosophy of this work is akin to that of Noy-Meir [27], Eagleson [9,10], Eagleson and Tellers [11], Eagleson and Segarra [12], and Paruelo and Sala [28] among others.

2. Scale issues and stochastic fluctuations in soil moisture dynamics

There are two characteristics which make especially daunting the quantitative analysis of this problem: (1) the very large number of different processes and phenomena which make up the dynamics, and (2) 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 modeling scheme while still preserving the most important features of the dynamics. The second of the above characteristics imposes a probabilistic description of the processes controlling the overall dynamics. Thus the soil moisture evolution throughout time and space needs to be characterized by means of a probabilistic framework. The objective is to extract features of order from the apparent disorder of the data. Typically these features will be probability distributions – or their moments – of the soil moisture evolution and of some of its most relevant attributes.

The scale issue is of crucial interest in the modeling of soil moisture dynamics as the controlling variable in many processes in ecohydrology. How frequently we should sample soil moisture content in time and space depends on the local and regional characteristics of soil, vegetation, and climate which control the probabilistic structure of soil moisture. What the relative importance of those characteristics is and how this importance changes from an ecosystem to another is at the heart of the modeling effort which in many ways is guided by the principle that "the purpose of models is not to fit the data but to sharpen the questions" [16]. These considerations are crucial for the temporal and spatial scales at which the dynamics is to be studied. The choice of large spatial scales, of the order of kilometers, over which average conditions are to be established, drastically decreases any kind of spatial variability in soil moisture and increases the temporal scale at which the processes are effectively correlated. Those larger scales, although very useful for climatologically oriented studies, are not very illuminating for the study of vegetation response and the accompanying hydrologic dynamics which is controlled by fluctuations at much smaller temporal and spatial scales. One is tempted to suggest a simile with the use of macroeconomics indicators in developing countries – which are frequently at very acceptable levels – to infer the quality of living conditions, the latter being in the realm of microeconomics and most commonly at unacceptable levels.

A further goal is to build the necessary elements for investigating the effects of the spatial scale on the fluctuation characteristics of the soil moisture dynamics. The analysis in this paper refers to a spatial scale of a few meters, characteristic of the domain of a typical plant, where vegetation and soil are assumed to be homogeneous. The commanding features of the spatial scales arise from the spatial variability of the soil and vegetation condition. Soil composition and soil properties, which are very important for the resulting soil moisture dynamics, generally vary at much smaller spatial scales than the rate of arrival of storms during the growing season or the average depth of the rainfall events. How large the spatial changes in soil type are varies from region to region, but both the main characteristics of the soil field as well as its spatial variability need to be accounted for when linking climate and vegetation through soil moisture dynamics. Moreover, climatic fluctuations both inside the year and of interannual character need to be taken into account. The result of this series of papers will be used under the above framework in the construction of a stochastic model involving spatial interactions at the local scale. The spatio-temporal model – presently under development – is framed via a cellular automaton whose space–time vegetation characteristics evolve throughout time under the influence of a varying climate.

In this series of papers we focus on the temporal dynamics of soil moisture to understand the role of different functional vegetation types on soil moisture dynamics and their resulting response to water stress. Plant physiologists studying water stress generally work at small temporal scales – e.g. hourly – which embed the multiple internal plant processes involved in the occurrence and development of water-induced stress. In terms of the hydrologic dynamics controlling ecological processes and patterns, one may attempt to study fluctuations in the daily average soil moisture at a site through functional representations of the main processes involved. These representations describe the dynamics at a daily time scale thus avoiding the explicit modeling of the hourly variations in the different parameters (e.g., internal storm structure, evapotranspiration diurnal variations, etc.). Thus, the stochasticity of rainfall as well as the response of vegetation and soil water dynamics are considered here at the daily time scale.

