Stochastic Dynamics of Plant-Water Interactions

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Abstract

Describing water flow from soil through plants to the atmosphere remains a formidable scientific challenge despite years of research. This challenge is not surprising given the high dimensionality and degree of nonlinearity of the soil-plant system, which evolves in space and time according to complex internal physical, chemical, and biological laws forced by external hydroclimatic variability. Although rigorous microscopic laws for this system still await development, some progress can be made on the formulation of macroscopic laws that upscale known submacroscopic processes and use surrogate stochasticity to preserve the probabilistic and spectral information content of the high dimensional system. The external hydroclimatic forcing is inherently intermittent with variability across all scales, thereby precluding the use of standard approximations employed in analysis of stochastic processes (e.g., small noise perturbations). Examples are provided to show how superposition of stochasticity at multiple space-time scales shapes plant-water interactions.

It is surely one of the triumphs of evolution that Nature discovered how to make highly accurate machines in such a noisy environment.

(Phillips & Quake 2006)

1. INTRODUCTION

We explore the stochasticity in plant-water dynamics with emphasis on its consequences for deriving laws for plant-water interactions at larger scales (referred to as macroscopic laws) starting from what is known at the smaller scales. The theme of this review purposely resembles a centuries-old problem whose answer led to the development of statistical mechanics and linkages to thermodynamics (see Nelson 2004 for a clear introduction to the applications of thermodynamics and statistical mechanics to biological systems; Dewar 2003, Martyushev & Seleznev 2006, Ozawa et al. 2003, Roderick 2001, and Whitfield 2005, among others, advocate thermodynamic principles to explain macroscopic behaviors in complex natural systems). The original problem considered whether knowledge of molecular matter via microscopic laws permitted description of macroscopic behavior. Naturally, the large number of molecules that make up macroscopic systems and their stochastic motion invites statistical treatment. Although plant-water interactions share attributes with molecular systems, including their high dimensionality (because of the large number of interacting processes impacting water movement within the soil-plant system), there are fundamental differences that prevent immediate applications of statistical mechanics to plant-water interactions:

1. The fundamental submacroscopic laws describing water movement within the plant system are not entirely known (e.g., water flow at the root-soil interface, in the xylem, and in the leaf);
2. Averaging the individual properties of these submacroscopic laws may not provide a meaningful description for the next hierarchical level because of nonlinear interactions and lack of scale separation (i.e., presence of significant variability at all scales); and
3. The drivers of many macroscopic laws remain stochastic because the soil-plant system is open to external environmental forcing such as rainfall, temperature, and radiation. In other words, the soil-plant system is open and far from equilibrium.

Our main objective is to present what is known about plant-water interactions within a stochastic framework, building on recent advances in dynamical systems theory, complex systems science, and stochastic processes. Long-term field measurements at various time and spatial scales are becoming increasingly available thereby providing unprecedented details of the spatial and temporal statistics of plant-water interactions (e.g., long-term ecosystem water vapor flux measurements via eddy-covariance methods, gas-exchange measurements, sapflow and soil moisture measurements, tree-ring reconstruction of net primary productivity, and space-borne leaf area index measurements, to name a few). In the absence of a theory for microscopic dynamics, such a stochastic framework may be a first step that inspires the future statistical mechanics theory in ecology and plant-water dynamics.

2. REVIEW OF REVIEWS

Previous reviews of plant-water interactions have been conducted by Noy Meir (1973) for desert ecosystems and Lathwell & Grove (1986) for tropical ecosystems. The former primarily dealt with space-time stochasticity in rainfall, whereas the latter dealt with the physical and chemical properties of soils that impact ecosystem productivity.

At the plant scale, a wealth of review articles has also dealt with physical, chemical, and physiological aspects of plant-water interactions, primarily the effects of water stress on physiological processes in various organs, gas exchange processes, and plant hydrodynamics. We mention in particular the reviews of Hsiao (1973) on plant-water stress, Sack & Holbrook (2006) on leaf hydraulics, and Sperry (2000) and Sperry et al. (2002) on hydraulic constraints to leaf water supply, as well as several books that summarize the state of knowledge up to the past two decades or so (e.g., Jones 1992, Kramer & Boyer 1995, Larcher 1995, Nobel 2005, Steffen & Denmead 1988).

At the watershed scale, a number of reviews presented the consequences of plant-water interactions on the hydrologic cycle with emphasis on potential feedbacks on the climate system (Brutsaert 1982, Eagleson 2002) and biogeochemical cycling (Eagleson 2002, Schlesinger 1997). The interplay between stochasticity and nonlinear dynamics in ecosystems has also received significant attention—evidenced by a recent special issue of *Oecologia* (in 2005; see also Austin et al. 2004, Schwinning & Sala 2004). Finally, the stochastic aspects of hydroclimatic forcing and their propagation within water-limited ecosystems were also the subject of several recent reviews (Kull & Jarvis 1995, Porporato & Rodriguez-Iturbe 2002, Porporato et al. 2002, Rodriguez-Iturbe & Porporato 2004). The scope of this review diverges from these earlier reviews by focusing on stochasticity and how it arises in plant-water dynamics. We also discuss what the consequences are of incorporating such stochasticity in sample contemporary ecological problems.

3. STOCHASTIC PROCESSES: AN ALEATORY ORIENTATION

The soil-plant-atmosphere system can be considered a stochastic dynamical system evolving in space and time according to its internal physical, chemical, and biological laws and subject to external variability. We speak of stochasticity in a broad sense, referring to the practical impossibility of precisely modeling and predicting temporal evolution and spatial configuration of the system at all spatial and temporal scales. We avoid the philosophical discussion on the true nature of this unpredictable and irregular behavior (Ford 1983) and whether it should be attributed to high dimensionality, instabilities, and sensitivities to initial conditions (Boffetta et al. 2002, Cross & Hohenberg 1993, Eckmann & Ruelle 1985), or to simple ignorance of the detailed functioning of the system that by itself requires a statistical approach (Clark & Gelfand 2006, Jaynes 2003, Kass & Raftery 1995, Sivia & Skilling 2006). To some extent, all these are present and somewhat interlinked in each compartment of the soil-plant-atmosphere system.

Stochastic fluctuations are often referred to as random noise, and solutions of equations with random parameters (or random dynamical systems) are called stochastic processes or random functions. The novice may be easily disoriented and daunted

by the vast literature in this branch of mathematics, which was inspired by different disciplines such as physics, chemistry, theoretical finance, communication and information theory, hydrology, etc., and which benefited from fundamental contributions by mathematicians and scientists such as Laplace, Poisson, Maxwell, Bolzmann, Einstein, and Kolmogorov, to name a few. The following is an incomplete orientation list of references for applications of random functions (Bendat & Piersol 1971, Papoulis 1991, Vanmarke 1983), stochastic processes (Cox & Miller 1977, Gardiner 2004, Horsthemke & Lefever 1984, Larson & Shubert 1979, van Kampen 1992) and their applications in the natural sciences (Sornette 2004).

