Climate Variability and Ecohydrology of Seasonally Dry Ecosystems

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Dissertation submitted in partial fulfillment of the requirements for the degree of Doctor of Philosophy in the Department of Civil and Environmental Engineering in the Graduate School of Duke University
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Abstract

Seasonally dry ecosystems cover large areas over the world, have high potential for carbon sequestration, and harbor high levels of biodiversity. They are characterized by high rainfall variability at timescales ranging from the daily to the seasonal to the interannual, and water availability and timing play key roles in primary productivity, biogeochemical cycles, phenology of growth and reproduction, and agricultural production. In addition, a growing demand for food and other natural resources in these regions renders seasonally dry ecosystems increasingly vulnerable to human interventions. Compounded with changes in rainfall regimes due to climate change, there is an urgent need to better understand the role of climate variabilities in these regions to pave the way for better management of existing infrastructure and investment into future adaptations.

In this dissertation, the ecohydrological responses of seasonally dry ecosystem to climate variabilities are investigated under a comprehensive framework. This is achieved by first developing diagnostic tools to quantify the degree of rainfall seasonality across different types of seasonal climates, including tropical dry, Mediterranean, and monsoon climates. This global measure of seasonality borrows from information theory and captures the essential contributions from both the magnitude and concentration of the rainy season. By decomposing the rainfall signal from seasonality hotspots, increase in the interannual variability of rainfall seasonality is found, accompanied by concurrent changes in the magnitude, timing, and durations
of seasonal rainfall, suggesting that increase in the uncertainty of seasonal rainfall may well extend into the next century. Next, changes in the hydrological partitioning, and the temporal responses of vegetation resulting from these climate variabilities, are analyzed using a set of stochastic models that accounts for the unpredictability rainfall as well as its seasonal trajectories. Soil water storage is found to play a pivotal role in regulating seasonal soil water hysteresis, and the balance between seasonal soil water availability and growth duration is found to induce maximum plant growth for a given amount of annual rainfall. Finally, these methods are applied in the context of biodiversity and the interplay of irrigation and soil salinity, which are prevailing management issues in seasonally dry ecosystems.
To Gen, who shows me difficult things were only that, and hardly impossible
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Acknowledgements

This work would not have been possible without the mentorship and steadfast encouragements of my adviser Amilcare Porporato. I want to also thank my committee members Gaby Katul, Ignacio Rodriguez-Iturbe, Jim Clark, and John Albertson for their crucial support.

This research was funded by the U.S. National Science Foundation Graduate Research Fellowship Program and CBET grant 1033467. Pierre Landolt and Fazenda Tamandua hosted visits to the Paraiba state of Brazil. Antonio Antonino and Rodolfo Souza of Universidade Federal de Pernambuco, and Eduardo Souza of Universidade Federal Rural de Pernambuco provided support during visits to Pernambuco state of Brazil. Giulia Vico of Swedish University of Agricultura Sciences and Stefano Manzoni of Stockholm University provided valuable discussions on this topic.
Seasonal variations in climatic inputs (in particular, rainfall and potential evapotranspiration) have garnered considerable attention in recent years as controlling factors for mean annual soil water partitioning (Chen et al., 2013; Gerrits et al., 2009; Potter et al., 2005; Hickel and Zhang, 2006), plant responses and adaptive strategies (Gentine et al., 2012; Vico et al., 2014), regional vegetation distribution, carbon fluxes, and primary productivity (Scott et al., 2009; Rohr et al., 2013; Stephenson, 1990; and Robinson, 2013), with further implications for agriculture and land management (Wani et al., 2009). These scientific emphases on the role of climate seasonality come at a time of discernible climate change. For instance, increase in the global mean temperature compounded with significant drying in some regions is likely to lead to increase in the frequency and the intensity of seasonal droughts (Hartmann et al., 2013). Meanwhile, rainfall seasonality and its interannual variability have been observed to change in magnitude, timing, and duration in the tropics (Feng et al., 2013; Pascale et al., 2014). Thus, it is important under these contexts to be able to evaluate the extent to which intra-annual variations in climate inputs may influence various ecohydrological processes.
1.1 A common framework for seasonal climates

Climate seasonality is a defining feature of many dry ecosystems, often characterized by a distinct non-uniformity in their timing of annual rainfall. This results in one or two wet seasons during which most of the annual rainfall occurs, separated by prolonged dry periods. Such seasonal rainfall variations are regularly found in tropical dry, monsoon, and Mediterranean climates (Critchfield, 1974). In terms of potential evapotranspiration, tropical dry and monsoon climates exhibit high year-round net radiation with little fluctuation between the seasons due to their presence in the lower latitudes, while Mediterranean climates, which are typically found on the western continental margins of the mid-latitudes, experience larger seasonal variations. Mediterranean climates are also marked by out-of-phase cycles of rainfall and potential evapotranspiration which manifest as hot, dry summers and cool, wet winters; this is particularly challenging for plant life, since high productivity is limited to the beginning of the summer season before soil moisture depletes (Viola et al., 2008). It is rare in the study of these climates (and their coexisting ecosystems) to reference commonalities shared with other seasonally dry regions, perhaps due to their collectively expansive geographical extent and disparate meteorological drivers. However, it is reasonable from an ecohydrological standpoint to treat them under a common framework due to their similarly large hydroclimatic contrast between the seasons (Chapter 2).

1.2 Extending stochastic ecohydrology to nonstationary systems

The field of stochastic ecohydrology initially developed in the context of water scarcity and vegetation adaptation in water-limited ecosystems (e.g., Rodriguez-Iturbe et al. (1999), Rodriguez-Iturbe and Porporato (2004)), where the intermittent and unpredictable nature of the hydrologic drivers were explicitly modeled through
stochastic processes. This helps to preserve the probabilistic information in the original environmental forcings and propagate them into different components of the soil-plant system. This approach has had widespread success in rigorously accounting for role of climate variability, under stationary conditions, in hydrologic partitioning (Porporato et al., 2004), biogeochemical cycling (Manzoni and Porporato, 2007; Manzoni et al., 2014), plant water stress and water use strategies (Laio et al., 2001; Rodriguez-Iturbe et al., 2001; Daly et al., 2004), and ecosystem structure (van Wijk and Rodriguez-Iturbe, 2002; Fernandez-Illescas and Rodriguez-Iturbe, 2004). Nevertheless, due to the a priori assumption of stationarity, the probabilistic information contained in the system can capture the effects of variability at only particular timescales (e.g., the daily and the interannual; see also the method of superposition adopted in Porporato et al. (2006)). This is most appropriate when the drivers of the exogenous factors remain constant, such as in a non-seasonal climate, or during the growing season, or without changes induced through anthropogenic means. However, the lack of clear separation in the timescales of the external environmental forcings (e.g., in rainfall, temperature, radiation), combined with the propensity of the soil-plant system to respond to the full spectral range of variability (from the daily to the interannual) (Katul et al., 2007), means that the parameters governing the dynamics of the system must be allowed to change over time. A main contribution of this dissertation is to investigate the soil-plant system through the lens of nonstationary, seasonal climates (Chapters 3, 4, and 5), and to extend the stochastic soil moisture models to yield seasonal evolutions of probabilistic soil moisture and other relevant hydrological fluxes (Chapter 4).

1.3 Chapter overviews

In this dissertation, the degree of rainfall seasonality in many climate types across the world are first quantified in Chapter 2 using an objective index—based on information
theory—that accounts for both the amount of rainfall and its annual concentration. The seasonality index is then used to identify regions across the tropics with highly seasonal regimes. By further decomposing rainfall seasonality into its magnitude, timing, and duration components, it is shown that the interannual variability of seasonality over many parts of the dry tropics has increased, implying increasing uncertainty in the intensity, arrival, and duration of seasonal rainfall over the past century. This is further accompanied by shifts in its seasonal magnitude, timing, and duration, underscoring the importance of analyzing seasonal rainfall regimes in a context that is most relevant to local processes.

In Chapters 3 and 4, the effects of climate seasonality is analyzed in the context of soil water partitioning—of rainfall inputs into evapotranspiration versus deep percolation and runoff—using simple stochastic soil moisture models. Chapter 3 derives analytical expressions guided by dimensional analysis while Chapter 4 aims to generalize the use of such stochastic soil moisture models into conditions in which the exogenous drivers are nonstationary and/or desynchronized. Changes to the classical Budyko’s curve are discussed, showing a decrease in the annual evapotranspiration ratio under increasing climate seasonality. The role of soil water storage between the seasons are also highlighted; the transfer of soil moisture between the wet to the dry season is found to be responsible for hysteresis in the hydrological response, with asymmetrical trajectories in the mean soil moisture and in the transient Budyko’s curves during the “dry-down” versus the “rewetting” phases of the year.

Then, in Chapter 5, the stochastic soil moisture model from Chapter 3 is coupled to a minimalist plant growth model to examine how climate seasonality might influence plant responses. It is shown that in seasonally dry climates, a maximum in biomass is to be expected for a wet season of optimal length, for which the limitations imposed by both water availability and duration of growth are at a minimum.

Finally, the implications of such climate variability are investigated in the context
of salinization in Chapter 6 and of biodiversity in Chapter 7. Secondary salinization is partially induced through over-irrigation and coincide with areas around the world where agriculture is practiced under arid or semi-arid climates. The coupled dynamics of soil moisture and soil salt solutes is driven not only by stochastic rainfall events at the daily level, but also by the frequency of irrigation and the quality of the irrigation water. As such, the partitioning of the water inputs into plant uptake or leaching (as discussed in Chapters 3 and 4) plays a strong role in determining the quality of soil, especially in drier climates. Hydrologic variability can also determine plant species richness at larger scales. This is because in water-limited regions, the relationship between species richness and water resources can be moderated not only through the mean resource amount, but also by its variability—and the different configurations of temporal and spatial niches that may be created due to that variability. Both secondary salinization and the maintenance of biodiversity are prevailing issues in seasonally dry regions, as water related constraints to food production and natural resource extraction are imposed against a backdrop of population growth and increasing resource demands. Such issues can benefit from the type of quantitative treatments presented in Chapters 6 and 7.
Changes in rainfall seasonality in the tropics


2.1 Introduction

Climate change has altered not only the overall magnitude of rainfall but also its seasonal distribution and interannual variability worldwide (Easterling, 2000; Trenberth et al., 2007; Zeng et al., 1999). Such changes in the rainfall regimes will be most keenly felt in arid and semiarid regions (Weltzin et al., 2003), where water availability and timing are key factors controlling biogeochemical cycles (Austin et al., 2004), primary productivity (Huxman, 2004; Briggs and Knapp, 1995), and the phenology of growth and reproduction (Dirzo et al., 2011; Singh and Kushwaha, 2005; Walther, 2002), while also regulating agricultural production (Wani et al., 2009). Life in these seasonal biomes is uniquely challenged by the requirement to cope with the uncertain arrival and duration of adverse conditions and to flourish during favorable conditions. In the tropics, seasonal rainfall has distinctly shaped a mosaic
of highly diverse ecosystems—from the tropical dry forests to open woodland forests to savannas (Dirzo et al., 2011)—which support species with a variety of adaptive strategies. Most of these ecosystems are extremely sensitive to not only the annual rainfall amount but also to other aspects of seasonal rainfall—such as the arrival of rain at the beginning of the wet season, which determines the timing of important life stages such as leaf flushing and flowering; and the wet season length, which contributes to the timing of leaf fall and thus the total transpiration period (Borchert, 1994; Eamus, 1999; Schwartz, 2003). The same rainfall seasonality, with its associated drought and flood risks, also poses huge challenges to local populations, making agricultural efforts and sustainable management of soil and water resources more difficult (Wani et al., 2009; Rockstrom et al., 2003).

Seasonality in the rainfall regime can be associated with the magnitude, timing, and duration of the wet/dry seasons and is often quantified by analyzing the monthly rainfall climatology (Borchert, 1999). On one hand, the literature has produced a confounding number of metrics—such as the relative lengths and rainfall amounts of the wet and dry seasons and the arrival dates of the 25 and 75th percentile rainfall (Adejuwon, 2012; Walsh and Lawler, 1981)—which are often tailored for specific locations and research purposes but rarely applied systematically over larger regions. Other studies, when juxtaposing different locations, tend to focus on their differences in rainfall amount (Trenberth et al., 2007) while neglecting its temporal distribution.

2.2 The Seasonality Index

As a starting point for a global analysis of seasonal rainfall regimes, we propose a generalized seasonality index that consolidates the rainfall amount with its annual distribution. To isolate patterns stemming from seasonal rainfall variability from those related to temperature variability, we take a section around the equator between 20°S and 20°N and compute seasonality indices using monthly rainfall data from 2715
stations in the Global Historical Climatology Network (Vose et al., 1992).

For each station, we first compute its long-term mean monthly rainfall and then normalize by the mean annual rainfall \( R \), resulting in a discrete probability distribution of monthly rainfall \( p_m \) for each month \( m \) (see Appendix A). The relative entropy (Cover and Thomas, 2006) of \( p_m \) (denoted by \( D \)) with respect to the uniform distribution \( q_m = 1/12 \) for all \( m \) quantifies the extent of rainfall concentration in the wet season and can be found using \( D = \sum_{m=1}^{12} p_m \log_2 \frac{p_m}{q_m} \). The dimensionless long-term seasonality index \( S \) for each station is then constructed by combining multiplicatively its mean annual rainfall, normalized by the observed maximum mean annual rainfall in the dataset, \( R_{\text{max}} \), with its relative entropy, i.e.,

\[
S = D \frac{R}{R_{\text{max}}}
\]  

(2.1)
such that \( S \) is 0 when \( R \) is distributed uniformly throughout the year and maximized (at \( \log_2 12 = 3.585 \)) when \( R_{\text{max}} \) is concentrated in a single month. As shown in Figure 2.1, a desert environment such as in Chad has a low seasonality index despite the intermittent nature of its rainfall (high \( D \)) because mean annual rainfall \( R \) is low. Similarly, in a humid environment like Papua New Guinea where rainfall is high year round, the seasonality index can nevertheless be diminished by the low contrast between the seasons (low \( D \)). Thus, a low seasonality index can be attributed to a reduction in either the rainfall amount or its relative entropy (Figure 2.1).

Because mean annual rainfall and relative entropy can be negatively correlated, the highest seasonality indices are found in areas with intermediate levels of mean annual rainfall. These hotspots of rainfall seasonality appear in the northeast region of Brazil, western sub-Saharan and central Africa, northern Australia, and parts of Southeast Asia and the Central America (Figure 2.1). These findings can be corroborated by replicating the analysis on a gridded dataset (Mitchell and Jones, 2005) (Figure 2.2; Appendix A), which additionally point to central Brazil and parts of
Figure 2.1: Seasonality index in the tropics. (Top panel) The seasonality index ($S$) is shown for stations in the GHCN-Monthly data set as a function of normalized mean annual rainfall ($\bar{R}/\bar{R}_{\text{max}}$) and relative entropy ($D$). The insets show qualitative differences in the monthly rainfall distribution between locations with high $\bar{R}$, high $D$ and high $S$, indicated by orange boxes. Green shading indicates low seasonality index, lightening to yellow as $S$ increases. (Bottom panel) The seasonality indices for all the stations in the top panel are shown, with the locations of the inset plots outlined in green.

Amazonia as seasonality hotspots. Furthermore, trend analysis on yearly time series of seasonality reveals areas which have experience marked changes in their seasonality from 1930-2002 (Figure 2.2; Appendix A) due to a combination of changes in their mean annual rainfall and/or its monthly distribution. In particular, western Africa and central Brazil stand out as highly seasonal regions that have undergone marked decreases in their seasonality due to decreases in their rainfall amounts (western Africa) and distribution (central Brazil), while the increase in seasonality in north-
western Australia can be traced to large increases in the rainfall total. Furthermore, changes in the rainfall regimes on continental Africa have notably resulted in latitudinal bands alternating between increases and decreases in their seasonality (Figure 2.2).

2.3 Changes in rainfall seasonality and its interannual variability

We are now in a position to focus on a subset of these seasonality hotspots—in northeast Brazil, western and central Africa, and northern Australia—and examine in more detail the changes over time in the magnitude, timing, and duration of their seasonal rainfall regimes. To this purpose, a set of statistical measures are adopted for decomposing available station series. Specifically, the following indicators are used to quantify each of the seasonality components for each year: (1) the annual rainfall (for the magnitude), (2) the centroid of the monthly rainfall distribution (for the timing), and (3) the spread (for the duration), which is a measure of the temporal
Figure 2.3: Decomposition of a monthly rainfall series.