In the ecological discussion as well as in the examples and applications, we will concentrate on a growing season which is assumed to be statistically homogeneous. It is frequently the case that the statistical characterization of the rainfall varies during the course of the growing season, with the frequency and intensity of storms undergoing significant changes throughout the period of several months. This is also the case for the average daily temperature, which is crucial for the estimation of evapotranspiration conditions. Although it is feasible to implement a modeling framework which incorporates a continuous Fourier representation of the parameters describing the rainfall and evapotranspiration dynamics during the season, it has been found that, in most cases where the above is needed, acceptable results are obtained by simply representing the growing season in two different periods: early growing season and late growing season [37]. Rainfall modeling parameters are then estimated for each period as well as the maximum evapotranspiration characteristics of the existing vegetation types.

Most of the analytical results presented in this series of papers refer to statistically steady-state conditions. This implies that the effects of the initial soil moisture condition last for a relatively short time and the probability distribution of the soil water content settles in a state independent of time. This has important implications for the applicability of some of the analytical results. The role of the initial condition in the characterization of the soil moisture temporal dynamics during the growing season is very different between, say, the savannas of Nylvsley in South Africa and the forests of Oregon in northwestern USA. In the case of 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. The forests of northwestern USA have a relatively dry growing season 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. In terms of plant response the case of Nylvsley is likely to be well represented by the statistically steady-state properties of the soil moisture process. In the forests of northwestern USA the statistically transient properties are crucial and especially important is the statistical characterization of the time it takes for the soil moisture to reach the wilting point or any other important threshold when starting from a given or random initial condition. These important transient properties and their impact on vegetation will be presented elsewhere.

3. Topographic effects and interaction with the water table

In this series of papers the temporal dynamics of soil moisture is modeled at a point without consideration of either the effects due to lateral moisture contribution or those resulting from the structure of the root vertical distribution. The point water balance is thus

$$nZ_r \frac{\mathrm{d}s(t)}{\mathrm{d}t} = R(t) - I(t) - Q[s(t),t] - E[s(t)] - L[s(t)], \tag{1}$$

where n is porosity; Z_r depth of active soil or root depth; $s(t)$ relative soil moisture content $(0 \leqslant s(t) \leqslant 1)$; t time; $R(t)$ rainfall rate; $I(t)$ rate of losses due to canopy interception; $Q[s(t),t]$ runoff rate; $E[s(t)]$ and $L[s(t)]$ rates of evapotranspiration and leakage, respectively.

As will be seen in Part II [19] rainfall input will be modeled as a marked Poisson process, and the losses as state dependent and nonlinear. Eq. (1) is therefore a nonlinear, stochastic, ordinary differential equation for the state variable $s(t)$. The complete analytical solution will be given in Part II for the case of steady-state conditions.

The vertical partition of soil moisture has been shown to be less important with respect to vertical niches of soil moisture availability than what was believed until recently (in this regard see the discussion on the stability of savannas in [39,40]). In many cases vertically integrated models like the one proposed here can provide an accurate enough description in what concerns vegetation stress and ecosystem function.

Moreover, we will make no consideration of the effect on soil moisture dynamics of lateral fluxes resulting from topographic features. In generally flat areas these effects tend to be very local but, wherever there exist relevant topographic features or a river basin with a drainage network and its accompanying hillslope system, the lateral fluxes are a most important factor for the spatial distribution of soil moisture and its temporal evolution. An analytical solution for the vertically integrated soil moisture at a hillslope site (i.e., with lateral contributions) subject to random precipitation inputs and nonlinear losses from evapotranspiration and leakage is not yet available. The problem is indeed quite difficult: with the inclusion of the lateral spatial dimension, the dynamics is described by an equation of the type

$$nZ_r \frac{\partial s}{\partial t} = R(t) - I(t) - Q(s,t) - E(s) - L(s) + \Phi_{\mathrm{lat}}, \tag{2}$$

where Φ_{lat} is the net flux due to lateral contributions. The latter can be modeled as

$$\Phi_{\mathrm{lat}} = Z_r \frac{\partial}{\partial x}\left[K_{\mathrm{lat}}(s)\left(S(x) + \frac{\partial \Psi_s}{\partial x}\right)\right], \tag{3}$$

where x is the horizontal dimension, $S(x)$ the local slope, $K_{\mathrm{lat}}(s)$ the lateral hydraulic conductivity, and Ψ_s the soil water potential.