The mathematical modeling of noisy dynamics typically requires a considerable degree of abstraction and simplification. In general, when the analysis is limited to the temporal domain, the existing literature is sufficiently developed for some classes of noise. If the governing (or state) variables are or can be approximated as discrete, one can employ the well-established theory of Markov chains (Cox & Miller 1977, Norris 1998); more typically, the state variables are time continuous and one must resort to so-called stochastic differential equations (SDEs). The most typical building blocks of continuous-state stochastic processes are either Gaussian noises (Brownian motion or Wiener process), used when the irregular fluctuations do not appear to be pulsing and intermittent, or jumps compounded with suitable point processes, used when the pulsing components and the space-time intermittency become dominant (e.g., hourly or daily rainfall). The basic models just mentioned are characterized by random independent increments so that they do not add new memory to the system. Because of their flat power spectrum, they are also called white noises. Their use always entails some subtle mathematical aberrations at very fine scales such as discontinuities in the state variables, as is the case for jump processes, or in the first derivative, as is the case for Brownian motion and its relatives (Cox & Miller 1977, Gardiner 2004). Two manifestations of these aberrations appear when analyzing the trajectory of a Brownian particle at infinitely small temporal scales using one stochastic differential equation. The first manifestation is its discontinuous velocities, which is interpreted as being produced by an unrealistic infinite force, and the second is that the trajectories cross a given level infinitely many times in an infinitesimal time interval. These pathologies are the necessary price paid for simplicity, and may be acceptable so long as no special physical meaning is attributed to the fluctuations at such short timescales.

Loosely speaking, white noises give rise to Markovian processes or processes in which future states do not directly depend on past states. They can be described mathematically as either SDEs for the state variables, emphasizing a specific realization (e.g., one possible outcome) of the stochastic process, or the ensemble of realizations (e.g., all possible outcomes) in terms of partial differential equations (PDEs) for the probability density functions of the state variables described by the SDEs (Gardiner 2004, Horsthemke & Lefever 1984, van Kampen 1992).

The use of non-Markovian (or colored noises), fractional Brownian motion, and Levy-type processes has gained recent popularity because of their ability to describe fine temporal dynamics, presence of scaling (e.g., power-laws), and long-term memory effects signified by slowly decaying temporal autocorrelations (Horsthemke & Lefever 1984, van Kampen 1992). Unfortunately, this standard mathematical

machinery becomes difficult to implement analytically for nonlinear systems with two or more degrees of freedom (Arnold 2003), and even more difficult when considering space-time processes (Bouchaud & Georges 1990, Cross & Hohenberg 1993, Durrett & Levin 1994, Falkovich et al. 2001, Sagues & Sancho 2004).

We conclude this orientation by noting that the presence of noise in the context of plant-water dynamics may not be necessarily a source of disorder within the system but can be a stabilizing factor (e.g., promoting coexistence among plants), a pattern generator, or a mechanism responsible for phase transitions (e.g., abrupt changes such as extinctions and catastrophic shifts), all of which are now gaining attention in a number of fields (D'Odorico et al. 2005, Horsthemke & Lefever 1984, Porporato & D'Odorico 2004, Rietkerk et al. 2004, Sagues & Sancho 2004, Scheffer et al. 2001, Sornette 2004, Vandenbroeck et al. 1994).

4. STOCHASTIC DYNAMICS

The genesis of stochasticity in the dynamics of plant-water uptake may be traced back to both internal and external factors. To illustrate the origins of internal factors, consider the conceptual diagram in **Figure 1** showing on the abscissa the dimensionality of the system and on the ordinate the degree of nonlinearity of the equations describing the interactions among its variables. As we discuss below, water movement in the soil-plant system typically resides in the high-dimensional and nonlinear region of this figure. When the dynamics of these interactions is approximated by a few coupled equations, the high dimensionality is replaced by stochasticity to preserve the probabilistic and spectral information content present in the natural system. As a result the stochasticity appears in model parameters of the simplified system (e.g., hydraulic conductivity of the soil pores and plant conduits, foliage distributions, stomatal properties, etc.) as well as in the external variability of the hydroclimatic forcing (e.g., rainfall, wind, temperature, radiation).

This stochastic representation of plant-water dynamics is logical in the context of propagating projected climatic fluctuations—an example of external forcing—on ecosystem processes. Vitousek's (1992) review "Global Environmental Change" pointed out some of the problems and difficulties in propagating climate projections to ecosystem processes with the current modeling framework. This difficulty is driven by the fact that ecosystems respond to the full range of hydroclimate variability (particularly the extremes). Hence, there are two practical benefits in considering the plant-water system in a stochastic but simplified framework: (*a*) reduced complexity and (*b*) proper accounting of hydroclimatic variability.

4.1. Origin of Internal Stochasticity

Movement of water in the soil-plant-atmosphere system (**Figure 2**) begins with water migrating from wetter to drier soil pores adjacent to the rooting system following potential energy gradients. Once it has reached and entered the rooting system through a patchy and heterogeneous root membrane, water flows through a tortuous and complex network within the xylem. It experiences phase transition within the leaves,
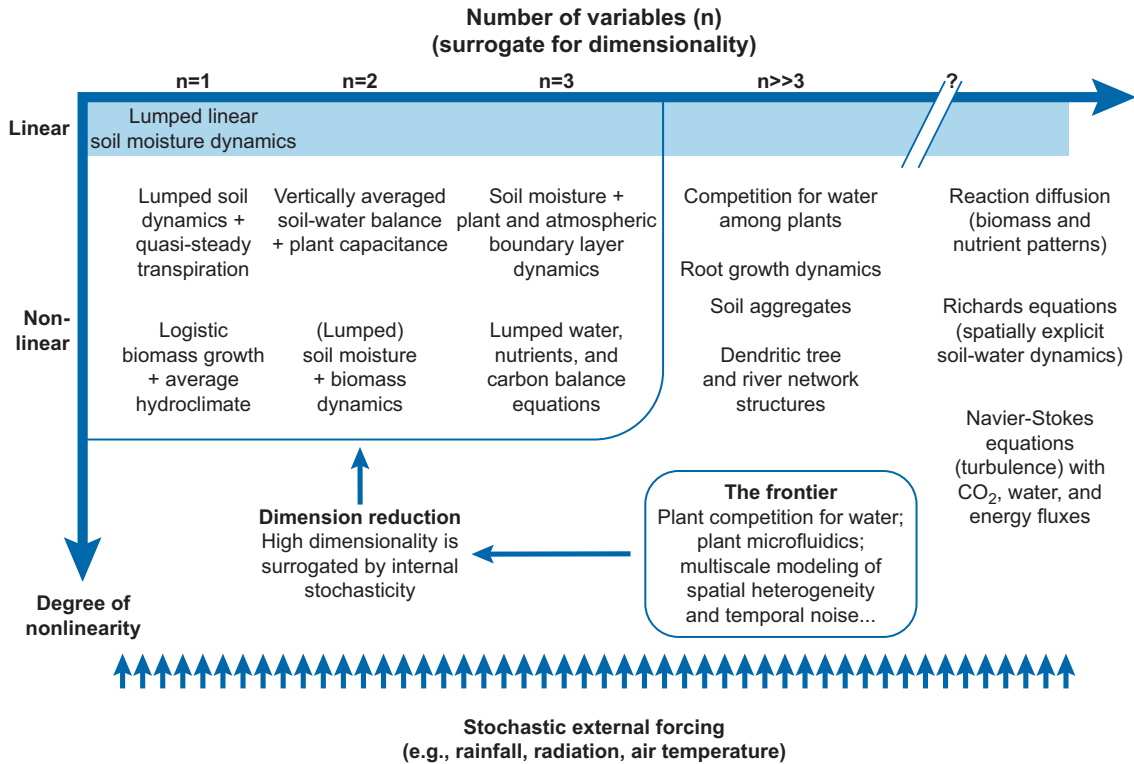
Number of variables (n)
(surrogate for dimensionality)