The monthly rainfall series for Parau, Brazil (5.78°S, 37.1°W) span 60 years (1930-1990), with each year’s distribution plotted next to each other (thin blue lines). The long-term average monthly rainfall distribution is shown in brown, with the beige area spanning the standard deviation. The projection for the annual rainfall is indicated in red. The centroid (dark green line) and the spread (light green area) are also shown.

deviation from the centroid of the monthly rainfall distribution (see Appendix A).

The decomposition of the seasonal rainfall signal for a single station in Parau, Brazil (5.78°S, 37.1°W) into its indicator series is shown in Figure 2.3.

For each indicator series (3 per station), we find its slope using linear or circular regression to assess temporal trends in the magnitude, timing, and duration of seasonality (see Appendix A for dealing with gaps in data). Next, to find changes in its temporal variability, we compute the standard deviation of the residuals with a moving 12-year window (with windows of different lengths producing qualitatively similar results) and then find the slope of the resulting series by linear regression. The slopes for the trend and variability of each indicator series are assembled in box-
plot forms in Figure 2.4, and the significance of the mean deviation from no change in each region was evaluated with a Wilcoxon signed-rank test. The period of analysis is restricted to 1930-1990 due to data availability.

The results show statistically significant changes in the trends (Figure 2.4, top boxplots) and increases in the variability of seasonality (Figure 2.4, bottom boxplots) throughout most of the dry tropics. Northeast Brazil, in particular, exhibits increases in the variability of seasonal magnitude and timing to a greater degree, on average, compared to other regions. This increased uncertainty associated with regional rainfall seasonality has occurred concurrently with increasing rainfall magnitude (avg 6.7 [max 22] mm/year), delays in its timing (avg 0.045 [max 0.13] day/year), and expansion of the wet season over 1930-1990. Western Africa generally shows trends in the opposite direction, with considerable decrease in the rainfall magnitude (avg −4.3 [min −18] mm/year) and reduction in duration (avg −0.034 [min −0.14] days/year) which have contributed to the previously detected decrease in seasonality (Figure 2.2), while central Africa shows statistically significant increase in the variability of seasonal timing. The overall picture for parts of seasonal Africa is of a declining rainfall supply distributed over increasingly uncertain times. Northern Australias increase in seasonality can be attributed to increase in the rainfall magnitude (avg 1.2 [max 6.4] mm/year) with concomitant increase in duration (avg 0.026 [max 0.23] days/year). Nevertheless, due to the simultaneous increase in rainfall magnitude variability (avg 3.2 [max 11] mm/year), the expected rainfall amount in each season has become more uncertain. These results are corroborated with a second complementary set of indicators based on demodulation (Rodriguez-Iturbe et al., 1971; Bloomfield, 2000) and information theory.
2.4 Discussion and conclusions

To guide the interpretation of these results, we note that the slopes at a given station reflect long-term trends over the recorded period and thus should be summed over 60 years to determine their cumulative changes. We also verified that the trends produced from analyzing the data at the monthly scale can indeed be interpreted at
the daily scale, since these trends are almost equivalent to those analyzed directly at the daily scale. Additionally, while the spatial means reveal broader regional tendencies, these tendencies are driven by more extreme changes occurring at individual stations, which are working synergistically to alter local landscapes. The increase in the uncertainty in the seasonal timings, as seen for example in parts of northeast Brazil and central Africa, may desynchronize phenology and other biological responses throughout several trophic levels in the ecosystem (Dirzo et al., 2011; Schwartz, 2003). Likewise, the lengthening of the rainy season in northeast Brazil and central Africa may translate to an increase in the transpiration period (Yoshifuku, 2006) and shifts in the regional carbon budgets, and the decrease in seasonal rainfall seen in Africa may boost the competitive advantage of some plant functional types over others (e.g., deciduous species at the expense of evergreen species (Enquist and Enquist, 2011)). For systems living near the margin of tolerance for available water, the occurrence of extremely wet or dry years can determine major compositional shifts as well as threshold responses such as mass tree mortality and disease outbreaks (Allen et al., 2010).

In summary, we project that this increased variability in conjunction with changing seasonality trends, if sustained into the next century, may portend significant shifts in the timing of plant activities (Cleland et al., 2007) and ecosystem composition and distribution (Walther, 2002), with consequences for water and carbon cycling and water resource management in the tropics. To understand their full impacts, we must begin by detecting changes in all aspects of seasonality while recognizing their simultaneous contributions to informing the life strategies of individual species and to shaping overall ecosystem functioning. To that end, the framework introduced in this study can be broadly adopted for multi-dimensional analyses of seasonality, applicable not only to seasonally dry tropical regions, but also to Mediterranean and monsoonal climates where the annual rainfall is unevenly
distributed. The results can then be used to inform on management strategies for mitigating water resource shortages and addressing ecosystem vulnerability in seasonally dry regions.
3

Soil water partitioning under climate seasonality

This chapter is adapted from Feng, X., Vico, G. and A. Porporato (2012), On the effects of seasonality on soil water balance and plant growth, Water Resources Research, 48(5).

3.1 Introduction

Evapotranspiration has long been recognized as the result of synergistic interactions between climate, soil, and vegetation (e.g., Brutsaert (1982); Rodriguez-Iturbe and Porporato (2004)). It is strongly influenced not only by the plant type and species composition at a site, but also by the overall economy of available water and energy. Budyko (1974) observed that, under conditions of relative water abundance, long-term evapotranspiration becomes limited by the potential evapotranspiration (PET), while in arid regions, where the energy supply is high, precipitation is the main constraint to evapotranspiration. In the former case, water supply exceeds demand, while in the latter case water supply is outstripped by the demand. On these premises Budyko (1974) proposed a semi-empirical framework in which the ratio of
mean annual evapotranspiration to rainfall (the evapotranspiration ratio) is related to a monotonically increasing function of the annual dryness index ($D$), defined as the ratio of mean annual PET to rainfall. Other studies have introduced similar functions, based either on empirical observations (Pike, 1964; Choudhury, 1999) or on boundary conditions mathematically imposed by water and energy balances (Fu, 1981; Zhang et al., 2001, 2004; Yang et al., 2008).

The applicability of these water balance models is often limited by their implicit assumption of temporal steady-state (Porporato et al., 2004; Donohue et al., 2007). Budyko and Zubenok (1961) noted from empirical observations that basins characterized by the same mean annual dryness index can generate different amounts of runoff and that this variability is influenced by the seasonal patterns of precipitation and PET. For example, when the water and energy supplies are out of phase, observed mean annual evapotranspiration is lower than the amount predicted in the absence of seasonality, while it is higher when water and energy supplies are out of phase. Furthermore, an annual rainfall amount concentrated in a few wet months can result in drastically different hydrological behavior and vegetation compared to the same amount spread evenly over the year. Thus, an increasing number of authors have come to recognize the need to resolve climatic inputs at a seasonal time scale (Milly, 1994a,b; Potter et al., 2005; Hickel and Zhang, 2006; Gerrits et al., 2009). In a modeling framework describing the long term balance of precipitation and evapotranspiration, Milly (1994a) introduced an index of seasonality as the normalized difference between the amplitudes of precipitation and PET, predicting decreasing annual evapotranspiration with stronger in-phase seasonality, in accordance with Budyko’s observations. Milly (1994b) subsequently incorporated rainfall stochasticity as a Poisson process and described the dependence of the annual water partition on seven dimensionless parameters, including those that capture the plant-available soil water storage and the amplitude of seasonal variations in precipitation intensity,
storm arrival rate (frequency), and PET.

In the absence of seasonality, dimensional analysis highlights the importance of the storage index ($\gamma$)—soil water storage capacity relative to mean rainfall depth—in addition to Budyko’s dryness index, in defining the rainfall partition at the annual level (Milly, 1993; Porporato et al., 2004). Empirical observations further reveal the complex role played by soil water storage in rainfall-dominated seasonal climates. To distinguish between seasonal rainfall regimes that are in or out-of-phase with PET, Potter et al. (2005) extended the stochastic model developed by Milly (1994b) by adding a phase shift term to the sinusoidal functions previously used for precipitation intensity, frequency, and PET. The numerical solutions predicted that, for cases with the same mean annual dryness index, the evapotranspiration ratio for catchments with summer-dominant rainfall regimes (in-phase) was higher than catchments with winter-dominant rainfall (out-of-phase). However, this was found to be surprisingly in contrast with observed data. Potter et al. (2005) attributed this discrepancy to infiltration-excess runoff, which was not explicitly modeled and which may have effectively lowered the soil water storage during periods of intense rainfall in the summer. Using a larger set of catchment data and decomposing evapotranspiration into climate- and storage-controlled components, Hickel and Zhang (2006) corroborated the evidence that the average effective storage is indeed smaller in summer-dominant rainfall catchments (due likely to high runoff ratios during intense rain events in the summer, as already suggested by Potter et al. (2005)), and the climate-controlled component of evapotranspiration (which bypassed the effect of soil water storage) is higher for summer-dominant catchments, as predicted by most previous models. These studies show that the storage index can compensate for seasonal rainfall variability by mediating the portion of rainfall that is actually available for plant uptake, something also shown by Gerrits et al. (2009).

The importance of seasonality and the need to account for it have been observed
in the context of other ecohydrological traits, such as the distribution of plant communities in North America (Stephenson, 1990) and the fraction of coexisting annual and perennial grasses in Mediterranean ecosystems (Clary, 2008). Thus, the strong link known to exist between evapotranspiration and plant growth naturally suggests that climatic conditions that result in variations in evapotranspiration may necessitate concomitant adaptations in growth strategies (Stephenson, 1998; Viola et al., 2008).

In this study, we present an idealized framework based on dimensional analysis, to study the seasonality of rainfall and PET in terms of both intensity and duration. We couple this framework with a process-based model of stochastic soil moisture balance (Porporato et al., 2004; Rodriguez-Iturbe and Porporato, 2004) and derive analytical solutions for the mean annual water balance. As in previous works on the subject (Reggiani et al., 2000; Yokoo et al., 2008), the parameters of our model are chosen to describe Budyko’s curve and its modifications. Our approach however also offers causal explanations for the resulting curves as it clearly ties physical processes to model structure, allowing us to specifically investigate the importance of rainfall and PET seasonality as well as the relative durations of the wet and dry seasons under different soil water storage capacities in water-controlled seasonal climates. Finally, the implication of rainfall variability on biomass accumulation are explored using a simple growth model that is directly linked to the soil moisture model.

3.2 Stochastic and seasonal variability of soil moisture

At the daily scale, assuming negligible horizontal redistribution via topographic effects, soil moisture at a point is recharged through intermittent rainfall pulses of random depths, and depleted through evapotranspiration, drainage, and runoff. In what follows, we focus on the vertically averaged, plant available “effective” soil moisture, $x$, defined as $\frac{s-s_w}{s_1-s_w}$, where $s$ is the relative soil moisture, and $s_w$ and $s_1$
correspond respectively to the plant wilting point and the effective saturation level, above which soil water is assumed to be immediately lost to drainage or runoff. The range of \( x \)—between 0 and 1—is bracketed by the upper and lower limits of soil moisture available for plant uptake. With the above assumptions, the effective soil moisture balance, vertically averaged over the rooting zone, is (Rodriguez-Iturbe and Porporato, 2004)

\[
\frac{d}{dt} \left( w_0 dx(t) \right) = R(t) - ET(x(t), t) - LQ(x(t), t),
\]

where \( w_0 = (s_1 - s_w)nZ_r \) is the maximum plant-available soil water storage volume per unit ground area, \( n \) (dimensionless) is the vertically averaged soil porosity, and \( Z_r \) (e.g., cm) is the average rooting depth. The rate of change in the total volume of plant-available soil moisture \( \frac{d}{dt} \left( w_0 dx(t) \right) \) is governed by the rate of precipitation \( R \) (e.g., cm/day), evapotranspiration \( ET \) (e.g., cm/day), and leakage/runoff \( LQ \) (e.g., cm/day).

Rainfall and PET, the latter controlling the evapotranspiration rate \( ET \) in (3.1), fluctuate at different time scales and are characterized by intra-seasonal, seasonal, and interannual variability. Moreover, the unpredictable nature of rainfall calls for a stochastic framework in the analysis of the soil moisture balance (Rodriguez-Iturbe and Porporato, 2004; Katul et al., 2007). We will thus assume that the observed hydroclimatic processes are one realization of a stochastic ensemble given by the underlying random process. For seasonal climates, we will assume that embedded within this random variability is a deterministic seasonal component repeating itself with yearly period, \( T^{yr} \), and divided into two distinct seasons, a wet season followed by a dry season, \( T^{yr} = T^w + T^d \). The origin of time \( t \) is set at the beginning of a generic wet season.

The following notations will be used: the ensemble average of a generic variable \( u \in [u_{min}, u_{max}] \) with probability density function \( p(u, t) \) at a specific instant of
time is denoted by brackets, i.e., $\langle u(t) \rangle = \int_{u_{\text{min}}}^{u_{\text{max}}} up(u, t) \, du$; the temporal average over a time period $T$ (e.g., over an entire year or a season) is denoted by overbars, defined as $\overline{u}_T(t_0, T) = \frac{1}{T} \int_{t_0}^{t_0+T} u(t) \, dt$, where $t_0$ is the beginning time of interest. Note that $\overline{u}_T(t_0, T)$ is still a random variable; it is only when the ensemble average of the time average is taken, $\langle \overline{u}_T(t_0, T) \rangle$, that it becomes deterministic. Moreover, if the process is stationary, the long-term time average $\overline{u}^\infty = \lim_{T \to \infty} \frac{1}{T} \int_{-T/2}^{+T/2} u(t) \, dt$ becomes independent of $t_0$ and is the same as the ensemble average, i.e., $\overline{u}^\infty = \langle u \rangle$; in this case, the process is said to be ergodic. In what follows we will be interested in the ensemble averages of annual, wet-season, and dry-season averages, i.e., $\langle \overline{u}^{yr} \rangle$, $\langle \overline{u}^{w} \rangle$, and $\langle \overline{u}^{d} \rangle$, indicated for short as $\langle \overline{u}^{yr} \rangle$, $\langle \overline{u}^{w} \rangle$, and $\langle \overline{u}^{d} \rangle$, respectively.

### 3.3 Dimensional analysis of the annual water balance

We now use dimensional analysis to derive seasonal parameters governing the annual water balance. A key assumption in the dimensional analysis that follows is that only two parameters are needed to describe the instantaneous evapotranspiration: potential evapotranspiration ($ET_{\text{max}}$) and plant available effective soil moisture ($x$). Since $x$ is in turn governed by equation (3.1), it is necessary to include $w_0$, $R$, and $LQ$ for a more complete characterization of $ET$, although we will waive $LQ$ from the list of independent governing parameters when considering long-term averages since $LQ$ is complementary to $ET$ in that case. We make a further assumption that the rainfall regime at a given time can be described simply by the mean depth $\alpha$ and the frequency $\lambda$ of storm events. Note that this formulation does not take in account the role of groundwater in vegetation dynamics and assumes that the plant characteristics $s_1$ and $s_w$ are already known.
3.3.1 General formulation with no seasonality

In the absence of seasonality, the water balance is assumed to be at stochastic steady state and therefore ergodic, i.e., $\langle ET^{yr}\rangle = ET^{yr}$. According to the assumptions outlined at the beginning of the section, a general equation for the annual average evapotranspiration, $\langle ET^{yr}\rangle$, can be written as

$$\langle ET^{yr}\rangle = f(ET_{max}, \alpha, \lambda, w_0). \tag{3.2}$$

The Buckingham-Pi theorem with 5 dimensional parameters and 2 primary dimensions—length (e.g., cm) and time (e.g., day)—provides $5 - 2 = 3$ independent Π groups (see e.g., Barenblatt (1996)). Selecting $\alpha$ (e.g., cm) and $\lambda$ (e.g., 1/day) as the parameters that cover all the primary dimensions, the following dimensionless Π groups can be formed

$$\Pi_1 = \phi(\Pi_2, \Pi_3), \tag{3.3}$$

where $\Pi_1 = \frac{\langle ET^{yr}\rangle}{\alpha \lambda}, \Pi_2 = \frac{ET_{max}}{\alpha \lambda},$ and $\Pi_3 = \frac{w_0}{\alpha}$. By substituting the original parameters into functional form (3.3), a more meaningful relationship emerges, and the annual water balance in steady state becomes a function of Budyko’s dryness index ($D = \Pi_2$) and the storage index ($\gamma = \Pi_3$),

$$\frac{\langle ET^{yr}\rangle}{\langle R^{yr}\rangle} = \phi(D, \gamma), \tag{3.4}$$

where $\frac{\langle ET^{yr}\rangle}{\langle R^{yr}\rangle} = \frac{\langle ET^{yr}\rangle}{\alpha \lambda}, D = \frac{ET_{max}}{\alpha \lambda},$ and $\gamma = \frac{w_0}{\alpha}$.