At present we are conducting a full numerical exploration of Eq. (3) which, in addition to being important for the study of the probabilistic behavior of soil moisture, may also suggest acceptable approximations for the nonlinear stochastic partial differential equation (2). This line of research, which will not be presented in this paper, may provide the means 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 successfully modeled, in the interlocked systems of hillslopes and channels which make up the river basin [32]. As suggested by Rodriguez-Iturbe [36], "this approach will blend in a natural manner the temporal and spatial dynamics of the process, accounting at the same time for the statistical fluctuations in precipitation and for the statistical geometry of the basin".

All the analytical developments of this paper assume no interaction between the saturated zone and the active soil layer. Thus the water table is assumed to be located well below the root zone and leakage from the active soil layer has no feedback effects on the dynamic of the soil moisture. For practical purposes this means that our applications do not cover regions or sites where, either because of humid climate, adjacent water courses, topographic converging features, or any combination of the above, the water table has an active role on the moisture conditions of the active soil layer.

4. Soil moisture and the cycles of nutrients

In water-controlled ecosystems plant formations are developed mainly in response to the water balance of the ecosystem, although the structure is also modeled by the nutrient status of the soil [43]. In many regions of the world water availability is the key factor determining ecological function by controlling the duration of the period for which processes such as primary production and nutrient mineralization can occur. The life history of vegetation depends not only on the amount of rainfall but also on the dry periods of uncertain duration. The success of a species in relation to a particular environment depends on three different aspects: its ability to survive periods of adversity; its ability to compete for limiting resources; and its ability to efficiently convert those resources into growth and reproduction [40]. Survival and competitiveness are crucial in water-limited ecosystems, while efficiency is the key in relatively wet systems. In all cases nutrients are essential for the growth and functioning of living organisms. Most important among nutrients are nitrogen and phosphorus, whose cycles are intimately related to that of carbon.

The primary source of soil organic matter is plant residue, which undergoes three general reactions: (1) organic compounds are oxidized to release carbon dioxide, water, and energy; (2) essential elements like nitrogen, phosphorus, and sulfur are released and/or immobilized by reactions specific to each one of them; (3) compounds very resistant to microbial action are formed through microbial synthesis and modifications of the original plant tissues. Fig. 2 shows a simplified scheme of nitrogen dynamics in soils. The production of plant residues is in direct dependence with the growth of vegetation through its photosynthetic capacity. For example, there generally exists a considerable difference in the photosynthesis rates of evergreen and drought-deciduous species even when operating under the same climatic conditions. Drought-deciduous species have higher photosynthetic rates resulting from larger amounts of nitrogen in leaves on a dry-mass basis than evergreen. "Where nitrogen, and hence growth-rate, is limited, leaf turnover is reduced and, in fact, there is a selection toward increased leaf duration. The longest leaf durations generally occur in plants occupying the most nutrient-deficient habitat" [24]. Thus evergreen plants tend to exist in soils with lower nutrient status and where nutrients are more slowly recycled than in the case of drought-deciduous species.

The above discussion shows the dependence of the carbon cycle on the nitrogen status of the plant, which is itself directly linked to the existence of soil organic matter coming primarily from plant residues. Soil moisture is a vital component of all these intertwined cycles. The growth and evolution of plants, as well as photosynthesis itself, are controlled in most plants through the opening of the stomata on the leaves. This exchange of CO_2 and water vapor between the atmosphere and the plant is driven by the amount of moisture in the soil. Moreover, plant nitrogen availability is also highly dependent on soil moisture (Fig. 2). Soil nitrogen in organic compounds is better protected from loss but unavailable to plants which need to absorb it in inorganic forms (NH_4^+ and NO_3^-) after mineralization. The rate of mineralization depends largely on the moisture, temperature, and aeration status of the soil. Also, the plant uptake of the inorganic nitrogen mainly takes place through the soil solution.