Figure 1

Conceptual diagram showing the complexity of the soil-plant system viewed in the
dimensionality/nonlinearity plane. Stochasticity arises when simplified models attempt to
capture this complexity (revised from Strogatz 1994). Surrogate stochasticity is added to the
simplified models to preserve the probabilistic and spectral information content of the original
system. We refer to internal stochasticity as related to the presence of random parameters to
distinguish it from the external forcing, which is present at all scales and is stochastic in nature.
The "frontier" represents open problems lacking rigorous mathematical formulations.

and exits to the atmosphere in the form of water vapor through leaf stomata. The vapor
molecules are then transported by turbulent eddies from within the canopy into the
free atmosphere. The transporting energy and sizes of these eddies are partially set by
complex interactions among canopy attributes (e.g., leaf area and height), mesoscale
forcing (e.g., geostrophic winds and weather patterns), landscape heterogeneity, and
the airflow above the canopy.

   Resolving all spatial scales needed to describe the trajectory of water in the soil-
plant-atmosphere system necessitates a three-dimensional simulation domain span-
ning 0.1 μm to tens of kilometers, equivalent to requiring $\sim(10^{10})^3$ nodes per time
step. The time step must be sufficiently fine to resolve the fastest process, which is the
action of viscous dissipation on turbulent fluctuations in the atmosphere ($\sim$0.001 s).
This high dimensionality in space and time is well beyond the capacity of any
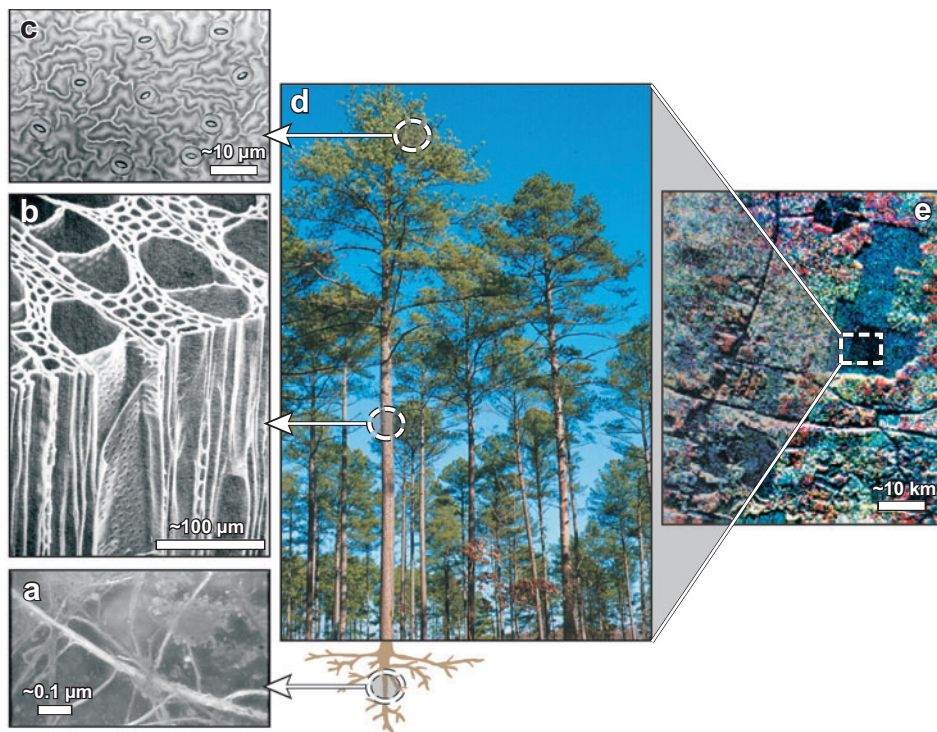
Figure 2

Water moves from the soil to the atmosphere through roots, xylem, and stomata: (*a*) The
root-soil system is heterogeneous at a wide range of scales (smallest ∼0.1 μm). (*b*) The xylem
within the individual branches generate a complex network whose precise details are rarely
known in plant-water dynamics modeling (scale ∼100 μm; after Zimmerman 1983).
(*c*) Plant-atmosphere gas exchange is controlled by stomata (scale ∼10 μm; from Grant &
Vatnick 2004). (*d*) Turbulent eddies transport water vapor from stomata to the free
atmosphere (scale ∼10 m). (*e*) Atmospheric states are modulated by the landscape
heterogeneity (scale ∼10 km). Note that stochasticity is present at all spatial scales.

brute-force computation at present and in the foreseeable future. Furthermore, there
are insurmountable scale issues in attempting to relate water flow in the soil-plant
system with its driving forces. For one, the constitutive laws currently used to describe
water movement in the soil, root, plant, and atmosphere systems do not share the
same representative elementary volume (REV), defined as the minimal spatial scale
of representation.

Consider the constitutive laws in each of the three compartments of the soil-plant-
atmosphere system:

1. Soil. Darcy's law and the water continuity equation are typically combined in
the Richards equation, which describes water movement in unsaturated soils near
the rooting zone at an REV scale containing a sufficiently large number of pore
spaces. This is a nonlinear partial differential equation that provides a space-time

description of water movement but averages out the variability of the soil and root matrix at scales smaller than the REV (Hillel 2004, Jury et al. 1991). It is a major theoretical challenge to up-scale this equation beyond the REV to include the effects of spatial heterogeneities in soil properties, macroporosity, and preferential flows of water and nutrients at discontinuities (e.g., large roots, rocks, etc.). Even the application of Darcy's law within a REV that includes such randomness and heterogeneities is questionable (Steffen & Denmead 1988). In particular, the origin of preferential flows and their impacts on the plant-water relationship remain open areas of research (de Rooij 2000).

2. Plant. Similar problems arise at the plant level. Laminar flow equations (e.g., Hagen-Poiseulle's law for capillary tubes) based on the continuum assumption in fluid mechanics are typically used to describe root and xylem water movement. These assumptions are now being challenged by recent research. For example, predictions of the onset of embolism in the plant xylem require microscale thermodynamic description of air and water microfluid dynamics not captured by Poiseulle's law; the derivation of observed vulnerability curves (Sperry 2000, Sperry et al. 2002) from first principles has not yet been tackled, and the connection between stomatal conductance and the plant-xylem system remains a subject of research (Katul et al. 2003, Oren et al. 1999, Sack & Holbrook 2006, Sperry & Hacke 2002, Sperry et al. 2002).