We note that the selection of the dimensionally independent governing parameters $\alpha$ and $\lambda$ is arbitrary; in this case, the resulting functional forms reproduce Budyko’s water balance relationship. If we instead select $ET_{max}$ and $w_0$, then the functional relationship becomes $\frac{\langle ET^{yr}\rangle}{ET_{max}} = \Phi(\gamma^{-1}, \frac{\lambda w_0}{ET_{max}})$. 

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3.3.2 Dimensional analysis with the inclusion of seasonality

We now follow the same approach in the case where mean annual climatic conditions are no longer constant. We divide the year into a wet and a dry season, assuming that together they encapsulate the most essential features of seasonal variability. Both seasons are now characterized by their own set of climatic and soil-plant parameters, initial soil moisture conditions, and lengths. The mean evapotranspiration over each season takes the following forms

\[
\langle ET^w \rangle = f_w(ET_{max}^w, \alpha^w, \lambda^w, w_0^w, x_0^w, T^w),
\]

\[
\langle ET^d \rangle = f_d(ET_{max}^d, \alpha^d, \lambda^d, w_0^d, x_0^d, T^d).
\]

The annual mean evapotranspiration and rainfall are now determined from the time weighed contributions from both seasons,

\[
\langle ET^{yr} \rangle = \frac{\langle ET^w \rangle T^w + \langle ET^d \rangle T^d}{T^w + T^d},
\]

\[
\langle R^{yr} \rangle = \frac{\langle R^w \rangle T^w + \langle R^d \rangle T^d}{T^w + T^d}.
\]

Combining equations (3.5) and (3.6) with the governing parameters from both seasons, and noting that the initial soil moisture conditions depend on the parameters of the previous season, the annually averaged evapotranspiration can be written as

\[
\langle ET^{yr} \rangle = f_s(ET_{max}^w, ET_{max}^d, \alpha^w, \alpha^d, \lambda^w, \lambda^d, w_0^w, w_0^d, T^w, T^d).
\]

In order to simplify the analysis, we assume that the maximum plant available soil water storage capacity remains constant across seasons, \( w_0 = w_0^w = w_0^d \), i.e., plant rooting depth and ability to capture soil water remains unaltered. We further assume that rainfall frequency \( \lambda \) is the dominant driver of rainfall variability and thus set the mean rainfall depth constant across seasons, i.e., \( \alpha = \alpha^w = \alpha^d \). Selecting the wet season as the reference state, we use \( \alpha \) and \( \lambda^w \) as the two parameters accounting for
all primary dimensions and normalize the remaining parameters using Buckingham-
Pi theorem to obtain the following functional form

\[
\frac{\langle ET^{gr} \rangle}{\alpha \lambda^w} = \phi_s(\Pi_2, \Pi_2^*, \Pi_3, \Pi_r, \Pi_t, \Pi_t^*),
\]

(3.8)

where \( \Pi_2 = \frac{ET^w_{\text{max}}}{\alpha \lambda^w}, \Pi_2^* = \frac{ET^d_{\text{max}}}{\alpha \lambda^w}, \Pi_3 = \frac{\lambda^d}{\lambda^w}, \Pi_r = \lambda^w T^w, \Pi_t = \lambda^w T^d, \) and \( \Pi_t^* = \lambda^d T^d. \)

Note that \( \Pi_2 \) and \( \Pi_3 \) are respectively the dryness index for the wet season, \( D^w, \) and the storage index \( \gamma \) found in (3.4). Of the other dimensionless groups, some combine parameters from the two seasons (e.g., \( \Pi_2^* \) and \( \Pi_t^* \)), a fact stressed by the use of the superscript *, while others have more complex physical meanings (e.g., \( \frac{\langle ET^{gr} \rangle}{\alpha \lambda^w} \)). By multiplying several dimensionless groups together, we can combine them into more intuitive forms amenable to physical interpretation, without altering the overall functional dependence. Using \( \langle R^w \rangle = \alpha \lambda^w, \langle R^d \rangle = \alpha \lambda^d, \) and equation (3.6), equation (3.8) can be expressed as a function of the mean annual water balance, \( \frac{\langle ET^{gr} \rangle}{\langle R^{gr} \rangle}, \) without introducing additional parameters. Likewise, the other dimensionless groups can be reorganized to give

\[
\frac{\langle ET^{gr} \rangle}{\langle R^{gr} \rangle} = \phi_s(D^w, \gamma, \rho, \tau, \epsilon, \beta^d),
\]

(3.9)

where \( D^w = \frac{ET^w_{\text{max}}}{\alpha \lambda^w}, \gamma = \frac{u_0}{\alpha}, \rho = \frac{\lambda^d}{\lambda^w}, \tau = \frac{T^d}{T^w}, \epsilon = \frac{ET^d_{\text{max}}}{ET^w_{\text{max}}}, \) and \( \beta^d = \frac{ET^d_{\text{max}} T^d}{u_0}. \) We will refer to this formulation throughout the rest of our developments. \( D^w \) is the dryness index in the reference (wet) season, \( \gamma \) is the storage index, \( \rho \) is the ratio of seasonal rainfall frequencies, \( \tau \) is the ratio of seasonal durations, \( \epsilon \) is the ratio of seasonal PET, and \( \beta^d \) is the dry season evaporative index, or the PET over the entire dry season normalized by the soil water storage capacity. The four dimensionless groups that appear in addition to \( D^w \) and \( \gamma \) are all associated with measures of seasonality. These dimensionless groups can be broadly adopted to analyze a variety of seasonal
climates, provided that these climates can be idealized as the alternation of a dry and a wet season. Explicit forms of the function $\phi_s$ will be obtained in Section 3.5. For subsequent use, we also define the mean annual dryness index as

$$D_{yr} = \frac{ET_{max}^w T^w + ET_{max}^d T^d}{\alpha \lambda^w T^w + \alpha \lambda^d T^d} = D^w \frac{1 + \epsilon \tau}{1 + \rho \tau}. \quad (3.10)$$

3.4 Classification of seasonal hydroclimatic regions

The previously introduced seasonality parameters can be used to quantitatively characterize rainfall dominated seasonal climates. We follow the widely used Köppen-Geiger classification system (Peel et al., 2007; Lydolph, 1985), focusing on climates with a pronounced dry season, especially tropical savanna (Aw), tropical monsoon (Am), and Mediterranean (Csa, Csb) climates.

The tropical savanna climate, known also as the tropical wet-and-dry climate, is found at latitudes roughly between 5° to 20° (Critchfield, 1974). Areas characterized by this climate type include western Central America, northwestern South America, interior Brazil, south-central and eastern Africa, Madagascar, India, southeast Asia, and northern Australia. Due to the influence of equatorial and tropical air masses and high year-round net radiation, temperatures are high throughout the year (the coolest month averages 18°C or higher), and seasonal variation in temperature is low. The precipitation regime, on the other hand, is marked by a stark seasonal contrast. In the equatorial regions the dry season is short, but at higher latitudes the dry season becomes longer and the PET may exceed precipitation year round.

Likewise, the tropical monsoon climate is found at low latitudes and has elevated temperature throughout the year. Its rainfall regime is comparable to the tropical savanna climates, characterized by a distinct and sustained dry season with low rainfall (albeit slightly higher than the driest monthly precipitation mark line set for tropical savanna climates). However, its annual total rainfall is much higher,
resembling more the tropical rainforest climate (typically over 1500 mm) (Critchfield, 1974). As a result, the contrast between the wet and the dry season may be even more drastic; typically, the dry months may receive less than 1/10 the rainfall of the wettest months.

The Mediterranean climates are found at latitudes between 30° to 45° on the western continental margins, including in the Mediterranean basin, California, Chile, the southern tip of Africa, and southwestern Australia. They are classified based on their temperature variability (warmest month above 10°C and coldest month above 0°C) as well as their precipitation variability (the dry months receiving less than 1/3 of the precipitation typical of the wet months; (Lydolph, 1985)). A chief feature of the Mediterranean climates is the dominance of the subtropical high air masses that result in hot, dry summers and cool, wet winters. Annual rainfall totals between 350 to 900 mm, with most of it falling during the cold winter season. The dry summers may last typically between five to six months.

These main features of the above climates can be summarized using the dimensionless groups defined in Section 3.3.2. The duration of the dry season for tropical savanna and monsoon climates can be more variable compared to that of Mediterranean climates, but it is around 6 months, corresponding to \( \tau \approx 1 \). PET is mainly driven by solar radiation and air temperature. Hence, the seasonal ratio in PET, or \( \epsilon \), hovers around 1 in tropical climates, where temperature and solar radiation do not significantly change throughout the year. On the other hand, in Mediterranean climates characterized by a hot summer and cool winter, \( \epsilon \) is more variable (often ranging between 2 and 3). With respect to rainfall, Mediterranean and tropical savanna climates are typically characterized by comparable annual totals, yet the contrast between the wet and the dry season rainfall for tropical savannas is more pronounced. Although the rainfall in monsoon and tropical savannas may have similar seasonal variability, the larger rainfall totals typical of the monsoon regions
Table 3.1: Typical range of seasonal parameters for seasonally dry climates. $\langle R^{yr} \rangle$ (mm/yr) is the average rainfall rate over a year. $ET^d_{\text{max}}$ (cm/day) is variable according to plant functional types; the values shown are typical for trees.

<table>
<thead>
<tr>
<th>Climate types</th>
<th>$\langle R^{yr} \rangle$</th>
<th>$ET^d_{\text{max}}$</th>
<th>$\rho = \lambda^d \chi^w$</th>
<th>$\epsilon = \frac{ET^d_{\text{max}}}{ET^w_{\text{max}}}$</th>
<th>$\tau = \frac{T^d}{T^w}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tropical savanna</td>
<td>400–1500</td>
<td>0.35–0.70</td>
<td>10</td>
<td>1</td>
<td>0.7–1.4</td>
</tr>
<tr>
<td>Monsoon</td>
<td>&gt; 1500</td>
<td>0.35–0.70</td>
<td>10</td>
<td>1</td>
<td>0.7–1.4</td>
</tr>
<tr>
<td>Mediterranean</td>
<td>350–900</td>
<td>0.30–0.60</td>
<td>3</td>
<td>2–3</td>
<td>0.7–1.4</td>
</tr>
</tbody>
</table>

results in a less intense dry season compared to the tropical savanna climates. The typical range of seasonal parameters for seasonally dry climates is summarized in Table 3.1.

3.5 Stochastic models

We use stochastic soil moisture models to link to the dimensionless groups in Section 3.3 and obtain explicit forms for the annual water balance ($\phi_s$ in equation (3.9)). Within each season, rainfall is idealized as a marked Poisson process, with the distribution of the times between precipitation events drawn from an exponential distribution of mean $1/\lambda^s$, different for each season (the superscript $s$ stands either for $w$ in the wet season or $d$ in the dry season), and the depth of rainfall drawn independently from an exponential distribution of mean $\alpha$ (Rodriguez-Iturbe et al., 1999). Accordingly, the effective soil moisture is a random variable with probability density function $p^s(x, t)$. The temporal evolution of the time dependent ensemble mean of soil moisture, $\langle x^s(t) \rangle$, can be obtained from the macroscopic equation (Laio et al., 2002; Rodriguez-Iturbe and Porporato, 2004)

$$
\frac{d\langle x^s(t) \rangle}{dt} = \frac{\lambda^s}{\gamma} - \int_0^1 \frac{ET^s(u)}{w_0} p^s(u, t) \text{d}u - \frac{\lambda^s}{\gamma} \int_0^1 e^{-\gamma(1-u)} p^s(u, t) \text{d}u. \hspace{1cm} (3.11)
$$

We will assume that the process has been started at $t \to -\infty$ and that $t = 0$ corresponds to the beginning of a generic wet season. Clearly the initial conditions of (3.11) are linked to those of (3.1). The terms on the right hand side in (3.11) are
the ensemble averages of rainfall input and soil moisture losses normalized by the storage capacity, i.e.,

\[ \frac{\lambda_s}{\gamma} = \frac{\langle R^s(t) \rangle}{w_0} \]  

(3.12)

\[ \int_0^1 \frac{ET^s(u)}{w_0} p^s(u, t) \, du = \frac{\langle ET^s(x) \rangle}{w_0} \]  

(3.13)

\[ \frac{\lambda_s}{\gamma} \int_0^1 e^{-\gamma(1-u)} p^s(u, t) \, du = \frac{\langle LQ^s(x, t) \rangle}{w_0}. \]  

(3.14)

With a simple assumption of a linear dependence of \( ET(x) \) on \( x \), from 0 at \( x = 0 \) to \( ET^s_{\text{max}} \) (depending on the season) at \( x = 1 \) (Porporato et al., 2004), equation (3.13) can be further simplified to

\[ \int_0^1 \frac{ET^s(u)}{w_0} p^s(u, t) \, du = \frac{ET^s_{\text{max}}}{w_0} \int_0^1 u p^s(u, t) \, du = \frac{ET^s_{\text{max}}}{w_0} \langle x^s(t) \rangle. \]  

(3.15)

On the other hand, the leakage and runoff term cannot be approximated easily. We apply two treatments of this term, one using a minimalist approach that leads to simple expressions, and another that uses a linear approximation of the \( \langle LQ(x, t) \rangle \) term (the linear LQ model) that can more accurately describes the soil water balance when the storage index \( \gamma \) is very high or low.

For the minimalist model, soil moisture is assumed to instantaneously reach stochastic steady state during the wet season and decay without leakage or runoff during the dry season (see Appendix B.1 for a more detailed exposition). Using equations (3.6), (3.15), and corresponding solutions for \( \langle x^s(t) \rangle \), the mean annual water balance can be recast as

\[ \frac{\langle ET^y_r \rangle}{\langle R^y_r \rangle} = \frac{1}{1 + \rho \tau} \left\{ G^w + \rho \tau \left[ 1 - \frac{1}{\beta_d} \left( 1 - e^{\beta_d} \frac{e - \gamma}{\rho} \right) \left( 1 - e^{-\beta_d} \right) \right] \right\}. \]  

(3.16)
where $G^w$ is the fraction of evapotranspiration in the wet season

$$G^w = \frac{\langle ET^w \rangle}{\langle R \rangle} = 1 - D^w \frac{\gamma \frac{\eta}{\eta^w} - 1 - e^{-\gamma}}{\Gamma \left( \frac{\eta}{\eta^w} \right) - \Gamma \left( \frac{2}{\eta^w}, \gamma \right)},$$

and $\Gamma(\cdot)$ is the gamma function and $\Gamma(\cdot, \cdot)$ is the incomplete gamma function (Abramowitz and Stegun, 1964; Porporato et al., 2004).

For the linear LQ model, $\langle LQ(x, t) \rangle$ is linearized by imposing a deterministic value at the beginning of each season and a long term value consistent with the stochastic steady state condition, as explained in Appendix B.2. Altogether, the water balance for the linear LQ model can be written as

$$\frac{\langle ET^w \rangle}{\langle R^w \rangle} = \frac{1}{1 + \rho \tau} (\Omega^w + \rho \tau \Omega^d),$$

where

$$\Omega^w = \langle x^w \rangle_{ss} D^w + \frac{D^w (x^w_0 - \langle x^w \rangle_{ss})^2}{\beta^w [x^w_0 D^w - 1 + e^{-\gamma(1-x^w_0)}]} \left[ 1 - e^{-\beta^w \left( \frac{x^w_0 D^w - 1 + e^{-\gamma(1-x^w_0)}}{D^w (x^w_0 - \langle x^w \rangle_{ss})} \right)} \right]$$

and

$$\Omega^d = \langle x^d \rangle_{ss} D^d + \frac{D^d (x^d_0 - \langle x^d \rangle_{ss})^2}{\beta^d [x^d_0 D^d - 1 + e^{-\gamma(1-x^d_0)}]} \left[ 1 - e^{-\beta^d \left( \frac{x^d_0 D^d - 1 + e^{-\gamma(1-x^d_0)}}{D^d (x^d_0 - \langle x^d \rangle_{ss})} \right)} \right]$$

are the evapotranspiration fraction during the wet and the dry season, respectively, with their corresponding soil moisture value $x^w_0$ at the beginning of each season and $\langle x^w \rangle_{ss}$ at stochastic steady state (see Appendix B.2), $D^d = \frac{D^w s}{\rho^s}$, and $\beta^w = \frac{\beta^d}{\beta^s}$.