Mineralization takes place through the action of soil microorganisms on organic matter to produce ammonium (NH_4^+), which is then further transformed into nitrate (NO_3^-). Plants can take up both ammonium and nitrate, although ammonium fixation by clay minerals generally makes nitrate a more important source for plant uptake. Relative soil moisture influences the balance of oxygen and water in the pore space of the soil and it constitutes an excellent overall variable to synthesize the impact of soil and climate condition on nitrification, ammonification, and denitrification (the last being the loss of nitrogen to the atmosphere when nitrate is converted to different gaseous nitrogen compounds through a series of chemical reductions). Fig. 3, from [6], shows how microbial activity, responsible for all the above processes, depends on relative soil moisture. The lack of oxygen, necessary of enzymatic

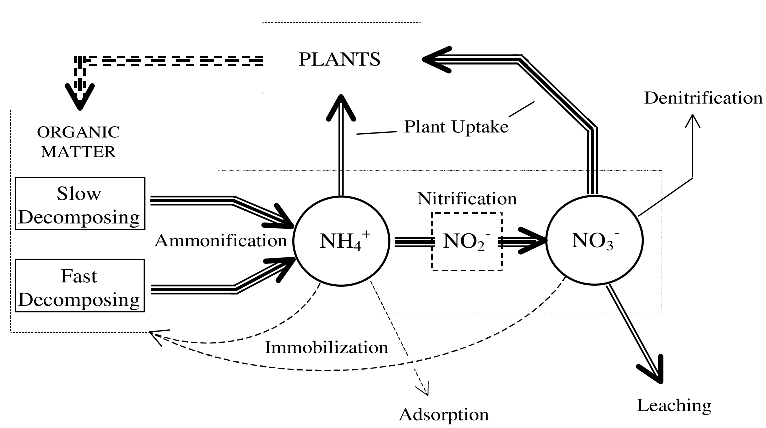

Fig. 2. Schematic representation of the main components of the nitrogen cycle in soil. The thickness of the arrows is related to the importance of the transformation within the soil nitrogen cycle; solid arrows refer to transformations where soil moisture plays an important role.

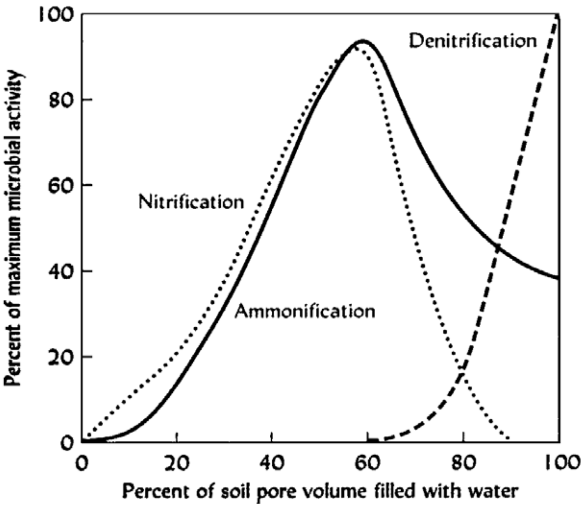

Fig. 3. Rate of microbial activity related to the various phases of nitrogen transformation as a function of soil water content (after Brady and Weil [6]).

oxidation, is responsible for the decay of the rates of nitrification and ammonification at high levels of relative soil moisture. In most water-controlled ecosystems, which undergo water stress during a considerable amount of time every year, water availability and its intermittent features act as a switch on nutrient uptake by vegetation.