3. Atmosphere. Mass, momentum, and energy exchanges between the canopy and the lower atmosphere are described by the Navier-Stokes equations and require detailed description of the boundary conditions at the plant-atmosphere interface. Describing the boundary conditions for these equations is complicated by stochasticity at multiple scales. Randomness, beginning with patchiness at the stomatal level and progressing to patchiness in stomatal conductance (Buckley et al. 1997), random leaf distribution, leaf area density, and onward to the atmosphere must be accounted for as dynamic boundary conditions to the Navier-Stokes equations (Albertson et al. 2001). Even for the simple case of a static boundary condition, the Navier-Stokes equations cannot be solved at all the necessary scales (Finnigan 2000).

These constitutive laws (the Richards equation, Poiseuille law, and Navier-Stokes equations) often provide reasonable approximations at a particular scale, typically where microscopic heterogeneities can be averaged out. However, a major challenge is the derivation of effective parameters in simplified models at larger scales (e.g., Bohrer et al. 2005, Chuang et al. 2006, Ewers et al. 2007, Katul et al. 1997). Clearly, novel tactics are needed to further the development of these constitutive laws for applications in the plant system at much finer scales (<10 μm), and of ways to properly scale them to coarser levels. Some answers may be found in microfluid dynamics, a field that is rapidly gaining attention (Squires & Quake 2005).

Formal applications of homogenization and averaging techniques (Torquato 2002) may guide the derivation of effective parameters for the current constitutive laws. Applications of such techniques to the set of equations described above are further complicated by three factors: (*a*) the inherent nonlinearities in the resistance to water flow, soil hydraulics, canopy turbulence, and plant responses to temperature and light, among others; (*b*) the fact that the external forcing can be highly intermittent (e.g.,
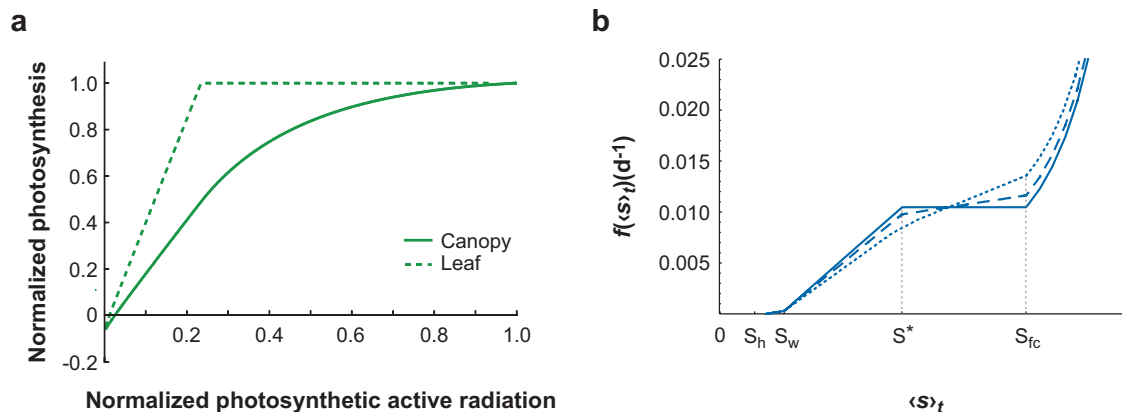
a

Normalized photosynthesis (y-axis)

Normalized photosynthetic active radiation (x-axis)

— Canopy
‑ ‑ ‑ Leaf

b

$f(\langle s \rangle_t)(d^{-1})$ (y-axis)

$\langle s \rangle_t$ (x-axis)

S_h S_w S^* S_{fc}

Figure 3

Examples of smoothing of nonlinearities appearing in macroscopic equations by averaging in
space and time. (*a*) Space: differences in leaf-and-canopy-photosynthesis response to light
when vertically averaging from leaf to entire canopy. A simplified version of the Farquhar
photosynthesis model (Farquhar et al. 1980) is used for leaf photosynthesis, whereas the
CANVEG model is used to scale it up for the canopy (Baldocchi 1992, Lai et al. 2000, Siqueira
et al. 2002); the CANVEG model is a multilayer representation of the canopy that includes
light attenuation, leaf physiology, leaf energy balance, and turbulent transport processes
(assuming mean air temperature, relative humidity, wind speed, and CO_2 concentration above
the canopy are unaltered). (*b*) Time: equivalent soil water loss function $f(\langle s \rangle_t)$ for the temporal
soil moisture mean $\langle s \rangle_t$ (Laio et al. 2002). The continuous line is the nonlinear loss function at
the daily level, whereas the dashed and dotted lines refer to long-term averages for different
noise levels representing rainfall variability. S_h, the hygroscopic point; S_w, the wilting point;
S^*, soil moisture at the onset of water stress; and S_{fc}, the field capacity.

rainfall, sunflecks, etc.), producing jumps that abruptly force the system toward dif-
ferent states; and (*c*) the rare presence of a clear scale separation. As a consequence, the
up-scaling smoothes and reduces nonlinearities but never eliminates them (as illus-
trated spatially for photosynthesis and temporally for soil water in **Figure 3**). Further-
more, the classic simplifying techniques, such as "small-noise and system-size expan-
sions," are not directly applicable in this context (Gardiner 2004, van Kampen 1992).

4.2. Origin of External Stochasticity

One of the main challenges in modeling the temporal dynamics of the soil-plant
system is the noise structure of the hydroclimatic forcing. Depending on the temporal
scale, some hydroclimatic components may be modeled as continuous Gaussian noise
or processes driven by Gaussian noise (e.g., annual rainfall, daily temperature, and
hourly wind velocity) and others may be modeled as intermittent jump processes (e.g.,
daily rainfall, subhourly photon flux density in the canopy understory). This strong
intermittency alone suffices to prevent direct applications of traditional techniques
used to simplify stochastic processes, such as small-noise expansions (Gardiner 2004,
van Kampen 1992).

Next we show examples of the complex noise structure at different scales of temperature, light and rainfall, which are among the most important hydroclimatic drivers of the soil-plant system. We start in **Figure 4** with measurements of air temperature above the canopy at scales ranging from interannual to fractions of seconds. Note the large and organized turbulent fluctuations around the diurnal cycle in mean air temperature (∼5°C). The figure shows that these excursions are intermittent and highly nonstationary during daytime as evidenced by progressive changes in the variance of air temperature. Even at sufficiently small timescales (∼10 s), large ramp-like temperature excursions are often detected (**Figure 4**). The latter ones are connected with bursts of air having high velocity and low temperature (so-called sweep events) that penetrate the canopy from above, exchange heat with the vegetation, and then are ejected back to the atmosphere (ejection events) with lower velocity and higher temperature (e.g., Katul et al. 2006). Such rapid changes in air temperature can significantly affect temperature-dependent kinetic constants in plant processes.

Light above the canopy may also become intermittent at short timescales because of the passage of clouds (Knapp 1993). Furthermore, within the canopy the light regime can be highly stochastic with intermittent pulses (**Figure 5**) at scales of seconds to minutes owing to random shading by the overlying canopy. This means that photosynthesis of the understory, which is a nonlinear function of light intensity, is driven by random sunflecks (see Naumburg et al. 2001, Pearcy et al. 1997), as can be seen in **Figure 5**.