The temporal evolution of the mean available soil moisture, $\langle x(t) \rangle$, obtained by the minimalist and linear LQ model are compared to one another and with the result of a numerical simulation in Figure 3.1a. The difference in $\langle x(t) \rangle$ from the minimalist and numerical simulation is most relevant for very shallow soils due to the non-negligible leakage/runoff at the beginning of the dry season and for very
Figure 3.1: Comparison of the minimalist and the linear LQ model applied to the seasonal soil water balance. (a) Temporal evolution of mean soil moisture $\langle x(t) \rangle$ using numerical simulations (dotted lines), the LQ model (solid lines), and the minimalist model (dashed lines), with $\gamma = 10.4$, $ET_{max}^d = ET_{max}^w = 0.45$ cm d$^{-1}$, $w_0 = 15.6$ cm, $\alpha = 1.5$ cm, $\lambda^w = 0.45$ d$^{-1}$, $\lambda^d = 0.15$ d$^{-1}$, and $\tau = 1$. (b) Corresponding soil water balance represented by the aseasonal Budyko’s curve for $\gamma = 10.4$ (black solid line) and seasonal curves using the minimalist model (gray dashed line) and the linear LQ model (gray solid line). Other parameters are as in (a) except for variations in $\lambda^w$. The soil water balance for the realizations (a) are represented by a single point in (b) (minimalist model, circle; linear LQ model, square).

Deep soils due to the slow recharge at the beginning of the wet season (Figure 3.1a). The restrictions related to the minimalist model is further discussed in Appendix B.1. The linear LQ model, on the other hand, is able to approximate the temporal evolution of soil moisture more closely to the numerical simulation for a wider range of parameters, and thus will be used in the rest of analyses for mean annual water balance, $\langle \frac{ET}{R} \rangle$. The parametric curves for $\langle \frac{ET}{R} \rangle$ are plotted as a function of the annual dryness index $D^\nu$ (equation (3.10)), generated by both analytical models in Figure 3.1b. As expected, the minimalist model performs well around intermediate dryness index values, but with extremely high or low soil water storage index or high dryness index, it tends to generate ratios of $\langle ET \rangle$ to $\langle R \rangle$ above 1. This is a direct consequence of the overestimation in evapotranspiration due to the higher-than-realistic soil moisture obtained with the minimalist model already observed with the specific choices of parameters in Figure 3.1a.
3.6 Effect of seasonality on Budyko’s curve

In the following analysis, we employ the results from the linear LQ model to explore the effects of climate seasonality on the annual average soil water balance by means of Budyko-like curves.

3.6.1 Role of rainfall variability and dry season length ($\rho$ and $\tau$)

Figure 3.2a shows the shift in the Budyko’s curve from the aseasonal case ($T^d = 0$; solid black line) to the seasonal case with increasing dry season length (the particular case of a 6-month dry season, i.e., $\tau = 1$, is represented by the solid gray line). We consider two alternative constraints on rainfall as the dry season length is increased: (1) total annual rainfall is kept constant by redistributing rainfall from the dry to the wet season, i.e., increasing $\lambda^w$ while keeping $\lambda^d$ constant (resulting in a decrease in the ratio of rainfall frequencies $\rho$; dashed lines) and (2) $\lambda^w$, $\lambda^d$ and hence $\rho$ are kept constant by decreasing total annual rainfall (dotted lines). As the dry season length (and thus $\tau$) is increased, a single point on the aseasonal Budyko’s curve (black solid line) will shift to the right, following one of two trajectories associated the previously described rainfall constraints, with different rates of change for both the annual dryness index, $D^{yr}$, and evapotranspiration ratio, $\frac{E T^{yr}}{R^{yr}}$. Points at equal intervals along the Budyko’s curve are used to show these relative rates of increase for the two cases. For a fixed $\tau$, all the endpoints of these trajectories fall onto the same line (solid gray line for $\tau = 1$). As such, the seasonal curve is independent of the method used to generate it: a single point on the Budyko’s curve may trace out different trajectories, but their endpoints for a given $\tau$ will always coincide on the same curve regardless of the path they followed from Budyko’s.

An important consequence of the results shown in Figure 3.2a is that, at a given annual dryness index, the overall effect of increasing the dry season length, with or
Figure 3.2: The effects of seasonality parameters on Budyko’s curve. (a) Effect of dry season length with $T^d$ increasing from 0 (black line) to $T^d = 180$ days (i.e., 6 month long dry season; $\tau = 1$, gray solid line), with constant total annual rainfall (dashed lines) and constant rainfall frequency $\rho$ (dotted lines). (b) Effect of seasonal ratio of PET, $\epsilon$: $\epsilon = 1$ (gray solid line), $\epsilon = 2$ (gray dashed line), and $\epsilon = 3$ (gray dotted line). Symbols represent typical values from each climate type. (c) Effect of the storage index $\gamma$: $\gamma = 2$ (light gray), 5.5 (gray), and 50 (black) with and without seasonality (dashed and solid lines, respectively). Dots denote the intersections between a dashed and a solid line. All results are obtained with the linear $LQ$ model. Unless otherwise specified, $\tau = 1$, $\epsilon = 2$, and $\gamma = 10.4$. Dry season parameters are always set to $\alpha = 1.5$ cm, $\lambda^d = 0.15$ d$^{-1}$, and $ET_{max}^d = 0.45$ cm d$^{-1}$. 
without a concomitant increase in seasonal rainfall variability (i.e., \( \rho \)), is a decrease in the evapotranspiration ratio. This effect is especially accentuated around the intermediate dryness indices, where the difference between aseasonal and seasonal evapotranspiration is greatest.

3.6.2 Impact of variability in potential evapotranspiration (\( \epsilon \))

Tropical \( \left( ET_{\text{w max}} \approx ET_{\text{d max}}; \epsilon \approx 1 \right) \) and Mediterranean climates \( \left( ET_{\text{w max}} < ET_{\text{d max}}; \epsilon > 1 \right) \) can be compared by modifying the potential evapotranspiration ratio, \( \epsilon \). By assuming that the dry-season PET is not significantly different between tropical and Mediterranean climates, we focus our analyses on the effect of a decrease in \( ET_{\text{w max}} \) while \( ET_{\text{d max}} \) is kept constant (resulting in \( \epsilon \) increasing to values greater than 1). As discussed in the previous section, an increase in dry season length and/or seasonal rainfall variability decreases the evapotranspiration ratio at a given annual dryness index compared to when the same total annual rainfall is distributed evenly throughout the year. As apparent in Figure 3.2b, this effect is further enhanced in Mediterranean climates \( \left( \epsilon > 1 \right) \) relative to tropical climates \( \left( \epsilon \approx 1 \right) \). Due to rainfall and PET being out of phase in Mediterranean climates, the evapotranspiration ratio further decreases as rainfall accumulate in the soil during the cold wet season without being used by plants, enhancing losses to runoff and deep percolation. In other words, an increase in \( \epsilon \) decreases \( \frac{ET_{\text{w}}}{R} \) beyond the limit already imposed by the length of the dry season \( (\tau) \) and/or degree of rainfall seasonality \( (\rho) \).

3.6.3 Impact of the soil water storage index (\( \gamma \))

The storage index \( \gamma = \frac{w}{\alpha} \) is an explicit function of several plant and soil parameters—soil porosity \( (n) \), plant rooting depth \( (Z_r) \), plant wilting point \( (s_w) \), and maximum soil water retention point \( (s_1) \)—and how they compare to average rainfall depth \( \alpha \). In the absence of seasonality, higher \( \gamma \) implies a larger proportion of rainfall
stored and retained in the soil rather than lost as runoff or deep percolation (either due to higher soil water storage capacity or shallow rainfall events that tend not to saturate the soil). Thus, larger $\gamma$ in aseasonal climates results in a larger percentage of rainfall used for evapotranspiration, represented by an upward shift in Budyko’s curve ([Porporato et al., 2004]; Figure 3.2c, gray to black solid lines).

The role of the storage index $\gamma$ is more complex in seasonal climates, where it also represents the inertia with which soil moisture changes between seasons. For a fixed $\alpha$, soil and plant parameters ensuring a higher storage index not only results in a higher steady state soil moisture value but also in a slower rate of change in response to climatic inputs, especially apparent at the junctions between the wet and dry seasons. Because larger inertia associated with larger $\gamma$ results in a more moderate range of soil moisture values year-round, the decrease in leakage/runoff (due to soil moisture values farther from saturation) combined with higher storage can yield higher evapotranspiration ratios even in seasonal climates (Figure 3.2c, dashed lines).

A comparison of seasonal and aseasonal Budyko’s curves also suggests that the impact of seasonality and storage index on the evapotranspiration ratio depends on the dryness index of the climate under consideration. Toward drier end of the curves, deeper roots in seasonal climates can result in higher evapotranspiration compared to shallower roots in aseasonal climates at a given dryness index. This is likely due to the added water storage capacity provided by deeper roots. Toward wetter climates, however, deeper roots in seasonal climates eventually lose their advantage. In fact, wetter seasonal climates are associated with a tremendous concentration of rainfall during the wet season, which causes soil moisture to quickly reach stochastic steady state; the higher losses to leakage/runoff that ensue can effectively lower the evapotranspiration ratio to an extent that cannot be compensated by an increase in storage. These trade-offs are apparent in the locations of the intersections between
aseasonal and seasonal curves of different storage indices (marked by dots in Figure 3.2c). The most important consequence is that the decrease in evapotranspiration due to climate seasonality can be balanced by higher storage indices, e.g., by developing deeper roots; this in turn can be more easily accomplished in drier climates than in wetter climates (Figure 3.2c). A caveat of this analysis is the assumption that typical rooting depths and climate conditions are independent. Nevertheless, roots are generally deeper in arid and seasonally dry climates (Schenk and Jackson, 2002b); this correlation may serve to offset the large differences in the evapotranspiration ratio between different storage indices in drier climates.

3.7 Discussions and conclusions

In this study we use dimensional analysis to develop a generalized framework for evaluating the role of seasonal climatic variability on soil moisture and mean annual evapotranspiration in rainfall dominated, surface water dependent systems. Assuming that the year consists of a distinct sequence of a wet and a dry season, we define a set of dimensionless quantities describing the seasonality of rainfall occurrence and plant activity. By combining this framework with a stochastic soil moisture balance model, the mean annual soil water balance can be analytically obtained. Generally, a stronger seasonality (e.g., due to longer dry seasons or stronger variability in rainfall or PET between the two seasons) results in more runoff and percolation losses and lower evapotranspiration ratio.

Our model shows that the influences of seasonal climate and soil water storage on evapotranspiration observed by Hickel and Zhang (2006) and Gerrits et al. (2009) can also be explained through the compensatory role played by soil water storage for changes in annual evapotranspiration resulting from rainfall seasonality. In seasonal climates, the effect of an increase in plant-available soil water storage capacity (chiefly driven by rooting depth) depends on the dryness index at the site (Figure
3.2c). In drier seasonal climates, the increase in total annual evapotranspiration achieved through deeper roots and more soil water storage easily overtakes the decrease due to rainfall seasonality. On the other hand, in wetter seasonal climates, the concentration of rainfall in the wet season saturates the soil despite increased storage, resulting in an overall decrease in evapotranspiration ratio. Care should be taken when comparing the evapotranspiration ratios across soil water storage indices because this model assumes rooting depths act independently from climate conditions (even though deeper roots are generally found in more arid and seasonal climates (Schenk and Jackson, 2002b,a)) and across plant types (when rooting depth can sometimes correlate with other plant characteristics such as stomatal conductance, leaf area index, and PET).

The present analysis uses an idealized representation of seasonality. In particular, the temporal variability of rainfall and PET are captured at the seasonal scale only, using two constant levels to represent the relative magnitudes of the climatic drivers across seasons. The assumption in this model of a fixed duration of the seasons as well as their fixed start and finish times have implications for plant phenology and its ensuing effects on evapotranspiration. One extension could be the inclusion of temporal variability of hydroclimatic signals at different scales, from intra-annual to interannual fluctuations, as well as a finer resolution of their relative timing (beyond being either in-phase or out-of-phase) and uncertain arrivals. Other controls such as vegetation dynamic can also prove revealing, by incorporating feedbacks from plant biomass to soil moisture, soil nutrient dynamics, plant resource allocation, and life strategies. Altogether, these additions will lend further insights into the roles of variable hydroclimatic forcing and soil-plant conditions in seasonally dry ecosystems.
4

Soil water partitioning in nonstationary environments: a general framework


4.1 Introduction

Previously in Chapter 3, we have studied the effect of climate seasonality on soil water balance, which complemented the results from existing analytical models (e.g., (Milly, 1994a)) as well as other more complex models (Yokoo et al., 2008; Woods, 2003). Others have adopted phenomenologically derived relationships based on boundary conditions imposed by water or energy balances (Potter et al., 2005; Chen et al., 2013). Soil water storage has been found to play an important role in seasonal climates in reducing losses through leakage and deep percolation, though such losses can be increased when seasonal rainfall and potential evapotranspiration are
out-of-phase, as in Mediterranean climates (Milly, 1994a; Potter et al., 2005). The problem of quantifying the mean pathways within the water cycle remains a challenging one, requiring suitable characterization of random-like hydroclimatic forcings which are simultaneously embedded in a periodic seasonal cycle.

Our main contribution in this chapter is to extend a physically-based, stochastic model of soil moisture (Porporato et al., 2004) into a generalized nonstationary context. Previously, this model has been used to analyze the effect of climate, soil, and vegetation on various quantities of interest, including the mean soil moisture, plant biomass, and carbon uptake and storage (Laio et al., 2002; Porporato et al., 2004; Feng et al., 2012; Rohr et al., 2013), though the descriptions of climate seasonality have so far been kept piecewise-linear to allow for mathematical tractability. The novelty of the work presented here is in integrating the daily and seasonal variabilities consistently within a stochastic framework. This bypasses the ad hoc use of seasonally “averaged” forcings (e.g. from monthly data) as driving factors in the soil water balance, since most soil water dynamics occur at a much shorter (e.g., daily) timescale. In addition, our simple models bring out new insights on seasonal soil moisture without resorting to impractically large numerical simulations. We construct not only the long-term evapotranspiration ratio but also transient departures from Budyko’s curve at the intra-annual scale, showing hysteresis in the mean soil moisture that is mediated by seasonal soil water storage. We neglect the contribution of capillary rise from groundwater or deeper layers and consider only surface water dependent systems where groundwater is either very deep or its amount negligible. We also neglect the contribution of lateral flow. These additional complexities would require substantial modifications to the existing model and are left for future studies. Here, we focus on cases where soil moisture dynamics are dominated by seasonally varying, stochastic rainfall.

In the following sections, we begin by introducing the stochastic mean soil mois-
ture model with three approximations for mean leakage/runoff and the corresponding Budyko’s formulation. Next, the model results are presented using climatic parameters typical of tropical dry and Mediterranean climates, with attention to the role of the phase difference between rainfall and potential evapotranspiration. Then, we highlight seasonal hysteretic behavior in the transient evapotranspiration ratio and other hydrological terms as results of seasonal soil water storage and trace their projections along Budyko’s framework. Finally, the effect of climate seasonality on the annually averaged Budyko’s curve is presented.

4.2 Modeling mean soil moisture and Budyko’s curve at the seasonal level

4.2.1 Mean soil moisture dynamics

At the daily scale, assuming negligible horizontal redistribution via topographic effects, soil moisture at a point is recharged through intermittent rainfall pulses of random depths, and depleted through evapotranspiration, leakage, and runoff. We neglect any contribution from groundwater and focus only on surface water dependent systems. In what follows, we focus on the vertically averaged, plant available “effective” soil moisture, $x$, at the daily time scale. The range of $x$ brackets the upper and lower limits of soil moisture available for plant uptake, with $x = 0$ occurring at the plant wilting point $s_w$, and $x = 1$ at $s_1$, which is the threshold above which all soil water is assumed to be immediately lost through leakage and runoff. The threshold $s_1$ is physically related to soil properties and is typically situated between field capacity and complete soil saturation (Milly, 1993; Porporato et al., 2004). Thus, $x$ is simply a standardized version of relative soil moisture $s$, defined by $x = (s - s_w)/(s_1 - s_w)$. With the above assumptions, the effective soil moisture balance, vertically averaged over the rooting zone, is (Rodríguez-Iturbe et al., 1999;
where \( w_0 = nZ_r(s_1 - s_u) \) is the maximum plant-available soil water storage volume per unit ground area, and \( n \) is the vertically averaged soil porosity and \( Z_r \) is the rooting depth (e.g., cm). The rate of change in the total volume of plant-available soil moisture \( w_0 \frac{dx(t)}{dt} \) is governed by the rate of rainfall \( R(t) \) (e.g., cm/day), evapotranspiration \( ET(x(t), t) \) (e.g., cm/day), and leakage/runoff \( LQ(x(t), t) \) (e.g., cm/day).