Due to its negative charge, nitrate may be lost by leaching because it is not held strongly on the cation exchange surfaces of the soil. Soil moisture plays again a fundamental role in these losses, which in water-controlled ecosystems are generally very sporadic due to the relatively minor importance of percolation in the soil water balance. Thus nitrate leaching in these environments tend to happen only after major rain events or when the soil has a low water-holding capacity. A quantitative characterization of the soil water balance is the best way to evaluate the importance of leaching.

Phosphorus is another essential nutrient that with nitrogen is essential for the existence of all plants and organisms. Without going into any details of its cycle, it is important to point out the strong similarly with the case of nitrogen and the important control of soil moisture on its dynamics. Thus, the rate of phosphorus uptake by plants is constrained by the rate of release of inorganic phosphorus from organic matter into the soil solution through the process of mineralization (e.g. [40]).

From the above discussion it is clear that soil water content impacts plant growth and function in many crucially important ways. Stomata opening and the water condition of the mesophyll are directly dependent on soil moisture; leaf nitrogen content and thus photosynthetic capacity also depend on soil moisture, which controls both the rate of nitrogen mineralization and the rate of plant uptake; the presence of other vital nutrients like phosphorus is similarly affected. Thus primary production, a most important characteristic of vegetation ecosystems, is intimately related to soil water availability through many vital links. Although in many ecosystems like savannas and seasonally dry forests primary productivity is frequently constrained by nutrient availability, the mineralization and uptake of such nutrients are controlled by the dynamics of soil water. The random and intermittent nature of the phenomena makes it necessary that we investigate the problem with a stochastic approach which, in addition to a probabilistic characterization of soil moisture, allows also the study of the frequency, duration, and intensity of deficit – or supply – of soil moisture with respect to levels important for the processes described above.

We will concentrate here on the modeling of the soil moisture dynamics and the stress that lack of soil moisture can directly induce in plants. The linkage of the results obtained here with the process of mineralization and nutrient uptake, as well as the probabilistic characterization of nutrient-related stresses as a function of climate, soil, and vegetation, will be presented elsewhere.

5. Scope of the study

This series of papers is organized in four parts. After this general outline, the second part [19] deals with the role of climate, soil, and vegetation on the soil moisture dynamics. There, a review is presented of Rodriguez-Iturbe et al. [33], where a similar stochastic model for soil moisture dynamics was proposed and analytically solved for steady-state conditions. Some components of the model are improved here to provide a more realistic description of the dynamics, and a detailed discussion of the simplifying hypotheses is presented in order to minimize possible risks of generalization and oversimplification. The resulting model is a nonlinear, stochastic differential equation of soil moisture dynamics driven by a marked Poisson process representing infiltration from rainfall. The analytical solution is obtained in terms of the probability density function of soil moisture, wherein the combined influence of climate, soil, and vegetation appears in mathematical form. The role of soil texture as well as the relative importance of the timing and amount of rainfall on soil moisture dynamics are investigated in relation to the physiological characteristics of different functional vegetation types.

The concept of plant functional types is a necessary one in the attempt to capture the essential dynamics of ecosystems and a more general application of modeling schemes. We will use the term to group plants that respond in a similar way to a syndrome of environmental factors [13]. Although recognizing the existence of major differences among species and individuals of each particular group, we will refer in generic terms to trees, grasses, and shrubs assigning different types of dynamic responses to each group to emphasize their different use of the resource and the impact that soil moisture fluctuations have on them.

In the third paper [29], following the approach adopted in [30,34,35], the soil moisture dynamics is related to the plant physiological characteristics to study the vegetation response to water stress. In particular, vegetation water stress is linked to soil moisture levels which mark important changes in the physiological activity of plants. Two important thresholds are the moisture content below which transpiration (and thus also photosynthetic activity) starts being reduced and the moisture level at which plants begin to wilt ([5,14,26] and references therein). The statistical description of periods of water stress, both in their intensity as well as in their duration, is based on the crossing analysis of the above-mentioned soil moisture thresholds, leading to an objective linkage of the intensity and duration of water stress to soil, climate, and vegetation characteristics. A measure of vegetation mean water stress is then proposed which incorporates the different important aspects that moisture scarcity may have over the whole growing season including number, duration, and severity of water stress periods.