The effects of these intermittent and high-frequency variations in light levels on the spatial and temporal water movement within various plant organs have not been sufficiently studied (see Ewers et al. 2007, Oren et al. 1998). Intracrown shading can reduce transpiration of some leaves or branches but more water becomes readily available to support higher water fluxes of the better-illuminated branches. Some evidence of this compensation may be graphically demonstrated in **Figure 5**, where stem-level fluxes do not significantly vary in space and appear better behaved in following the overall diurnal cycle of light variations when compared to the branches downstream. The combination of recent advances in plant hydrodynamic models of water movement in trees and stochastic models of light attenuation within canopy has been employed to successfully represent such variability and its integrated effects on stomatal conductance and branch and tree transpiration (Ewers et al. 2007), and may be employed to a similar end in representing carbon uptake.

Finally, **Figure 6** shows rainfall variability from daily to century timescale. The annual rainfall can be decomposed into several embedded stochastic processes (D'Odorico et al. 2000, Porporato et al. 2006). Similar to temperature, at annual timescales the rainfall process is less intermittent (and near-Gaussian), while at the daily timescale it is highly intermittent. The propagation of such rainfall fluctuations to plant dynamics is gaining increasing usage for predicting an ecosystem's response to future climatic shifts or for explaining historical responses to climatic variations. It is now recognized that changes in total rainfall amounts are not sufficient to explain changes in net primary productivity (Knapp et al. 2002). Shifts in rainfall distributions,
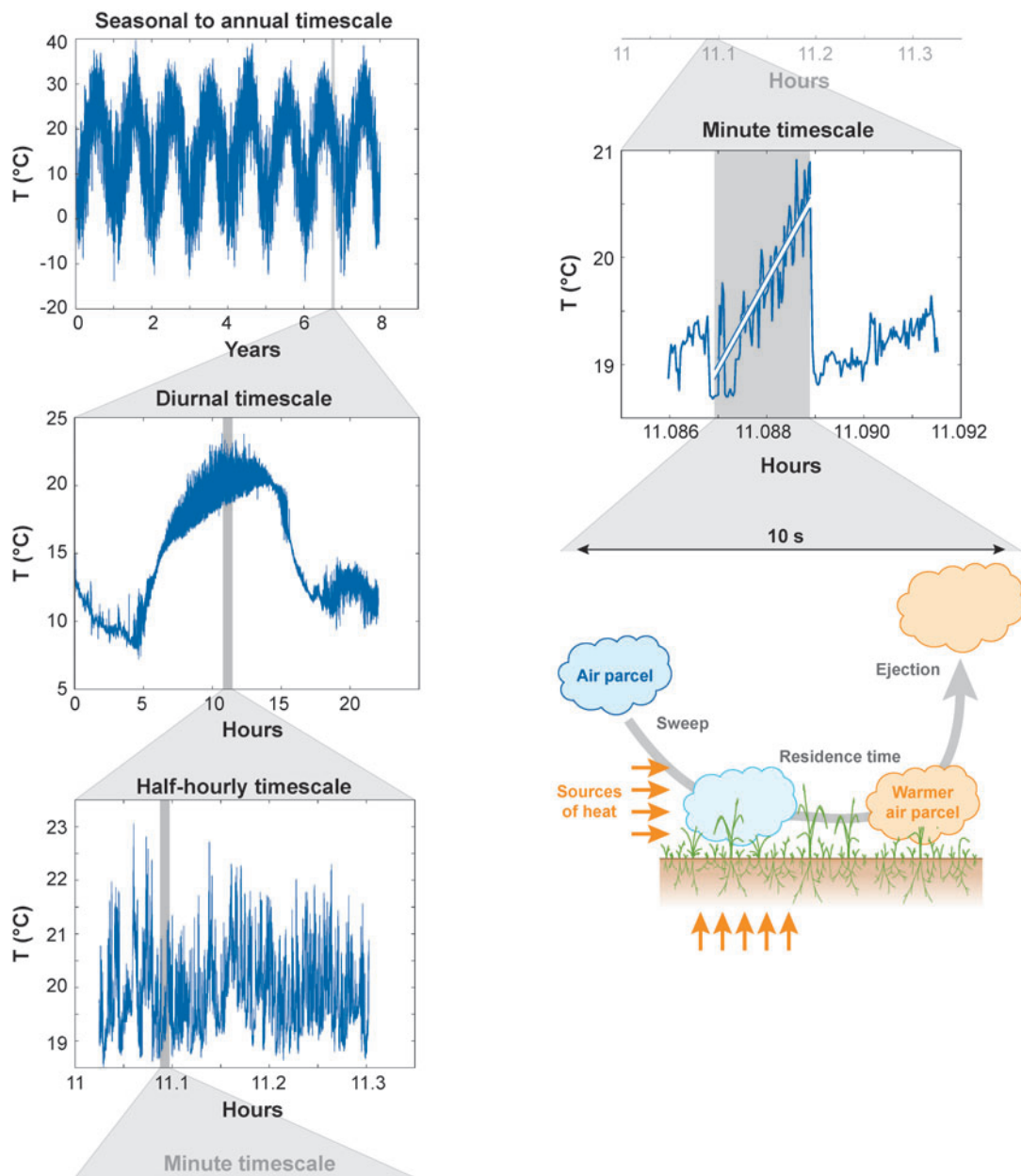
Figure 4

Illustration of the complexity in the hydroclimatic forcing using measured air temperature
fluctuations: (*top-left*) variations at seasonal-to-annual, (*middle-left*) daily, (*bottom-left*)
half-hourly, and (*top-right*) minute timescales. Note the increasing intermittency at shorter
timescales. Data were collected using sonic anemometry at the Duke Forest, near Durham,
North Carolina, from 1997–2005 (see Stoy et al. 2006).
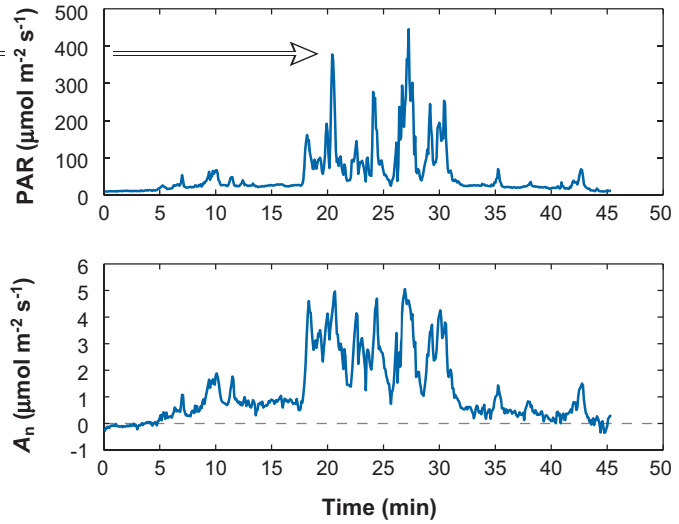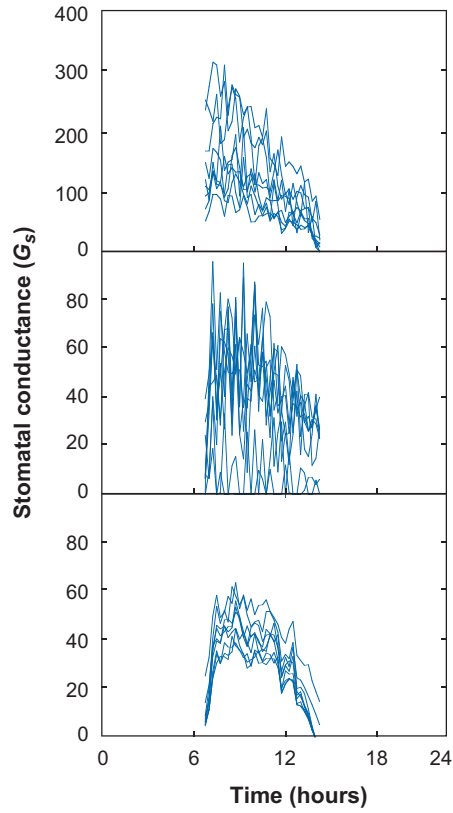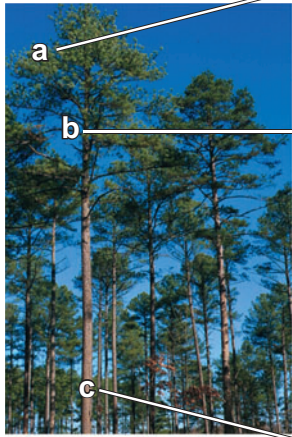
including extremes, cannot be ignored. These shifts remain unreliably predicted by climate models, and reconstructing the full distributional properties from mean projected scenarios continues to be problematic.