Rainfall is considered as a time-dependent stochastic process and, at the daily scale, idealized as a marked Poisson process that is non-homogeneous in time, with a time-dependent rate parameter \( \lambda(t) \) and the depth of rainfall drawn independently from an exponential distribution of mean \( \alpha(t) \) (Rodriguez-Iturbe et al., 1999). The sources of seasonality may come from gradual changes in the mean frequency of rainfall and in the parameters that control evapotranspiration.

Given the stochastic nature of all variables presented in equation (4.1), it is useful to introduce some notation here to distinguish between ensemble averages and time averages. The ensemble average of a generic stochastic variable \( u(t) \in [u_{\min}, u_{\max}] \) with associated pdf \( p(u, t) \) at time \( t \) is denoted by brackets as \( \langle u(t) \rangle = \int_{u_{\min}}^{u_{\max}} u' p(u', t) du' \); this can be applied to all soil water partitioning terms in equation (4.1). Furthermore, each time-dependent pdf \( p(u, t) \) has an associated quasi steady state pdf \( p_{ss}(u, t) \), which is produced by applying the instantaneous conditions found at \( t \) constantly over an extended period of time, until \( p(u, t) \) has reached steady state, yielding \( p_{ss}(u, t) \). The resulting ensemble average produced from \( p_{ss}(u, t) \) will be denoted by \( \langle u_{ss}(t) \rangle \). In parallel, we also make use of temporal averages which are represented by overbars, defined as \( \bar{u} = \frac{1}{T} \int_{t_0}^{t_0+T} u(t) dt \), where \( t_0 \) and \( T \) are the initial time and period of interest. In the analyses that follow, temporal averages are taken of the ensemble average \( \langle u(t) \rangle \) over a year \( (T = T_{year}) \), which is the natural
Figure 4.1: Evolution of the soil moisture trajectories and pdfs over a year. Gray lines represent single realizations of stochastic soil moisture according to equation (4.1). The thick black line is their ensemble average, and the dashed line is its time average over a year. The pdf on the right panel is compiled for values over the entire year, while the pdfs along the trajectories correspond to a particular day of the year.

period over which seasonal climatic variations occur. As such, once we neglect initial transients and consider only the seasonally periodic stochastic process, the temporal average of the ensemble over a year will be equivalent to the long term temporal average; both will be designated by \( \langle u(t) \rangle \). Figure 4.1 is a schematic showing the evolution of the stochastic soil moisture trajectories \( x(t) \) in gray, their associated pdf \( p(x, t) \) at six points in the year, their ensemble average \( \langle x(t) \rangle \) as a bold line, and their long term average as a dashed line.

The mean soil moisture balance corresponding to equation (4.1) can be written in its normalized form as

\[
\frac{d\langle x(t) \rangle}{dt} = \frac{\langle R(t) \rangle}{w_0} - \frac{\langle ET(x(t)) \rangle}{w_0} - \frac{\langle LQ(x(t), t) \rangle}{w_0},
\]

with the macroscopic equation accounting for the mean effects of random rainfall as (Laio et al., 2002; Rodriguez-Iturbe and Porporato, 2004),

\[
\frac{d\langle x(t) \rangle}{dt} = \frac{\lambda(t)}{\gamma(t)} \int_0^1 \frac{ET(u)}{w_0} p(u, t) \, du - \frac{\lambda(t)}{\gamma(t)} \int_0^1 e^{-\gamma(t)(1-u)} p(u, t) \, du,
\]
where $\gamma(t) = \frac{u_0}{a(t)}$.

When considering averages over a large area of heterogeneous soil and vegetation, evapotranspiration may be assumed to depend linearly on $x$, taking a value of 0 at $x = 0$ to $ET_{\text{max}}$ at $x = 1$ (Porporato et al., 2004). Thus, the evapotranspiration term on the right hand side of equation (4.3) can be simplified as

$$\int_0^1 \frac{ET(u)}{w_0} p(u, t) \, du = \frac{ET_{\text{max}}(t)}{w_0} \int_0^1 u p(u, t) \, du = k(t) \langle x(t) \rangle,$$  \hspace{1cm} (4.4)

where $k(t) = \frac{ET_{\text{max}}(t)}{w_0}$. We adopt a simplified notation in the rest of the paper, where the time dependence of a function is denoted by a subscript $t$. Equation (4.3), now approximating evapotranspiration, can be reduced to

$$\frac{d\langle x_t \rangle}{dt} = \frac{\lambda_t}{\gamma_t} - k_t \langle x_t \rangle - \frac{\lambda_t}{\gamma_t} \langle e^{-\gamma(t)(1-x_t)} \rangle,$$  \hspace{1cm} (4.5)

where

$$\langle e^{-\gamma(t)(1-x_t)} \rangle = \int_0^1 e^{-\gamma(t)(1-u)} p_t(u) \, du.$$  \hspace{1cm} (4.6)

Equation (4.5) is not closed because the last term, in which the ensemble average is taken over the exponential of soil moisture instead of over the soil moisture itself, is not known in terms of $\langle x_t \rangle$.

Since it will be used later, we note here that the pdf of $x$ and its ensemble mean are already known under steady state conditions for constant parameters, in the form of a truncated gamma distribution with shape parameter $a$ and rate parameter $b$ (Porporato et al., 2004),

$$p_{ss}(x) = \frac{b^a x^{a-1} e^{-bx}}{\Gamma(a) - \Gamma(a, b)}, \quad \langle x \rangle_{ss} = \frac{a}{b} - \frac{b^{a-1}}{\Gamma(a) - \Gamma(a, b)} e^{-b},$$  \hspace{1cm} (4.7)

where $a = \frac{\lambda}{\kappa}$ and $b = \gamma$ are constant values, and $\Gamma(\cdot, \cdot)$ indicates a truncated gamma function (Abramowitz and Stegun, 1964).
4.2.2 **Approximating the average leakage/runoff ($LQ_t$)**

The complication of solving equation (4.5) under fully seasonal conditions arises from the nonlinear time dependency in each of the parameters, and our lack of information on the full pdf $p_t(x)$ at every time point, which is required to quantify the leakage/runoff term, which in turn governs the evolution of mean soil moisture. In this section, we present, in order of increasing complexity, four treatments of the $LQ_t$ term in equation (4.6). These approximations reduce equation (4.5) into an ordinary differential equation (ODE) for $\langle x_t \rangle$.

We start by considering cases where $\langle LQ_t \rangle$ can be effectively neglected. Such an assumption is justified when the mean rainfall depth $\alpha_t$ is low relative to the soil root depth $w_0$ or if rainfall is infrequent, corresponding to small $\lambda_t$. Such is often the case in extremely dry climates or during the dry season. Equation (4.5) subsequently becomes

\[
\frac{d\langle x_t \rangle}{dt} = \frac{\lambda_t}{\gamma_t} - k_t \langle x_t \rangle.
\]  

(4.8)

We can explicitly solve this simple ODE with initial value $x_0$ if all parameters are considered to be constant (e.g., within the same growing season), resulting in an analytical solution of

\[
\langle x_t \rangle = \frac{\lambda}{\gamma k} + \left( x_0 - \frac{\lambda}{\gamma k} \right) e^{-kt}.
\]  

(4.9)

Indeed, the full solution to the stochastic differential equation (4.1), $p_t(x)$, is available when constant parameters are assumed for this case (Viola et al., 2008). However, since these assumptions do not place an upper bound on the value of $\langle x_t \rangle$, they also result in significant overestimation of $\langle x_t \rangle$ when there is leakage or runoff. Other implications for soil moisture and plant water stress are extensively discussed in Viola et al. (2008) under constant climate conditions for the growing season. The next three cases are newer improvements on equation (4.5) that approximate $\langle LQ_t \rangle$.
using various assumptions for \( p_t(x) \).

**Quasi steady state approximation**

The first treatment approximates the instantaneous pdf of soil moisture by its quasi steady state pdf as determined by the corresponding environmental parameters, 

\[ p_t(x) \approx p_{t,ss}(x), \]

where the shape and rate parameters from equation (4.7) are now \( a_t = \lambda_t/k_t \) and \( b_t = \gamma_t \). That is, the parameters found at each instant \( t \), i.e., \( \lambda_t, k_t \), and \( \gamma_t \), are “frozen” as constants and applied to a parallel homogeneous stochastic process until it has reached steady state, represented by \( p_{t,ss}(x) \). This is similar to assuming that the inhomogeneous process can instantaneously reach steady state at every point in time. Examples of \( p_{t,ss}(x) \) are shown in Figure 4.2 at different times of the year.

Hence, we substitute \( p_{t,ss}(x) \) in place of \( p_t(x) \) in the formula for mean leakage, shown in equation (4.6) as 

\[ \langle LQ_t \rangle = \frac{\lambda_t}{\gamma_t} \int_0^1 e^{-\gamma_t(1-u)} p_t(u) \, du. \]

It follows that the instantaneous ensemble leakage \( \langle LQ_t \rangle \) is approximated by the steady state leakage value \( \langle LQ_{t,ss} \rangle \), calculated using instantaneous environmental values at \( t \) and given by 

\[ \langle LQ_t \rangle \approx \langle LQ_{t,ss} \rangle = \langle R_t \rangle - \langle ET_{t,ss} \rangle = \langle R_t \rangle - ET_{\max,t} \langle x_t \rangle_{ss}. \]

Equation (4.5) can now be written by applying equation (4.7) for \( \langle x_t \rangle_{ss} \) as 

\[ \frac{d\langle x_t \rangle}{dt} = \frac{\lambda_t}{\gamma_t} - k_t \langle x_t \rangle - \frac{k_t}{\gamma_t} \Gamma \left( \frac{\lambda_t}{k_t} \right) \frac{\gamma_t}{\Gamma \left( \frac{\lambda_t}{k_t}, \gamma_t \right)} e^{-\gamma_t}. \quad (4.10) \]

The previous equation suggests that this particular form of leakage/runoff can be combined with the original rainfall process to be considered as a new censored marked Poisson process, where the equivalent rainfall frequency can now be defined as \( \lambda'_t = \)
\[ \lambda_t - k_t \gamma_t e^{-\gamma_t} / \left( \Gamma \left( \lambda_t / k_t \right) - \Gamma \left( \lambda_t / k_t, \gamma_t \right) \right) \], where \( \lambda'_t \) is strictly positive. Additionally, equation (4.10) can be cast into an equivalent form of

\[ \frac{d\langle x_t \rangle}{dt} = k_t (\langle x_{t,ss} \rangle - \langle x_t \rangle), \] (4.11)

where changes in the mean soil moisture is dictated by the difference between its current value \( \langle x_t \rangle \) and its quasi steady state value \( \langle x_{t,ss} \rangle \). The approximation of \( p_t(x) \) by \( p_{t,ss}(x) \) is most appropriate when soil moisture can quickly adjust to changes in its environment, which is the case when soil water storage is small. Figure 4.2 also shows that the difference between true steady state soil moisture and \( p_{t,ss}(x) \) diminishes during persistently wet or dry periods. During the dry-down and wetting-up periods, the quasi steady state approximation predicts soil moisture values that are respectively lower and higher than true steady state values because it does not capture the effect of soil moisture transfer from previous times. Thus, this treatment of the leakage term is expected to work well at small \( \gamma_t \) values and in conditions where the environmental parameters do not change quickly. Since \( \langle x_{t,ss} \rangle \) can be calculated using environmental parameters only and do not depend on the state variable \( \langle x_t \rangle \), this approximation results in an inhomogeneous, linear, time-dependent ODE that can be formally solved (see, for example, page 14 of Bender and Orszag (1978)).

**Negligible fluctuations approximation**

The next treatment assumes that the soil moisture pdf itself is concentrated entirely on its mean value, represented by a Dirac delta function at \( \langle x_t \rangle \), i.e.,

\[ p_t(x) \approx \delta(x - \langle x_t \rangle). \]

These are shown as spikes at \( \langle x_t \rangle \) in Figure 4.2. The substitution of the Dirac delta function into the pdf in equation (4.5) results in \( \langle e^{-\gamma(1-x_t)} \rangle = e^{-\gamma(1-\langle x_t \rangle)} \) in the
leakage term, and correspondingly the new soil moisture equation becomes

\[
\frac{d\langle x_t \rangle}{dt} = \frac{\lambda_t}{\gamma_t} - k_t\langle x_t \rangle - \frac{\lambda_t}{\gamma_t} e^{-\gamma_t(1-\langle x_t \rangle)}. \tag{4.12}
\]

Since \( e^{-\gamma(1-x)} \) for any value of \( x \) is a convex function, by Jensen’s inequality, \( \langle e^{-\gamma(1-x)} \rangle \geq e^{-\gamma(1-\langle x \rangle)} \). While we thus know that the approximated mean leakage must be smaller or equal to the actual mean leakage at any given time point, the cumulative result of this estimation is more difficult to predict, since the evolution of \( \langle x_t \rangle \) necessarily depends also on the history of its seasonal variations. The difference between \( \langle e^{-\gamma(1-x_t)} \rangle \) and \( e^{-\gamma(1-\langle x_t \rangle)} \) decreases as the soil moisture pdf becomes naturally concentrated around its mean; this happens as the true value of soil moisture approaches its upper or lower bounds (for example, as during the wet period in Figure 4.2). Thus, we may expect this approximation to perform better in conditions that allow soil moisture to remain perennially close to its bounds, such as in extremely
wet or arid environments where soil moisture is continuously saturated or otherwise dry. Unlike the previous approximations, equation (4.12) is a nonlinear ODE. While an analytical solution is unavailable, its closed form allows numerical solutions to be easily found using simple ODE solvers.

Self-consistent truncated gamma approximation

The last treatment approximates the instantaneous soil moisture pdf $p_t(x)$ by a truncated gamma distribution with parameters consistent with the evolution of the mean soil moisture. The shape parameter of the truncated gamma distribution, which is the pdf of $x$ under steady state conditions (equation (4.7)), is constantly adjusted so that the resulting pdf will have its mean centered on the current value of $\langle x_t \rangle$. This combines the advantages of the quasi steady state approximation to better capture the overall shape of $p_t(x)$ with the negligible fluctuations approximation’s ability to track its mean.

The mean of the truncated gamma distribution with given shape parameter $a$ and rate parameter $b$ can be calculated using equation (4.7). To match it to the mean soil moisture value at any given time, we set the instantaneous rate parameter to $b_t = \gamma_t$ (similar to the quasi steady state model) and obtain an implicit function $a_t = f^{-1}(\langle x_t \rangle; \gamma_t)$ for the instantaneous shape parameter $a_t$ in terms of $\langle x_t \rangle$ and $\gamma_t$, where

$$f(a_t; \gamma_t) = \frac{a_t}{\gamma_t} - \frac{\gamma_t^{a_t-1}}{\Gamma(a_t) - \Gamma(a_t, \gamma_t)} e^{-\gamma_t} = \langle x_t \rangle. \quad (4.13)$$

The resulting truncated gamma distribution, $p^*_t(x)$, parameterized by $b_t = \gamma_t$ and $a_t = f^{-1}(\langle x_t \rangle; \gamma_t)$, where $f^{-1}$ is the inverse of equation (4.13), has its mean equal to $\langle x_t \rangle$ (Figure 4.2). The shape of the inverse function $f^{-1}$ is illustrated in Figure 4.3 for $\gamma_t = 5.5$.

Substituting the formula for $p^*_t(x)$ into equation (4.6), the governing equation
Figure 4.3: Inverse function of equation (4.13), used for the self-consistent truncated gamma approximation, shown for $\gamma_t = 5.5$. The dashed lines are used to indicate that $a_t = \lambda_t / k_t$ corresponds to $\langle x_t \rangle = \langle x_t \rangle_{ss}$. In fact, this is the value used for the parameter $a_t$ in the quasi steady state model in equation (4.10).

(4.5) becomes

\[
\frac{d\langle x_t \rangle}{dt} = \frac{\lambda_t}{\gamma_t} - k_t \langle x_t \rangle - \frac{k_t}{\gamma_t} \frac{\gamma_t^{a_t}}{\Gamma(a_t) - \Gamma(a_t, \gamma_t)} e^{-\gamma_t}, \quad a_t = f^{-1}(\langle x_t \rangle; \gamma_t). \tag{4.14}
\]

We emphasize here that the equations in (4.14) form a closed set; substituting $f^{-1}(\langle x_t \rangle; \gamma_t)$ in place of $a_t$ ensures that the ODE, as a function for $\langle x_t \rangle$, can be solved using simple numerical solvers in much the same way as equation (4.12). The additional complexity of this model comes only from having an implicit function embedded within the ODE. In fact, this ODE is similar to the ODE derived from the quasi steady state approximation (equation (4.10)), where the rainfall and leakage/runoff process can again be considered as a new censored rainfall process with an equivalent, strictly positive rainfall frequency, $X_t' = \lambda_t - k_t \gamma_t^{a_t} e^{-\gamma_t} / (\Gamma(a_t) - \Gamma(a_t, \gamma_t))$, which is now also dependent on the current value of mean soil moisture through $a_t = f^{-1}(\langle x_t \rangle)$. We have chosen to solve for $a_t$ as function of $\langle x_t \rangle$ while keeping $b_t = \gamma_t$ because the runoff generation mechanism acts as a censoring of the rainfall process; in a censored process the size of the marks (e.g. rainfall depths) can be drawn from an exponential distribution with the same normalized mean of $\gamma_t$ as the
original process, due to the memoryless property of exponential distributions (Ross, 2014). Furthermore, the parameter $a_t$ for a given $b_t$ is directly proportional to the mode of the truncated gamma distribution, suggesting that the mode might be better used to summarize the effects of $p_t(x)$ instead of its mean.