Applying such a measure of vegetation water stress, different functional vegetation types living in the same environment turn out to have a similar level of normalized water stress, although they have quite different mechanisms of water use. Thus plants with high water-use efficiency (e.g. C_4 grasses), especially when combined with relatively shallow rooting depths, tend to have shorter yet more frequent periods of water stress compared to the longer but rarer ones of deeper-rooted plants with more "prudent" exploitation of soil moisture. These links of causes and effects in the plant responses to soil moisture deficits may turn out to be important in the understanding of the different strategies undertaken by plants to resist drought. They may also help to clarify the necessary environmental conditions for the possible coexistence of different functional vegetation types or for the existence of plant ecosystems in metastable states (i.e. delicate equilibrium conditions which under the influence of strong external disturbances may shift to new and different states).

The fourth part of the series [20] deals with particular applications of the modeling scheme to different types of water-controlled ecosystems. The selected case studies refer to sites where appropriate data are available. The first application concerns the warm savanna of Nylvsley in South Africa [40], where a relatively homogenous soil texture and rooting depth of trees and grasses, as well as the presence of different woody and herbaceous plants with well-documented physiological characteristics, make this location ideal to asses the role of different plant physiological properties on the water balance and vegetation stress. The second example is provided by the brushland of La Copita (TX), where the issue of tree–grass coexistence is complicated by a strong interannual climatic variability and markedly different rooting depths between trees and grasses. Here trees and grasses seem to coexist in a dynamic equilibrium which tends toward brushland in wet years and to grassland in the drier years, but with an evolution highly dependent on the particular succession of dry and wet periods. The last case study deals with a short-grass steppe in Colorado, where the grassland exists in fragile equilibrium between desert and forest encroachment. This makes particularly important the issue of the control of reproductive strategies by soil water availability as well as the dependence of these processes on soil properties.

Although aware of the risks of over-simplification involved in the ecohydrological model here discussed, we are nevertheless confident that this type of effort is necessary for the quantitative understanding of the complex climate–soil–vegetation interaction and the resulting response of vegetation ecosystems. Extensions under study involve the relaxation of some of the assumptions to include elements of spatial and seasonal dynamics. Once the plant response is analyzed during an average growing season, the vegetation response to interannual climatic fluctuations has to be considered. Preliminary results along this line have shown how nonlinearity in soil moisture dynamics may in some cases strongly enhance the effects of interannual climatic variability leading to a bimodal distribution of mean soil moisture values during the growing season [8,31]. It is expected that the elements provided by these analyses will allow the implementation of more realistic models for the study of the evolutionary dynamics of vegetation in water-controlled ecosystems. Such models will be implemented using a spatial field of fitness factors derived from soil, climate, and vegetation which evolve in time with climate fluctuations and effectively control the local interactions of existing vegetation. Thus the probability of death, reproduction, and colonization are naturally a function of the water stress condition and evolve throughout time allowing a linkage between vegetation patterns and a changing environment.