Models of rainfall that capture intermittency at daily timescales and the long-term variability at interannual timescale were embedded to describe interannual variability of plant productivity and its sensitivity to both rainfall amounts α and frequency λ (Porporato et al. 2006). Such hierarchical representation of rainfall variability can capture extreme events of storm intensity and drought duration. Interannual statistics of daily intensity and frequency of precipitation events also help explain the reconstructed annual net primary productivity (**Figure 6**).

Rainfall and, to a lesser extent, temperature, humidity, and radiation in turn control the statistics of water stress and carbon assimilation through soil moisture dynamics (Daly & Porporato 2006). Recently, the statistical properties of stochastic soil moisture models (Laio et al. 2001, Milly 1993, Porporato et al. 2004, Rodriguez-Iturbe et al. 1999) and plant water stress (Porporato et al. 2001) have been analytically derived assuming a nonlinear dependence between carbon assimilation and soil moisture at the daily level (Daly et al. 2004, Porporato et al. 2001). Ongoing research investigates how to link these soil moisture fluctuations to actual plant biomass growth and other biotic processes.

Competition for nutrients between plants and soil microbes is also mediated by stochastic dynamics of soil water availability (Kaye & Hart 1997). Characterization of small-scale water, root, and nutrient dynamics can be essential to quantifying plant-water interactions and strategies for carbon allocation and growth (Guswa et al. 2004, Jackson et al. 2000, Lai et al. 2002, Laio et al. 2006, Palmroth et al. 2006). In particular, fluctuating soil moisture conditions impact the cycling of nutrients and decomposition of organic matter in soils with important feedbacks on plants that can induce fluctuations at different timescales, possibly with self-sustained oscillations (D'Odorico et al. 2003, Ehrenfeld et al. 2005, Hogberg & Read 2006, Kaye & Hart 1997, Porporato et al. 2003, Yahdjian et al. 2006).

Figure 7 shows an example of modulations that may be triggered by variations in soil moisture using a simplified model of plant-soil microbial biomass competition (Manzoni & Porporato 2005, Porporato et al. 2003). This competition is quantified by the ratio between immobilization of mineral nitrogen by soil microbes (bacteria and fungi) and plant nitrogen uptake. Fluctuations of soil moisture create shifts in competitive advantage owing to the different responses of plants and soil microbial biomass to water stress. Rapid microbial responses to rewetting have also been

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Figure 5

Sap flux-scaled stomatal conductance (G_s) sampled on a 15-minute time step from (*a*) nine upper branches, (*b*) lower branches, and (*c*) stems. These measurements, taken from Ewers et al. (2007), are for a *Pinus taeda* stand situated in the Sandhills of North Carolina. (*d*) High intermittency in photon flux density measured as photosynthetically active radiation (PAR) and leaf-level photosynthesis (A_n) for *Acer rubrum* in the Duke Forest, North Carolina (Naumburg et al. 2001). Here, $t = 0$ is 11:00 AM local time.
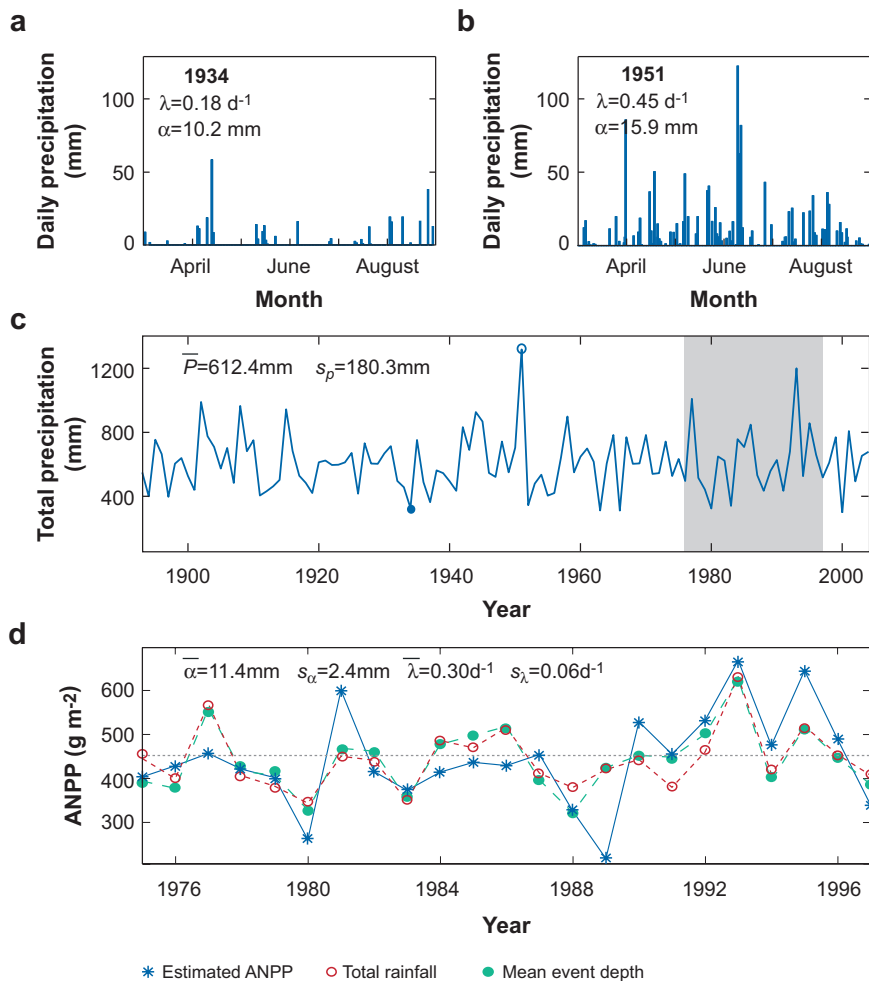
Figure 6