The difference between this approximation and the quasi steady state approximation is that the leakage/runoff term is no longer predetermined by environmental conditions but rather needs to be solved implicitly using current values of $\langle x_t \rangle$. This modification produces considerable improvements in the approximation to the true values (see e.g., Figure 4.2 and Appendix C). While relatively more computationally costly due to the inversion required for $f^{-1}$, it still reduces the problem to that of solving a nonlinear ODE and eliminates the need to simulate the full random processes associated with stochastic rainfall realizations.

4.2.3 Budyko’s formulation

In addition to the mean soil moisture evolution over a year, we are interested also in the partitioning of rainfall into evapotranspiration and leakage/runoff. A synthetic representation of the evapotranspiration ratio, defined as the ratio of evapotranspiration over rainfall, is provided through Budyko’s curve as a function of the dryness index, defined as the ratio of potential evapotranspiration over rainfall (Budyko, 1974). While Budyko first introduced this framework under steady state conditions using long term means, where $\lambda_t = \lambda$, $k_t = k$, and $\gamma_t = \gamma$ are considered constant, it is possible to apply his framework also to instantaneous and annually averaged quantities.

For example, the instantaneous partitioning terms using time dependent parameters are,

$$\langle D_t \rangle = \frac{\gamma_t}{\lambda_t} k_t, \quad \langle ET_t \rangle = \frac{\gamma_t}{\lambda_t} k_t \langle x_t \rangle.$$

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The annually averaged curve using seasonal parameters that change over time can be constructed by using the time average of the instantaneous dryness index and the evapotranspiration ratio, i.e.,

$$\langle D \rangle = \frac{1}{T_{\text{year}}} \int_t^{t+T_{\text{year}}} \gamma_t \frac{k_t}{\lambda_t} dt,$$

$$\frac{\langle ET \rangle}{\langle R \rangle} = \frac{1}{T_{\text{year}}} \int_t^{t+T_{\text{year}}} \frac{\gamma_t}{\lambda_t} k_t \langle x_t \rangle dt,$$

where $T_{\text{year}}$ is the length of the year. While $t$ is contained in the integral limits, the resulting quantifies do not depend on $t$ because the integrations are conducted over their natural period of variation, namely over a year. For that same reason, in the absence of interannual variabilities which is the case considered here, $\langle D \rangle$ is also the same as the classical, long term dryness index introduced by Budyko. Finally, Budyko’s evapotranspiration ratio using long term mean climatic parameters are shown as

$$\frac{\langle ET \rangle_{ss}}{\langle R \rangle_{ss}} = \frac{\gamma_t}{\lambda} \langle k \langle x \rangle \rangle_{ss}.$$

4.3 Results

4.3.1 Comparison with stochastic simulations

The three new approximations of the LQ term described in the previous section—quasi steady state, negligible fluctuations, and self-consistent truncated gamma—allow complete flexibility in the climatic inputs during modeling of seasonal soil moisture dynamics. Their results are compared here with numerical simulations using parameters typical of tropical dry and Mediterranean climates. We start each run with an arbitrary initial condition $x_0 = 0.5$. At each time step, changes in the effective soil moisture $x$ is determined by inputs from rainfall and output from $ET$ and $LQ$ as determined by the time-dependent climate parameters. Rainfall is generated according to a non-homogeneous, marked Poisson process with mean frequency $1/\lambda_t$ and mean intensity $\gamma_t$. We adopt sinusoidal forms to describe rainfall
Figure 4.4: Comparison of results from typical Mediterranean and tropical dry climates. The Mediterranean climate has out-of-phase rainfall and potential evapotranspiration inputs, while the in tropical dry climates they are in-phase (top panels). The bottom panels show results from simulations (averaged over 1000 runs; dots), the quasi steady state approximation (model 1; dashed lines), the negligible fluctuations approximation (model 2; solid lines), and the self-consistent truncated gamma approximation (model 3; dotted lines), for mean soil moisture $\langle x_t \rangle$, mean evapotranspiration $\langle ET_t \rangle$ and leakage/runoff $\langle LQ_t \rangle$, and the evapotranspiration ratio over dryness index, $\langle ET_t \rangle / \langle R_t \rangle$ versus $\langle D_t \rangle$. Parameter values are as described in the text.

and potential evapotranspiration inputs $\lambda_t$ and $k_t$, e.g.,

$$v_t = \mu_v + A_v \sin(\omega t + \phi_v),$$

(4.15)

where $v_t$ is a stand-in variable for $\lambda_t$ or $k_t$, $\mu_v$ is the annual mean, $A_v$ is the amplitude of seasonal variation, $\phi_v$ is the phase, and the period $\omega$ is set to a year. If rainfall
depth at a time exceeds soil water storage (i.e., 1 – x, with 1 being the upper bound of effective soil moisture), soil moisture is filled to its upper bound at x = 1 and the rest of rainfall is lost to leakage/runoff. Loss from evapotranspiration occurs as a linear function of x. The mean soil moisture \( \langle x_t \rangle \) is calculated over many iterations, with the initial transient state discarded.

Results from a representative tropical dry and Mediterranean climates are shown in Figure 4.4. For Mediterranean climates, specific climate parameters are set to \((\mu_\lambda, A_\lambda) = (0.3, 0.2)\) and \((\mu_k, A_k) = (0.03, 0.02)\), with the phase difference \(\phi_k - \phi_\lambda = 180^\circ\) to reflect a hot, dry summer and a cool, wet winter (top panel, Figure 4.4). For the tropical dry climate, potential evapotranspiration is set to high year-round with mild fluctuations, e.g., \((\mu_k, A_k) = (0.06, 0.02)\), with more dramatic changes in rainfall between the seasons, \((\mu_\lambda, A_\lambda) = (0.6, 0.575)\). Both climate types are set to a constant soil storage index of \(\gamma_t = 5.5\), consistent with a globally averaged effective rooting depth (Porporato et al., 2004).

The bottom panels of Figure 4.4 show comparisons of the simulation and the model outputs for mean soil moisture \( \langle x_t \rangle \), water partitioning components \( \langle ET_t \rangle \) and \( \langle LQ_t \rangle \), and an instantaneous Budyko-type partitioning, e.g., \( \langle ET_t \rangle / \langle R_t \rangle \) vs. \( \langle D_t \rangle \), for every time point of the year. As expected, the self-consistent truncated gamma approximation followed the trajectory of the simulations most closely for all terms of comparison. The other two models do well enough in capturing the time evolution of the mean leakage/runoff and mean evapotranspiration as well as the general arc of seasonal mean soil moisture evolution. For example in the Mediterranean climate, all three models were able to show the surge in evapotranspiration at the beginning and end of the summer season. Further analyses in Appendix C show that when considering annually averaged values, all three models are also able to capture the annual evapotranspiration ratio \( \langle ET \rangle / \langle R \rangle \) to within a threshold of 0.05 under more general conditions.
In addition, all three models also demonstrate hysteretic behavior, wherein the same climate condition may not result in the same hydrological response due to the effect of transient soil water storage. This can be seen in the “loop” of the transient Budyko curves, as well as a similar loop in the relationship between \( \langle x_t \rangle \) and \( \langle LQ_t \rangle \) (not shown). For any given dryness index \( \langle D_t \rangle \), the corresponding \( \langle ET_t \rangle / \langle R_t \rangle \) value can fall within two domains—one along the upper “dry-down” trajectory and one along the lower “rewetting” trajectory. The reason more evapotranspiration can occur on average during the “dry-down” trajectory is that stored soil moisture can be carried over in greater amount from a wet period than from a dry period, accentuating the role of soil water storage.

4.3.2 Transient departures from Budyko’s curve

The previously described hysteresis of mean soil moisture and evapotranspiration ratio is further explored in this section. Here, we expand the projected views in the bottom panels from Figure 4.4 with an additional dimension for time and show that increasing the phase difference between rainfall and potential evapotranspiration will further increase the asymmetry in the curves between the wet and dry season.

Figure 4.5 shows expanded views of the transient Budyko’s curves produced from the self-consistent truncated gamma approximation, parameterized by the same mean and amplitude for both rainfall and potential evapotranspiration inputs as in the Mediterranean (left) and tropical dry (right) climates shown previously in Figure 4.4. In other words, the difference between each transient curves are attributed only to the phase difference between rainfall and potential evapotranspiration, with the thick black line showing a phase difference of 0° and the thick grey line showing 180°. For comparison, the classical steady state Budyko’s curve and the annually averaged Budyko’s curves parameterized with seasonal climatic inputs are shown respectively as a thin black line and two dashed lines, black and grey, for a greater range of
the dryness index. While the instantaneous dryness index and evapotranspiration ratio for the transient curves might fluctuate over a range of values over the year, each transient curve collapses to only a single point placed on the annually averaged curves.

Figure 4.5 shows that in both climate types, increase in the phase difference results in a larger, more asymmetrical hysteresis loop between the two seasons. Since this is due to the transfer of stored soil water from the wet season to the dry season, it implies that seasonal soil water storage becomes more important as rainfall and potential evapotranspiration become more out-of-phase. In Mediterranean climates, there is a sizable part of the year during which the instantaneous evapotranspiration ratio is above 1, where the high evapotranspiration is sustained not only from rainfall inputs but also from residual soil water carried over from the wet season. This “water
deficit” portion of the curve diminishes as the climatic inputs become more in-phase, when as a consequence evapotranspiration occurs mostly when the rainfall input is also high. In tropical dry climates, even though the climatic inputs are in-phase, there is still a large excursion of the instantaneous evapotranspiration ratio above 1, because rainfall is so low during the dry season that even a small amount of stored water from the wet season will allow evapotranspiration to surpass the rainfall input during the dry season.

4.3.3 Annual Budyko’s curve

The annually averaged Budyko’s curves calculated from seasonal climatic inputs are shown in Figure 4.6 as a function of seasonal rainfall amplitudes, with the rainfall signal both in-phase (black) and out-of-phase (grey) with potential evapotranspiration. The evapotranspiration ratios \( \langle ET \rangle / \langle R \rangle \) are found using the quasi steady state approximation and calculated as the complement of \( \langle LQ \rangle / \langle R \rangle \); this is justified when mean soil moisture \( \langle x_t \rangle \) have reached periodic steady state over the year. The particular curves on which the Mediterranean and tropical dry climates shown in Figure 4.4 reside are highlighted as dashed curves. In fact, these dashed curves are exactly the same as the dashed seasonal curves shown in Figure 4.5 of the same color. The reason that the graphs do not extend to all \( \langle D \rangle \) values is that there is an effective upper bound to the rainfall amplitude allowed for each mean rainfall level (which corresponds to a dryness index value) due to the fact that rainfall frequency \( \lambda_t \) at any given point cannot fall below 0.

It can be seen that the annually averaged evapotranspiration ratio is lower for an out-of-phase climate than an in-phase climate, regardless of seasonal rainfall amplitude. In general, increasing seasonal rainfall amplitude decreases the annual evapotranspiration ratio. However, in some cases (left panel, at high \( \langle D \rangle \) values), when the the climatic inputs are in-phase, the annual evapotranspiration ratio can first in-
Figure 4.6: The annual Budyko’s curves are shown as function of rainfall seasonality. Both panels show curves that are derived from the same potential evapotranspiration input ($\mu_k$ and $A_k$) as those found in Mediterranean (left) and tropical dry (right) climates of Figure 4.4, with the black meshes for when rainfall and potential evapotranspiration are in-phase, and grey meshes for when they are out-of-phase. The particular cases shown in Figure 4.4 (with given rainfall means $\mu_\lambda$) are annually averaged to single points, residing on a seasonal Budyko’s curve (dashed line) with a corresponding rainfall amplitude. Both points coincidentally has a dryness index of $\langle D \rangle = 0.55$.

crease with increasing rainfall amplitude before decreasing. This means that in some dry conditions, rainfall seasonality can actually result in more annual evapotranspiration compared to non-seasonal climates experiencing the same mean conditions. This is again due to seasonal soil water storage which transfers rainfall in the wet season to be used during exceptionally dry periods, which is otherwise not possible in a uniformly dry year.

4.4 Discussions and conclusions

To facilitate the analyses of hydrological processes under seasonally varying climates, both at the annual and intra-annual time scales, we introduced three approximations to a stochastic soil moisture model which are used to construct relatively parsimonious ODEs that closely describes the seasonal trajectories of mean soil moisture and its associated pdfs. This links daily stochastic soil moisture dynamics to its
seasonal patterns in a direct and consistent way. It is also a considerable advantage
over having to simulate stochastically rainfall input at every time step and taking
the ensemble mean over many realizations, and moreover is amenable to analytical
formulations.

The resulting mean soil moisture trajectories are used to investigate the effect
of transient soil water storage in seasonal climates. The mean soil moisture and in-
stantaneous evapotranspiration ratio both exhibit hysteresis because of seasonal soil
moisture storage, whereby evapotranspiration occurs during the dry season using soil
moisture carried over from the wet season as supplements to minimal rainfall inputs.
This results in an significant portion of the year during which the instantaneous evap-
otranspiration ratio stays above 1, which can be further prolonged as rainfall and
potential evapotranspiration become more out-of-phase. In some dry environments,
the annual evapotranspiration ratio can increase under seasonal climates precisely
because soil water storage allows a more “efficient” mode of evapotranspiration by
transferring soil moisture between seasons.

The main results brought out by our models are consistent with those from other
empirical studies. The importance of monthly soil moisture carryover has previously
been pointed out by Jothityangkoon and Sivapalan (2009), who by incorporating
seasonality and soil water transfer between storm events were able to achieve a much
better match between observed and predicted interannual variability of water balance
for selected catchments in the United States, Australia, and New Zealand. Likewise,
inclusion of a monthly carryover factor in Gerrits et al. (2009) significantly improved
predictions of annual water balance in semiarid areas in Africa. While these studies
highlight the role of seasonal soil water storage on annually integrated quantities,
we have explicitly related soil water storage to their seasonal, hysteretic dynamics.
Petrie and Brunsell (2012) used the seasonality of potential evapotranspiration to
induce such hysteresis in the presence of soil water storage, but we have extended the
analysis here to account also for the complex interplay between seasonal magnitude and timing of rainfall and potential evapotranspiration (via their amplitude and phase difference). Our models also predict that increase in the phase shift between atmospheric demand and water supply (towards more Mediterranean-type climates) decreases the annual evapotranspiration ratio. This has been shown through first-order modeling exercises (e.g., Milly (1994a), Feng et al. (2012)) and has recently been corroborated with observations across a global network of flux towers (Williams et al., 2012).

While our approach captures well the hydrological influence of seasonal climate variability, the simultaneous contributions from seasonal variation in soil water storage (as a result of between-season changes in rooting depths or vegetation cover), groundwater, and interannual variability in the seasons, which are all known to affect annual soil water partitioning, remain to be explored. Vico et al. (2014) recently investigated plant water and carbon uptake based on different physiological and phenological strategies in seasonally dry ecosystems using a coupled model of soil water (including deeper, more persistent storage) and plant carbon balances. The versatility of the models introduced here can allow for similar future extensions to account for the role of groundwater dynamics and vegetation water uptake strategies on seasonal and annual water partitioning.
5

Plant growth under climate seasonality

This chapter is adapted from Feng, X., Vico, G. and A. Porporato (2012), On the effects of seasonality on soil water balance and plant growth, Water Resources Research, 48(5).