Acknowledgements

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Appendix A. List of symbols

b	parameter defining, along with $\bar{\Psi}_s$, the shape of the soil water retention curve, dimensionless
c	parameter defining, along with K_s, the power-law relationship between soil moisture and hydraulic conductivity, dimensionless
C	integration constant of the steady-state soil moisture pdf, d^{-1}
C_ζ	integration constant of the steady-state pdf of the static water stress, d^{-1}
e	absolute pressure of water vapor, kPa
e_s	absolute pressure of water vapor at saturation, kPa
$E[s(t)]$	evapotranspiration rate, cm d^{-1}
E_{max}	average daily evapotranspiration rate under unrestricted soil moisture conditions, cm d^{-1}
$E_{ns}(s)$	evapotranspiration by plants in non-stressed conditions (with $s > s^*$), cm d^{-1}
$E_s(s)$	evapotranspiration by plants under stress (with $s < s^*$), cm d^{-1}
E_w	average daily evaporation rate at $s = s_w$, cm d^{-1}
$f_T(\tau)$	probability density function of the interarrival time between rainfall events, d^{-1}.
$f_H(h)$	probability density function of the amount of precipitation per rainfall event, cm^{-1}
$f_Y(y, s)$	probability density function of the normalized amount of infiltration per rainfall event, dimensionless
$f_Z(\zeta)$	probability density function of the static water stress
$F_Z(\zeta)$	cumulative density function of the static water stress, dimensionless
${}_2F_1[\cdot,\cdot;\cdot;\cdot]$	hypergeometric function, Ref. [1], n. 15.1.1
g	gravitational acceleration, $g = 9.807$ m s^{-2}
g_L	leaf conductance, mmol m^{-2} s^{-1}
G	gravitational potential, MPa
G_a	atmosphere gravitational potential, MPa
G_p	protoplast gravitational potential, MPa
G_x	xylem gravitational potential, MPa
h	rainfall depth per rain event, cm
h'	net rainfall depth per storm event after subtraction of interception losses, cm
h_i	amount of precipitation of the ith rainfall event, cm
$I(t)$	canopy interception rate, cm d^{-1}
k	parameter used in the definition of the average dynamic stress to take into account plant resistance to water stress, dimensionless
$K(s)$	hydraulic conductivity, cm d^{-1}
$K_{lat}(s)$	lateral hydraulic conductivity, cm d^{-1}
K_s	saturated hydraulic conductivity, cm d^{-1}
$L[s(t)]$	leakage or deep infiltration rate, cm d^{-1}
m	parameter used in the representation of the leakage loss rate, d^{-1}
M	matric potential, MPa
n	soil porosity, dimensionless
n_ξ	number of crossings of the soil moisture threshold ξ during a growing season, dimensionless
$\bar{n}_{s_w}$	average number of crossings of the permanent wilting point during a growing season, dimensionless
$\bar{n}_{s^*}$	average number of crossings of s^* during a growing season, dimensionless
$\bar{n}_\xi$	average number of crossings of the soil moisture threshold ξ during the growing season, dimensionless
$p(s)$	steady-state probability density function of soil moisture, dimensionless
$p(s,t)$	time-dependent probability density function of soil moisture, dimensionless
$P(s)$	steady-state cumulative density function of soil moisture, dimensionless
q	parameter describing the degree of nonlinearity in the relationship between soil moisture deficit and static vegetation stress, dimensionless
$Q[s(t), t]$	rate of surface runoff, cm d^{-1}
R	universal gas constant, $R = 8.31436$ J mol^{-1} K^{-1}
R_v	gas constant for water vapor, $R = 461.499$ J kg^{-1} K^{-1}
$R(t)$	rainfall rate, cm d^{-1}
s	relative soil moisture, dimensionless
s_{fc}	soil field capacity, dimensionless
s_h	hygroscopic point or soil moisture level below which water can not be extracted from the soil through evaporation, dimensionless
s_w	permanent wilting point or soil moisture level below which plants stop transpiring and begin to wilt, dimensionless