Growing season (April to September) rainfall regime at Manhattan, Kansas. Daily precipitation during (*a*) a very dry and (*b*) a very wet season; (*c*) total annual rainfall, *P*. (*d*) Time series of measured annual net primary productivity (ANPP) at the Konza Prairie Long Term Ecological Research (LTER) Program in Kansas (*asterisks*; **http://intranet.lternet.edu/cgi-bin/anpp.pl**). Also shown are the estimated ANPP obtained with a multiple linear regression model using only the total rainfall (*open circles*, $r^2 = 0.40$) versus the mean event depth, α, and the mean frequency of rainfall events, λ (*solid circles*, $r^2 = 0.47$). Overbars are interannual averages and s_λ is the standard deviation of λ. Redrawn after Porporato et al. (2006).

observed in arid ecosystems and trigger a pulse in nitrogen availability for plants (Austin et al. 2004, Schwinning & Sala 2004). However, prolonged dry conditions or frequent drying-rewetting cycles may damage the microbial community and increase its recovery time (Fierer & Schimel 2002, Schimel 2001).
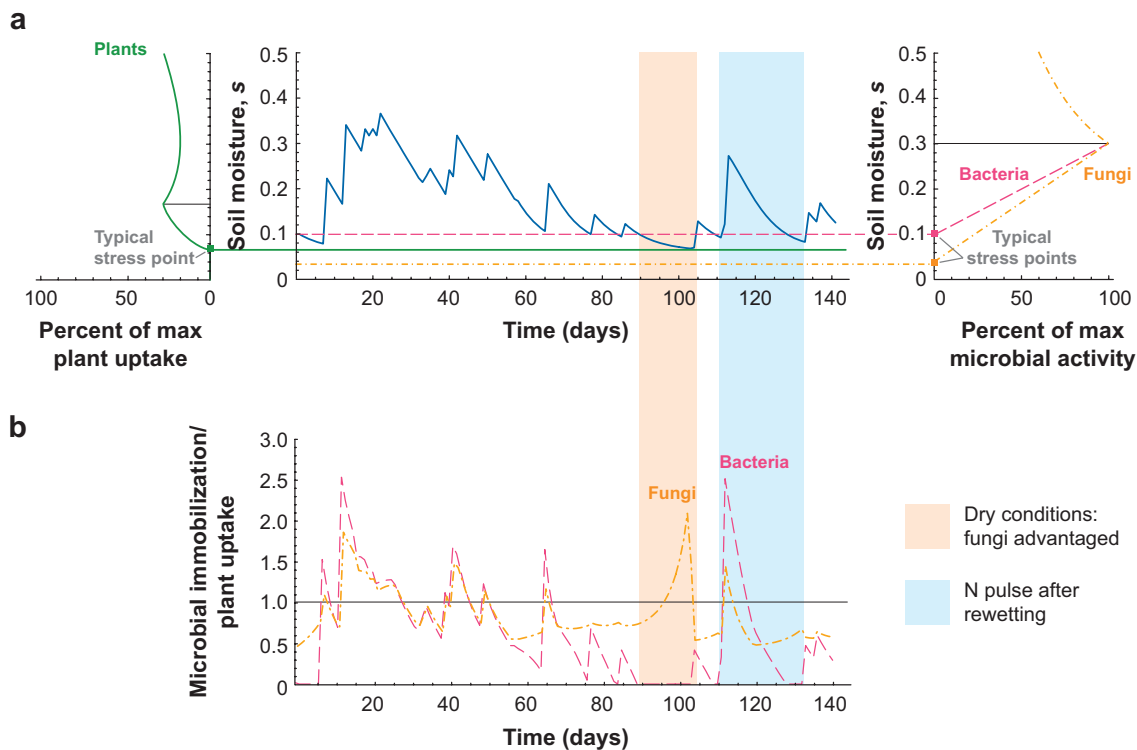
Figure 7

(*a*) Stochastic evolution of soil moisture *s* (*continuous line*) along with stress moisture levels for plants (*continuous line*) and microbes, bacteria (*dashed line*) and fungi (*dot-dashed line*). Left panel shows the plant nitrogen uptake and right panel shows microbial nitrogen (N) immobilization as a function of soil moisture. (*b*) Ratio between microbial immobilization and plant uptake for fungal-dominated (*dot-dashed line*) and bacterial-dominated (dashed line) microbial communities, illustrating the effect of soil moisture pulsing on this competition. Redrawn after Manzoni & Porporato (2005).

5. THE ISSUE OF SPATIAL DYNAMICS

Although so far our examples of external forcing have emphasized stochasticity in time, analogous problems exist in space. The random spatial variability in rainfall and soil moisture has been the subject of research within both hydrological and statistical sciences (Cox & Isham 1988, Rodriguez-Iturbe et al. 2006). However, recent analyses of vegetation spatial patterns arising from coupled carbon-water inter-action seem to have neglected stochastic heterogeneities in space and time (Gilad et al. 2004, Klausmeier 1999, Lefever & Lejeune 1997, Meron et al. 2004, Rietkerk et al. 2004, Ursino 2005). Typically, variability in vegetation patterns caused by changes in annual rainfall regimes has been studied deterministically using reaction-diffusion (or activation-inhibition) equations that mirror the coupled carbon-water dynamics

(see **Figure 1**), with one recent exception (D'Odorico et al. 2006a,b). An important extension of this line of work is to explore how spatial stochastic components may disrupt or enhance these vegetation patterns.

5.1. Plant-Water Interactions and Geomorphic Gradients

The up-scaling of local soil-plant dynamics to landscape and regional scales (e.g., 10–100 km) must account for topographic heterogeneities, hillslope and riparian processes, and river-network structures. Topographic position, slope, and aspect significantly vary in space within a watershed, influencing incident solar radiation, and hence, evapotranspiration and photosynthesis, which in turn impact water availability and vegetation distribution (Jones 1992, Ridolfi et al. 2003, Rodriguez-Iturbe & Porporato 2004, Western et al. 2002).

An example of a digital elevation model (DEM) analysis for the Konza prairie LTER site (7 km × 5.7 km) is reproduced in **Figure 8**. The stochastic dendritic structure of the landscape is clearly visible, notwithstanding the small elevation differences of the region. **Figures 8***b* and **8***c* provide examples of the frequency distributions of slope and aspect computed for the 30-m × 30-m grid elements of the DEM. The regularity of these histograms is suggestive of the possibility of a probabilistic description of the variations in vegetation properties across regional scales, building upon the framework of statistical geomorphology (e.g., Rodriguez-Iturbe & Rinaldo 1997, Western et al. 2002). Few analyses of this type have been conducted (e.g., Caylor et al. 2005, Istanbulluoglu & Bras 2006), and the field remains a fruitful area for research.