5.1 Introduction

We apply the results presented previously in Chapter 3 to a simple model of plant growth, and use them to extrapolate the effects of altered seasonality at the ecosystem level. Because of the strong coupling between transpiration and CO$_2$ assimilation, evapotranspiration has strong connections to plant growth (Rosenzweig, 1968; Major, 1967) and morphology (Stephenson, 1990). Thus the effect of seasonality on plants follows inevitably from its effect on soil moisture and evapotranspiration. For Mediterranean climates, on the basis of vegetation surveys, Clary (2008) has already established a correlation between the seasonality of rainfall (in particular the relative strength of the summer drought) and the species composition, independent of other factors. In semi-deciduous tropical forests of southeastern Brazil, OliveiraFilho and
Fontes (2000) found the floristic composition to be most strongly correlated with proxies of increasing rainfall seasonality. In the following analyses, we explore the consequences for plant biomass of altering the season lengths while maintaining a constant total annual rainfall, effectively concentrating rainfall into the wet season as the dry season length is increased. The two end member scenarios encountered by the plants are a mild water stress imposed over a prolonged period of time (i.e., a long “wet” season and short dry season, resulting in soil moistures mostly under mild to moderate stress), and extreme stress during a long dry season with relatively high soil moisture during a short wet season.

5.2 A minimalist model of plant growth

To assess the effect of rainfall seasonality on the temporal evolution of plant biomass $B$ and to explore the possible existence of an optimal duration of the wet season for a given total annual rainfall, we couple the previous minimalist stochastic soil moisture model in Section 3.5 to a plant growth model. Because of the simplifications inherent in the soil moisture model, the obtained results are applicable to the case where vegetation is unable to access additional water stores, such as groundwater, and is fully dependent on rainfall and soil water availability to meet its evapotranspiration demands. In order to isolate the effect of rainfall seasonality from other drivers of growth (e.g., temperature in Mediterranean climates), we focus our analysis on tropical climates where the wet season coincides with the growing season. Defining $B$ as the maximum attainable biomass at a single time point under ideal conditions, encompassing also the biomass lost to litter production, root secretion, and consumers, the relative growth rate, $\frac{1}{B} \frac{dB}{dt}$, can be written as

$$\frac{1}{B} \frac{dB}{dt} = k(A - R), \quad (5.1)$$
where $A$ is the gross assimilation rate, $R$ is the respiration rate, and $k$ is the product of the specific leaf area (leaf area per leaf mass) and leaf mass ratio (leaf mass per unit plant biomass).

To proceed quantitatively, we assume that assimilation and respiration rates are driven by the ensemble mean effective soil moisture, $\langle x(t) \rangle$. Although plant response depends on the full distribution of soil moisture (as well as its temporal structure), this approximation allows us to capture the main effect of water stress without excessively complicating the analytical treatment. Following Daly et al. (2004), we assume analogous drought responses in all climates and adopt a piecewise-linear dependence of gross assimilation rate on the mean ensemble effective soil moisture, with a maximum assimilation rate of $A_{\text{max}}$ under well-watered conditions ($\langle x \rangle \geq x^*$) and falling to zero under intense stress ($\langle x \rangle = 0$). The soil moisture threshold $x^*$ represents a mean soil moisture level below which plants reduce growth due to water stress (Hsiao, 1973; Porporato et al., 2001; Larcher, 2003). This pattern is supported by empirical observations across Mediterranean (Gimenez et al., 1992; Galmés et al., 2007b; Peguero-Pina et al., 2009; Shane et al., 2010) and semi-arid tropical species (Gindaba et al., 2004; Muthuri et al., 2009). Consistent with the general decline observed across many species in assimilation-to-respiration ratio with increasing water stress, we further assume respiration decreases from a fraction of the assimilation, $R_{\text{max}}$ (anywhere between 20-70% of $A_{\text{max}}$ depending on the plant type and climate zone), to a minimum, non-zero value $R_{\text{min}}$ (Larcher, 2003; Flexas et al., 2005, 2006; Ribas-Carbo et al., 2005; Galmés et al., 2007a). We introduce another soil moisture threshold $x_{\text{cr}} < x^*$ at which net assimilation is zero, i.e., $A(x_{\text{cr}}) = R(x_{\text{cr}})$. No feedback of $B$ on soil moisture, specific leaf area, or leaf mass ratio is considered.
5.3 Maximizing biomass as function of rainy season length and annual rainfall

The temporal evolution of plant biomass can be obtained by solving equation (5.1), with $\langle x(t) \rangle$ encapsulating the effects of seasonality in rainfall. For a given total annual rainfall, biomass $B$ increases at the maximum rate during the wet season; such rate will be $A_{max} - R_{max}$ when $\langle x \rangle$ is above $x^*$. After the end of the wet season, as the mean soil moisture drops, the relative growth rate gradually diminishes along with net assimilation, $A(\langle x \rangle) - R(\langle x \rangle)$, until the threshold $x_{cr}$ is reached (Figure 5.1a). The biomass at $\langle x(t) \rangle = x_{cr}$ corresponds to the peak biomass for the year. A further decrease in soil moisture below $x_{cr}$ results in negative net assimilation, and theoretically to a decrease in $B$. Since plant response at this stage varies widely, from drought dormancy to deciduousness and even death, our minimalist model cannot capture plant adaptations beyond this point. We will instead focus on the seasonal peak in biomass, $B_p$ (reached at $\langle x(t) \rangle = x_{cr}$), for a given ratio of dry season to wet season length, or $\tau = T^d/T^w$. For a short dry season, annual rainfall is redistributed over a long wet season during which the soil moisture is relatively low; thus the peak biomass is reached via slow but steady growth, limited by water availability (Figure 5.1a, light gray line). Conversely, for a long dry season, rainfall is concentrated over the short wet season, resulting in transiently high soil moisture. The absence of water limitations results in a rapid biomass growth (at maximum rate), which however does not last long because of the subsequent onset of the dry season. Thus, the peak seasonal biomass depends on the relative lengths of the seasons, with a maximum occurring under an optimal wet season of intermediate length, in which the total rainfall is distributed in such a way that allows for plants to take advantage of abundant water during most of the growing season. A longer dry season ($\tau > \tau_{opt}$) means that plant growth is limited by time, while a longer
Figure 5.1: Effect of rainfall seasonality on biomass accumulation. (a) Temporal evolution of biomass, $B$, for different lengths of the wet season, for mean annual rainfall rate $\langle R' \rangle = 450$ mm/yr. Each line corresponds to a wet season length from $T_w = 10$ (black line) to $T_w = 360$ (light gray line) in 50 day intervals; the maximum biomass is attained for $T_w = 210$ days (mid gray line). Dashed lines are used to indicate theoretical changes in biomass beyond the peak point. Other soil and climatic parameters are $\alpha = 0.50$ cm, $\lambda^d = 0.05$ d$^{-1}$, $\lambda^w = 0.25$ d$^{-1}$, $ET_d^{max} = ET_w^{max} = 0.50$ cm d$^{-1}$, $w_0 = 10$ cm, and $x^* = 0.55$. Plant parameters refer to Panicum virgatum (switchgrass) (Shipley, 2002): net assimilation rate $A_{net} = 0.0018$ g cm$^{-2}$ day$^{-1}$ ($A_{max} = A_{net}/0.4$, $R_{max} = 0.6A_{max}$, $R_{min} = 0.1A_{max}$), leaf mass ratio = 0.46, and specific leaf area = 325 cm$^2$ g$^{-1}$. Initial biomass $B_0$ is set to 100 g. (b) Maximum attainable (peak) seasonal biomass, $B_p$, as function of wet season length $T_w$, for different annual rainfall rates. All the other parameters are as in (a). The black line has the same annual rainfall rate used in (a) and, when superimposed to (a), would connect the peak biomass points.

Wet season ($\tau < \tau_{opt}$) means that plant growth is limited by water availability. With the choice of parameters in Figure 5.1a (i.e., for an annual rainfall of 450 mm), such maximum in peak biomass is attained for wet season length $T_w = 210$ days, i.e., $\tau_{opt} \approx 0.7$.

The achievable peak in $B$ clearly depends as well on the total annual rainfall. This is made evident by plotting the peak seasonal biomass $B_p$ (a single point for each line in Figure 5.1a) for different amounts of total annual rainfall and wet season length (Figure 5.1b). Overall, peak biomass is low when the dry season becomes too long and the wet season rainfall is too concentrated, or when the total annual rainfall is low. For a given total annual rainfall, the maximum peak biomass is obtained at an
intermediate ratio of $T^d/T^w$, showing the existence of an optimal duration of the wet season. Increasing total annual rainfall relieves the restriction on water availability during the wet season and, as can be seen in Figure 5.1b, allows for a longer period of maximum growth (and thus a decrease in $\tau_{opt}$).

5.4 Discussions and conclusions

In conclusion, our framework shows the existence of an optimal wet season length given constant annual rainfall (related to $\tau_{opt}$, see Figure 5.1) that conciliates the trade-off between water-limited growth rate and growing season length, in the absence of additional rainfall-independent water stores available to vegetation. The existence of such optimal wet season length could be tested by comparing biomass indices (e.g., NDVI) from regions with the same annual rainfall but differing in their seasonal distributions. The simultaneous influence of annual rainfall totals and seasonality has already been demonstrated in India, where humid forest types are differentiated from each other based on their dry season lengths, while the driest ecosystems such as thornbush savannas and deserts were more defined by their total annual rainfall (Walter et al., 1971). Guan et al. (2014) also empirically corroborated the dependence of tree fraction cover on annual rainfall total and rainy season length in the savannas and woodlands of sub-Saharan Africa using satellite data. Changes in the ecosystem response based on intra-annual rainfall shifts is then expected to have a significant impact on ecosystem functioning and biosphere-atmosphere fluxes of energy, water, and carbon.
Effects of climate variability and irrigation in salt-affected regions


6.1 Introduction

The problem of soil salinization has affected human societies since historic times and has been one of the main causes of collapse for some of the most developed ancient societies (Hillel, 1998). Szabolcs (1989) estimates that 10% of arable land in over 100 countries, and nine million square km are affected by salinization, especially in arid and semi-arid regions (see also Sakadevan and Nguyen (2010)). Salinization refers to high concentrations of highly soluble salts in soil water causing ion-specific and osmotic stress, which may reduce plant productivity and quality (Chaves et al., 2009).
As the salinity of the soil water increases, the soil water potential is lowered and water becomes less available for plant uptake; at the same time, excessive Na\(^+\) and Cl\(^-\) ions disturbs the ionic balances in plants and induces ion-specific effects on proteins and membranes (Larcher, 2003). The uptake of other mineral nutrients such as NO\(^3-\), K\(^+\), and Ca\(^2+\) is reduced, photosynthesis is impaired, and growth may become inhibited, resulting in lower yields and early senescence (Larcher, 2003; Munns and Tester, 2008). The problem of salinization is usually categorized into primary and secondary salinization, depending on whether the process occurs naturally or as the result of human intervention.

Primary salinization occurs under natural conditions, such as through deposition of oceanic salt carried inland or via precipitation or by reduced leaching of salts made available by rock weathering. In coastal areas, additional causes of salt accumulation are tsunamis and capillary rise of saline water (the latter may be triggered by the overexploitation of freshwater aquifers). Under natural conditions, salt from atmospheric or rainfall deposition is accumulated in the soil as water is lost via evapotranspiration, and flushed out during percolation/runoff events due to high rainfall. Nevertheless, salt is liable to become concentrated in soils and groundwater reservoirs, especially in arid regions when the potential for evapotranspiration is higher than the amount of precipitation and salt flushing is insufficient, or in areas where natural drainage is poor due to low topographical relief or other soil characteristics.

Secondary salinization is anthropogenic and often caused by use of relatively saline irrigation water with poor drainage. In these cases, prevention or remediation of soil salinity is usually achieved by leaching salts through over-irrigation (Hillel, 1998; Schleiff, 2008). Alternative amelioration strategies by phytoremediation (i.e., harvesting salt-accumulating plants) are possible although appear to be less effective (Qadir et al., 2000). A different issue is the rise of saline groundwater due to increased percolation caused by land-use changes. This is the case of several Aus-
tralian watersheds, where deep-rooted forests have been supplanted by pasture and farmlands; the subsequent decrease in transpiration and increase in recharge has caused groundwater rise and created widespread water-logging and salt pans.

In the following sections, we investigate the conditions leading to the accumulation of salts in soils. Contrary to spatially explicit numerical models (Corwin et al., 2007; Schoups et al., 2005; Straw et al., 2005), which require precise site-specific parameterizations and may be computationally demanding, we take a parsimonious approach and describe the mass balance of soil solutes as a stochastic balance equation coupled to soil moisture dynamics. The long-term balance of soil salt mass, along with the dynamics of its moments, is investigated by explicitly accounting for the effect of leaching events, driven by stochastic rainfall. The role of irrigation in secondary salinization is later introduced.

6.2 Coupled soil moisture and soil solutes dynamics

The temporal evolution of the relative soil moisture $s(t)$, which ranges between 0 and 1, can be written similarly to previously presented forms in Chapters 3 and 4, as

$$n Z_r \frac{ds(t)}{dt} = R(t) + I(s(t)) - ET(s(t), t) - LQ(s(t), t), \quad (6.1)$$

where $R(t)$ is rainfall rate (minus canopy interception), $I(s(t))$ is irrigation rate, $ET(t, s(t))$ combines the rates of soil water evaporation and the plant transpiration, and $LQ(t, s(t))$ includes both percolation and runoff loss rates. The temporal evolution of the solute mass, $m$, dissolved in the soil solution per unit area of soil, can be described by the following mass balance equation

$$\frac{dm(t)}{dt} = I_n(t) + I_a(t) - \phi(s(t), t) - UP(s(t), m(t), t) - LE(s(t), m(t), t). \quad (6.2)$$
In equation (6.2), $I_n(t)$ is the rate of natural input by dry and wet deposition, $I_a(t)$ is the anthropogenic input rate, $\phi(t, s(t))$ is net exchange between soluble and insoluble fractions (e.g., nutrient mineralization from organic matter; adsorption/desorption; dissolution of salts), $UP(t, s(t), m(t))$ is the rate of nutrient/contaminant uptake by plants (linked in part to transpiration $ET$ in equation (6.1)), $LE(t, s(t), m(t))$ is the rate of solute loss due to leaching and runoff (associated with the leaching of soil water $LQ$). Most of these terms are coupled to the dynamics of soil moisture $s(t)$. These generic terms also take on more specific forms depending on the type of solute analyzed. Here, the anthropogenic input for dissolved salt is associated with the quality of irrigation water.

The external stochastic forcing through rainfall and the nonlinear coupling between soil moisture and solute make the behavior of the stochastic system (6.1) and (6.2) difficult to predict theoretically, despite the limited number of parameters. While numerical solutions of the two-equation system may already yield practical insights, theoretical analysis of suitable approximations may be especially useful to investigate general behaviors and understand the role of climatic drivers and internal dynamics. To do so we first invoke a separation of time scales to model leaching events as multiplicative jump processes in Section 6.3, then in Section 6.4 take a macroscopic approach to arrive at first order approximations of long-term soil salt concentration as a function of climate and irrigation.

6.3 Leaching of soil salt as multiplicative jump processes

When there is a clear separation of time scales between soil moisture trajectories and the duration of leaching events, it is possible to treat the two equations (6.1) and (6.2) separately by first solving the stochastic differential equation for soil moisture in (6.1) and then approximating the short-duration leaching events as independent, instantaneous events whose frequency is controlled by the probability of reaching
percolation thresholds. These leaching events are modeled as a marked Poisson process (Manzoni et al., 2011; Suweis et al., 2010), and when multiplied to typical values of soil moisture during leaching events, form the multiplicative jump process used to model the $LE$ term in equation (6.2). More detailed derivations can be found in Suweis et al. (2010) and Suweis et al. (2011).

In Mau et al. (2014), we used a simple system driven multiplicatively by white shot noise to model the dynamics of soil salt mass. We derived analytical solutions of the stationary probability density functions of the salt mass as well as the transient evolutions of its moments. Using these model results, the dynamics of the system was analyzed in two ways: solving a hierarchy of linear ordinary differential equation for the moments, which gives a time scale of convergence for the stationary probability density function of the salt concentration; and characterizing the crossing properties, such as the mean first-passage time and the mean frequency of threshold crossings.