s_0	initial soil moisture level of the soil-drying process, dimensionless
s^*	soil moisture level below which plants begin closing their stomata, dimensionless
$S(x)$	local slope at site x, dimensionless
t	time, d
t_i	time associated with the ith rainfall event, d
t'_i	time associated with the ith event reaching the soil after losses for interception are subtracted, d
$t_{s_{fc}}$	time to reach the condition $s = s_{fc}$ during the soil-drying process, d
t_{s_w}	time to reach the condition $s = s_w$ during the soil-drying process, d
t_{s^*}	time to reach the condition $s = s^*$ during the soil-drying process, d
T	absolute temperature, K
T_{seas}	duration of the growing season, d
T_ξ	duration of an excursion of the trajectory of soil moisture below ξ, d
$\bar{T}_{s_w}$	average duration of an excursion of the trajectory of soil moisture below s_w, d
$\bar{T}_{s^*}$	average duration of an excursion of the trajectory of soil moisture below s^*, d
$\bar{T}_\xi$	average duration of an excursion of the trajectory of soil moisture below ξ, d
u	dummy variable of integration
V_w	partial molal volume of pure water, $V_w = 18 \times 10^{-6}$ m^3 mol^{-1}
y	normalized infiltrated depth of water per rainfall event, dimensionless
y_i	normalized infiltrated depth of water of the ith rainfall event, dimensionless
z	elevation above the reference level, m
Z_r	depth of active soil or root depth, cm
α	mean depth of rainfall events, cm
β	parameter defining, along with K_s, the relationship between soil moisture and hydraulic conductivity when an exponential law is used, dimensionless
γ	inverse of the normalized mean rainfall depth, $\gamma = nZ_r/\alpha$, dimensionless
$\Gamma[\cdot]$	complete gamma function, Ref. [1], n. 6.1.1
$\Gamma[\cdot,\cdot]$	incomplete gamma function, Ref. [1], n. 6.5.3
$\delta(\cdot)$	Dirac delta function; its dimension is the inverse of that of its argument
Δ	amount of precipitation intercepted by canopy cover for each rainfall event, cm
Δ_g	amount of precipitation intercepted by herbaceous vegetation for each rainfall event, cm
Δ_t	amount of precipitation intercepted by woody vegetation for each rainfall event, cm
$\zeta(t)$	static water stress, dimensionless
$\bar{\zeta}$	average static water stress during a growing season, dimensionless
$\bar{\zeta}'$	average static water stress of the periods when the plant is under stress, dimensionless
η	normalized average daily evapotranspiration rate under unrestricted soil moisture conditions, d^{-1}
η_w	normalized average daily evaporation rate at $s = s_w$, d^{-1}
$\bar{\theta}$	average dynamic water stress, dimensionless
Θ	total amount of rainfall during a growing season, cm
λ	arrival rate of rainfall events, d^{-1}
λ'	arrival rate of rainfall events that reach the ground without being completely intercepted by the canopy, $\lambda' = \lambda \exp(-\Delta/\alpha)$, d^{-1}
$\nu(\xi)$	frequency of the upcrossings events of the soil moisture threshold ξ, d^{-1}
ξ	generic threshold of soil moisture, dimensionless
Π	pressure potential, MPa
Π_a	atmosphere pressure potential, MPa
Π_p	protoplast pressure potential, MPa
Π_x	xylem pressure potential, MPa
$\rho(s)$	normalized water losses, d^{-1}
ρ_v	density of water vapor in moist air, kg m^{-3}
ρ_w	water density, kg m^{-3}
τ	interarrival time between rainfall events, d
τ_i	interarrival time between the ith and the $(i-1)$th rainfall events, d
τ'_i	interarrival time between the ith and the $(i-1)$th events reaching the soil after losses for interception are subtracted, d
$\varphi[s(t),t]$	rate of infiltration from rainfall, cm d^{-1}
Φ_{lat}	lateral soil moisture flux, cm d^{-1}
$\chi[s(t)]$	rate of water losses, cm d^{-1}
$\bar{\Psi}_s$	parameter defining, along with b, the shape of the soil water retention curve, MPa
Ψ	total water potential, MPa
Ψ_a	atmosphere water potential, MPa

Ψ_p	protoplast water potential, MPa
Ψ_s	soil water potential, MPa
Ψ_{s,s_h}	soil water potential at $s = s_h$, MPa
Ψ_{s,s_w}	soil water potential at $s = s_w$, MPa
Ψ_{s,s^*}	soil water potential at $s = s^*$, MPa
Ψ_x	xylem water potential, MPa
Ω	osmotic potential, MPa
Ω_p	protoplast osmotic potential, MPa
Ω_x	xylem osmotic potential, MPa

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