5.2. Plant-Water Interactions—Feedback to the Atmosphere

In previous examples (**Figures 6–8**), rainfall was considered entirely external to the soil-plant system. However, at sufficiently large spatial scales, ecosystems can modify their own precipitation regimes primarily because of two-way interactions between the soil-plant system and the atmosphere (Eagleson 1986). The strength of this two-way interaction can be quantified by examining how changes in land cover by human activities impact rainfall regimes (Chase et al. 2001, Kanae et al. 2002, Liston et al. 2002). Recent modeling efforts suggest that these impacts can be as large as those from other anthropogenic factors such as greenhouse gases and aerosols. For example, Roy et al. (2003) utilized a numerical model to show that land cover change in the United States over the past 300 years has significantly altered the local climate in July. Focusing on 1910 to 1990, they found that the increase in forested areas in the East Coast region of the United States resulted in lower surface temperature owing to higher evapotranspiration.

Higher evapotranspiration contributed moisture to the atmosphere thereby enhancing precipitation in the region (Roy et al. 2003). More broadly, precipitation recycling via evapotranspiration and the control that soil moisture exerts on the partitioning of sensible and latent heat fluxes can enhance the feedback between soil moisture and precipitation along a number of pathways (D'Odorico & Porporato
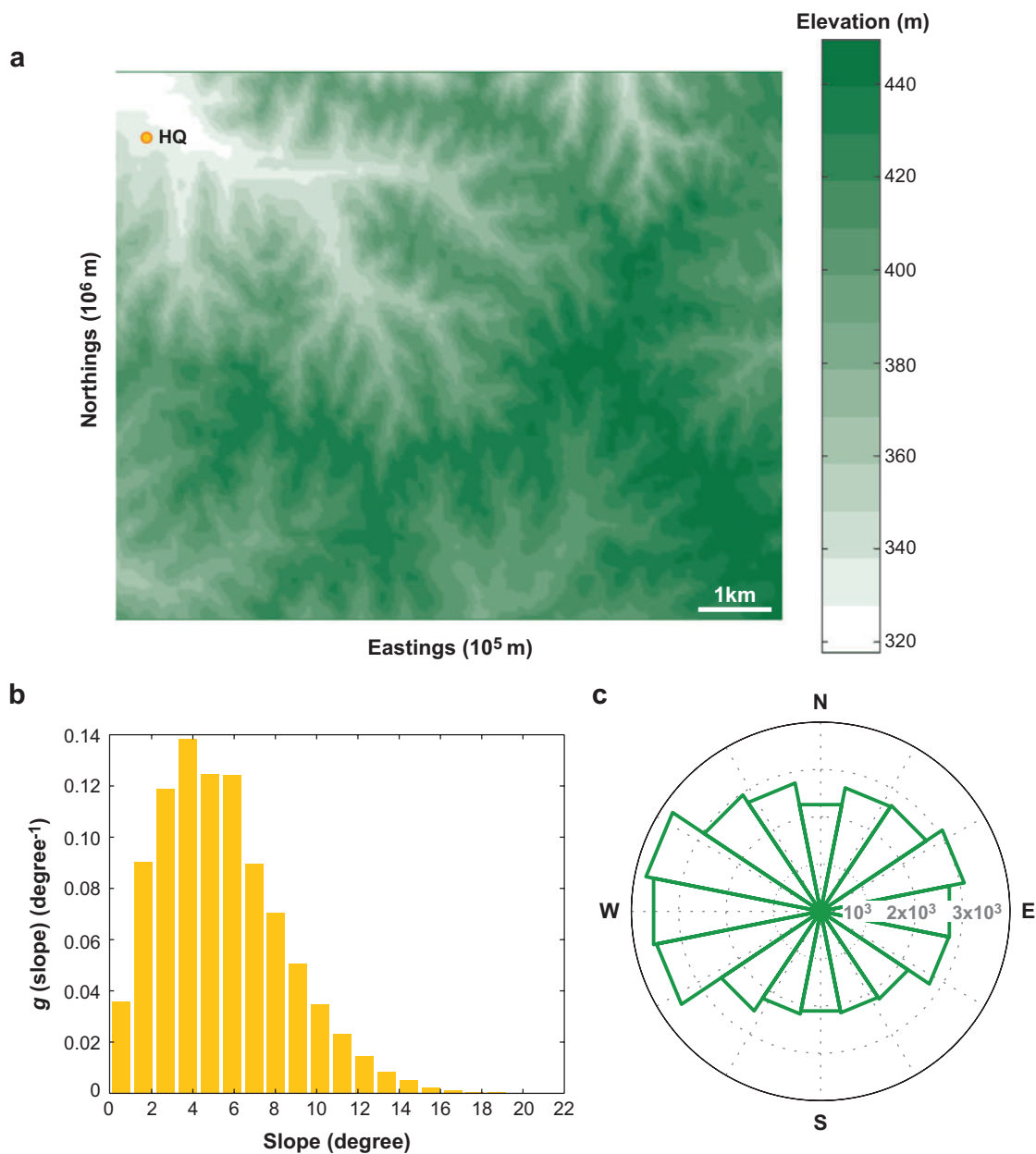
Figure 8

(*a*) Digital elevation map for an area of 7 km by 5.7 km in the Konza Prairie LTER site (HQ is
the position of Konza headquarters); (*b*) probability distribution of slope *g* represented using
histogram, and (*c*) of aspect represented using histogram in polar coordinates for the same
landscape. The spatial probabilistic distribution of these geomorphologic properties affects
solar radiation and soil moisture and thus plant growth.

2004; Entekhabi & Brubaker 1995; Findell & Eltahir 2003a,b; Freedman et al. 2001; Juang et al. 2007a,b; Wu & Dickinson 2005). In short, at sufficiently large scales, plant-water interactions can impact rainfall patterns, which thus can no longer be treated as mere external forcing.

6. CONCLUSIONS

The fundamental barrier to progress in plant-water interaction can be distilled to two main issues: (*a*) we do not know how to describe microscopic water movement in the soil-plant system, although microfluidics might offer a blueprint of how to proceed, and (*b*) we do not know how to scale up, spatially and temporally, these microscopic descriptions coherently, while preserving the effects of nonlinearity and stochasticity. The approaches reviewed here should be viewed as initial steps toward filling these knowledge gaps, with a bias toward the second knowledge gap. We discussed how existing equations for the soil-plant system, when averaged, are not scale-independent in time or space (Nykanen & Foufoula-Georgiou 2001) and remain subject to external stochasticity. With availability of long-term measurements and progress in nonlinear time series analysis, it is conceivable that low-dimensional nonlinear components of the dynamics of the soil-plant-atmosphere system can be extracted from data, thereby guiding the choice of model complexity.

These limitations notwithstanding, all representations must consider external stochasticity originating from the hydroclimatic forcing to the plant-soil system. This forcing is inherently intermittent with variability across all scales, which precludes the use of standard approximations often used in analysis of stochastic processes (e.g., small noise perturbations). Superposition of stochasticity at multiple scales (e.g., rainfall) can intensify extremes and must be taken into account for a reasonable description of ecosystem dynamics. Moreover, when propagated into the soil-plant system, such stochasticity may give rise to noise-induced oscillations and patterns, especially because the water-carbon-nitrogen cycles are tightly coupled.

DISCLOSURE STATEMENT

The authors are not aware of any biases that might be perceived as affecting the objectivity of this review.

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Errata

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