Using parameters from a sandy-loam soil in a semiarid climate subject to dry deposition of salt, we found the stationary probability density function of the salt mass, normally a beta distribution, to approach a gamma distribution in the limit of no plant uptake. It takes $\sim 10$ years for the mean salt mass to come within 2% of its steady state value. We also calculated the mean first passage time for soil salinity to reach critical levels that may impair the growth of common crops. For pepper ($Capsicum annum$) and sweet potato ($Ipomoea batatas$), it takes $\sim 7$ years, and for tomato ($Lycopersicon esculentum$) and cucumber ($Cucumis sativus$) it takes $\sim 80$ years before salinization at this site reaches a level that would require remediation measures to ensure the adequate growth of these crops.
6.4 Macroscopic formulations of soil salinization

Alternatively, one can resort to a macroscopic approach and take the ensemble average of each term in equations (6.1) and (6.2):

\[
\frac{nZ_r}{dt} \frac{d\langle s \rangle}{dt} = \langle R \rangle + \langle I \rangle - \langle ET \rangle - \langle LQ \rangle
\]

\[
\frac{d\langle m \rangle}{dt} = \langle I_n \rangle + \langle I_a \rangle + \langle \phi \rangle - \langle UP \rangle - \langle LE \rangle.
\]

(6.3)

Analyzing this system requires overcoming the so-called closure problem. Because of the nonlinearities, the flux terms cannot be expressed in terms of the means \(\langle s \rangle\) and \(\langle m \rangle\) but involve higher-order, joint moments of \(s\) and \(m\). Thus, to evaluate equation (6.3), simplifying assumptions are needed on the functional forms of these ensemble fluxes. This was discussed extensively in Chapters 3 and 4 for seasonal changes in \(\langle ET \rangle\) and \(\langle LQ \rangle\). Examples for salinization are presented in the following sections for specific management and environment scenarios.

6.4.1 Role of climate and the prevalence of primary salinization

As a minimalist ecohydrological model including salinity effects, we illustrate the prevalence of salt-affected soils in semiarid regions by using the macroscopic equations (6.3), rewritten for natural (not irrigated) conditions and at steady state as

\[
\langle R(t) \rangle = \langle ET(t, s(t)) \rangle + \langle LQ(t, s(t)) \rangle,
\]

\[
\langle I_n(t) \rangle = K_d \kappa \langle C(t) \cdot ET(t, s(t)) \rangle + K_d \langle C(t) \cdot LQ(t, s(t)) \rangle.
\]

(6.4)

Here \(K_d\) is the partition coefficient between adsorbed and dissolved fractions, \(\kappa\) the transpiration stream concentration factor or the ratio of the concentration in the transpiration stream to that in soil water (Dietz and Schnoor, 2001), and \(C = m/(nZ_r s)\) is the concentration of dissolved salts in the soil. We approximate plant uptake to be linearly dependent on soil moisture over large spatial areas,
where \( PET \) is the potential evapotranspiration, thus \( \langle ET \rangle = PET\langle s \rangle \). We also approximate leakage/runoff using a modified first term of its Taylor expansion (Feng et al., 2015; Laio et al., 2002) such that \( \langle LQ \rangle = \frac{\lambda}{\gamma} e^{-\gamma\epsilon(1-\langle s \rangle)} \), where \( \gamma \) is a normalized soil rooting depth defined by \( \gamma = nZ_r/\alpha \) and \( \epsilon \) accounts for the bulk effects of other soil features. Furthermore, we assume negligible cross-covariance between salt concentration and soil water fluxes, such that \( \langle C \cdot LQ \rangle \approx \beta \langle C \rangle \cdot \langle LQ \rangle \) and \( \langle C \cdot ET \rangle \approx \beta \langle C \rangle \cdot \langle ET \rangle \), where \( \beta \) serves as a linear correction factor. The effect of the climate is conveyed through the non-dimensional dryness index, defined as the ratio of long-term potential evapotranspiration to rainfall, i.e., \( D = PET/R \). Then the steady state ensemble average concentration of salt under these conditions can be found as a function of the dryness index,

\[
\langle C \rangle = \frac{\langle I_n \rangle}{K_dPET\beta(\kappa\langle s \rangle + De^{-\gamma\epsilon(1-\langle s \rangle)})}.
\]

(6.5)

The results are shown in Figure 6.1, where the steady state salt concentration \( \langle C \rangle \) is plotted against increasing dryness index \( D \) for different values of the potential evapotranspiration. The increase in \( D \) comes as a result of decreasing mean rainfall frequency \( \lambda \) while mean rainfall depth \( \alpha \) is kept constant. Primary salinization is especially pronounced in drier climates (high \( D \)) where potential evapotranspiration greatly exceeds rainfall that may leach salt out of the soil. Indeed this trend is even more accentuated in locations with lower potential evapotranspiration where, at the same \( D \), rainfall rates are comparatively even lower.

### 6.4.2 Effect of irrigation on secondary salinization

A more general theoretical analysis of irrigation and soil salinization under stochastic rainfall can be carried out using the coupled dynamics of equation (6.1) and (6.2). In the second equation, \( m \) is the amount of salt in the soil solution, balanced by salt inputs from atmospheric and rainfall deposition in addition to those dissolved in the
irrigation water, and output from leaching events caused by rainfall and irrigation as well as plant uptake from transpiration. Intuitively, irrigation can be thought of as playing simultaneously opposing roles in regulating soil salt concentration. On the one hand, irrigation introduces an additional source of salt through those dissolved in the irrigation water. On the other hand, irrigation increases soil moisture, which leads to increase in leaching and salt flushing from the soil that may eventually overcome the effects of increased salt input into the soil.

To explore these tradeoffs, a macroscopic approach can again be employed to study the mean behavior of the coupled system in the case of secondary salinization, in which the generalized anthropogenic input $\langle I_a \rangle$ in equation (6.3) now designates the concentration of salt in the irrigation water. Using similar approximations as those adopted in equation (6.4) for primary salinization, the macroscopic equation describing salt concentration under secondary salinization, under negligible primary

**Figure 6.1:** The steady state concentration of salt $\langle C \rangle$ (in dS/m) as defined in equation (6.5) plotted against the climatic dryness index $D$ (or the ratio of potential evapotranspiration to rainfall). Each line corresponds to changes in the potential evapotranspiration (in mm/day) varying from low (dark lines) to high (light lines). Mean rainfall intensity is kept constant at $\alpha = 10$ mm, primary deposition at $\langle I_n \rangle = 30$ mg m$^{-2}$ day$^{-1}$, $\kappa = 0.1$, $K_d = 0.6$, $\epsilon = 0.1$, and $\beta = 16$. 
salt input, is now given by

$$\langle C \rangle = \frac{\langle I_a \rangle}{K_d PET\beta(\kappa \langle s \rangle) + D e^{-\gamma(1-\langle s \rangle)}} = \frac{C_I n Z_v \langle I \rangle}{K_d PET\beta(\kappa \langle s \rangle) + D e^{-\gamma(1-\langle s \rangle)}}$$

(6.6)

where the connection between anthropogenic input of salt, $\langle I_a \rangle$, through irrigation $\langle I \rangle$ is established by setting $\langle I_a \rangle = C_I n Z_v \langle I \rangle$, where $C_I$ gives the concentration of salt in the irrigation water.

The results for the salt concentration in the soil $\langle C \rangle$ described by equation (6.6) are shown in Figure 6.2 as a function of the average irrigation rate $\langle I \rangle$ for different values of the dryness index $D$. As can be seen in Figure 6.2a, the concentration of salt in the soil is determined by both the climate and the irrigation rate. Particularly under drier climates, a maximum for the soil salt concentration exists at an intermediate rate of irrigation. This is due to the opposing effects of irrigation and leaching. In drier climates, the amount of salt in the irrigation water added to already dry soil has an enormous effect on increasing the soil salt concentration. As the soil becomes more irrigated, however, increasing levels of leaching counterbalances the additional salt input, and soon the salt concentration decreases again. In wetter climates, on the other hand, leaching events due to naturally occurring rainfall already dominates the system such that the overall salt mass balance is not as drastically affected by the increase through irrigation. As such, the maximum observed in drier climates ceases to appear. A comparison of the approximate analytical solutions and the numerical simulation of the complete system, in which the covariance of salt mass and soil water fluxes (e.g., $\langle C \cdot L \rangle$ and $\langle C \cdot ET \rangle$) are explicitly taken into account, reveals that the behavior of the system and the existence of the maximum concentration are consistent across different climate regimes (Figure 6.2b and 6.2c).

Extensions of the previous analysis could include plant feedbacks on soil salinity. In some salt tolerant species (e.g., dates and some vegetables), a moderate increase in salinity may actually promote growth, which nevertheless decreases at extreme
Figure 6.2: (a) Mean salt concentration $\langle C \rangle$ (in dS/m) as a function of irrigation rate $\langle I \rangle$ for different climate conditions (using the macroscopic equation (6.6)), where “Drier” and “Wetter” conditions span the range respectively from $D = 50$ to $D = 0.55$. (b-c) Comparison of the salt concentration-irrigation rate relations obtained from the macroscopic solution of equation (6.6) (gray lines) and its corresponding numerical solution in which the covariance of salt mass and soil water fluxes are explicitly simulated (black lines). The dryness index is $D = 5$ (b) and $D = 1$ (c). Other parameters: $C_I = 1000 \text{ mg/cm}^2$, $nZ_s = 15 \text{ cm}$, $PET = 0.5 \text{ cm/day}$, $\alpha = 1.0 \text{ cm}$, $\kappa = 0.1$, and $K_d = 0.6$, $\epsilon = 0.1$, and $\beta = 16$.

salt levels. However, in most species salinity at least triggers stomatal closure and reduced growth (Munns and Tester, 2008; Volpe et al., 2011). Therefore, reduced transpiration in saline conditions may affect the long term soil moisture balance. Analysis of long term salinization trends can also inform current efforts towards salt tolerant plants, and accounting for future climate scenarios will be key to assessing sustainability of agricultural practices at large scales, including groundwater dynamics (Hillel, 1998; Jobbágy and Jackson, 2001).
This chapter is adapted from Feng, X. and A. Porporato, Hydrologic variability controls global plant diversity patterns in arid and semi-arid ecosystems, in preparation.

7.1 Introduction

Accelerated changes in the global environment in recent years have prompted a surge in the long-standing effort to determine the mechanisms behind the maintenance of biodiversity. At broader spatial scales, species richness is primarily constrained by climate-related variables such as potential evapotranspiration or rainfall (Hawkins et al., 2003; Francis and Currie, 2003; Kreft and Jetz, 2007). For vast areas of the world under an arid or semi-arid climate, energy and water fluxes in plants are tightly coupled and are regulated by plant water status and available soil moisture (Noy-meir, 1973). The presence of strong hydrological fluctuations in soil moisture, resulting in the unpredictable timing, duration, and intensity of water stress, and combined with heterogeneities in space, has led to the evolution of plant species with
a variety of physiological and phenological adaptations, including different water use efficiencies, drought tolerance strategies, and trade-offs between competitive and dispersal abilities (Vico et al., 2014; Rodriguez-Iturbe and Porporato, 2004). In addition, plot-scale changes in net primary productivity, carbon cycling processes, and community composition of water-limited grasslands have already been observed as a result of changes in soil moisture variability, independent of total rainfall quantity over a season (Knapp et al., 2002; Nippert et al., 2005).

7.2 Role of soil moisture on plant biodiversity

Soil moisture synthesizes the combined effects of climate, soil, and plant properties, and, as a driving agent of vegetation dynamics in water-limited ecosystems, presents a compelling link to plant diversity. Here, using a combination of global biodiversity data and stochastic soil moisture models, we show how water stress and soil moisture fluctuations shape patterns of regional plant biodiversity, resulting in maximum biodiversity in regions where both mean and variance of soil moisture are relatively high. We use a globally gridded map of native vascular plants (Kreft and Jetz, 2007; Ellis et al., 2012) and relate it to the statistical properties of modeled soil moisture in water-limited regions (Figure 7.1). Plant species richness is estimated based on empirical predictors of 1032 regional data points worldwide (Kreft and Jetz, 2007). Soil moisture fluctuations—driven by the unpredictable nature of daily rainfall—the long-term averaged rainfall frequency and depth, combined with feedback from plant water uptake and soil water storage (Porporato et al., 2004). The resulting soil moisture distribution (in the form of a truncated gamma distribution (Abramowitz and Stegun, 1964)) is statistically simple yet capable of realistically characterizing the mean and variance under a wide range of stationary hydroclimatic regimes (Porporato et al., 2004).

As seen in Figure 7.2, plant species richness in water-limited ecosystems is orga-
Figure 7.1: Globally gridded values of native vascular plant richness (Kreft and Jetz, 2007; Ellis et al., 2012) plotted against the corresponding dryness index (ratio of potential evapotranspiration to rainfall) in global biomes (Olson et al., 2001). Biomes with strongly negative slopes ($<-0.2$) based on linear regression of the log-log relationship is marked with a red regression line.

Biomes are recognized into distinct patterns based on the statistical properties of regional soil moisture, with highest richness at intermediate levels of not only the mean but also the variance of the distribution. The humped shape of the mean-variance plot arises due to the correlation between the mean and variance of the soil moisture distribution. That is, the hydrological bounds at very low and very high rainfall amounts,
Figure 7.2: Scatter plot for the species richness in water-limited biomes against the mean and variance of soil moisture. Darker red colors show higher number of species, with a maximum at 5121.

corresponding respectively to complete soil water depletion and saturation, allow maximum spread of soil moisture only in the middle, resulting in high variance at intermediate mean values (Brocca et al., 2007). Within these hydrological boundaries, biodiversity patterns are influenced by both the mean and variance of soil moisture. By considering mean soil moisture as a proxy for rainfall and net primary productivity, the peak of species richness along the mean soil moisture gradient is suggestive of the unimodal form of the productivity-diversity relationship (Waide et al., 1999). One notable theory that aims to explain this relationship invokes the competition of multiple species for a few essential resources (Tilman, 1982; Chase and Leibold, 2003). It assumes that heterogeneity of the resources is higher at intermediate levels of the limiting resources (as is applicable here to soil moisture), and shows maximum biodiversity at intermediate productivity (Tilman, 1982; Chase and Leibold, 2003; Rosenzweig and Abramsky, 1993; Shmida et al., 1986). Nevertheless, it makes no prediction on the explicit role of resource variability.

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7.3 Linking local to regional community through resource variability

To gain insights into other governing mechanisms, we adopt a metacommunity model that incorporates resource variability to investigate its influence on regional community diversity. The concept of a metacommunity describes population dynamics and community composition in the context of ecological processes integrated over different spatial scales (Leibold et al., 2004). At the local scale, community composition is governed by species interactions such as competition and predation, and these localities are in turn linked at the regional scale through species dispersal (Leibold et al., 2004). Among the four paradigms outlined within the metacommunity framework, the species-sorting paradigm is most closely associated with the idea of niche diversification in the presence of environmental variability, with dispersal rates high enough to fill all suitable niches (Chase and Leibold, 2003; Logue et al., 2011). Adopting similar assumptions, we incorporate the role of resource variability into regional species composition using methods borrowed from superstatistics (Beck and Cohen, 2003),

$$p^\gamma(k) = \int p(k|R)f(R)dR,$$

where $p^\gamma(k)$ is the proportion of species $k$ in the metacommunity, $p(k|R)$ is the proportion of species $k$ in the local community with given resource level $R$, and $f(R)$ is the probability density distribution (pdf) of the resource within the region. The key premise here is that the local community composition are determined by a single resource amount, $R$. Additionally, while other models explicitly address the tradeoff between competition and colonization (Calcagno et al., 2006), we assume here that dispersal rates between each local community are high enough such that each species is able to reach localities associated with a preferred resource amount. Since the set of species within local communities collectively comprises the assemblage within the regional metacommunity, varying the local composition $p(k|R)$ and then superim-
posing with the regional resource distribution effectively changes the proportion of each species “mixed” within the regional pool. It must be noted that this hierarchical framework can be easily generalized to the distribution of limiting resources other than soil moisture. For now we have restricted our discussion of the resource distribution to a purely ensemble sense without specifically accounting for the space or time dimension.

Another important ingredient in our metacommunity model is the relationship between local species proportions and the resource amount, expressed through $p(k|R)$ in equation (7.1). While the type of species interactions dictating local community compositions can run the gamut from classical Lotka-Volterra competitions to density-dependent “neutral” random walks (Hubbell, 2001), the general idea that species are distributed according to their respective physiological response to environmental gradients can be traced back to the pioneering works of Whittaker (Whittaker, 1967) and systematically integrated within the species-sorting paradigm (Chase and Leibold, 2003). In particular, plants in water-limited ecosystems are known to physiologically respond to decreasing water availability by decreasing their stomatal conductance, transpiration rate, and assimilation rate, and can exploit a variety of strategies when implementing the timing and the rate of these responses (Vico et al., 2014; Larcher, 1995; Vico and Porporato, 2008). As a result, their successes—driven jointly by their individual functional traits and their interactions with neighbors—show strong association to environmental gradients (Toledo et al., 2012).

We use two prototypical examples to illustrate the effect of such responses to local and regional species composition. In the first case, species dominate exclusively within a limited soil moisture range, within which their growth rates are equivalent to all other species’. In the second case, they are independently limited in their growths across a soil moisture gradient; each species is defined by the tradeoff between its
maximum growth rate and the soil moisture threshold at which its growth declines. Thus, those that grow under a wider range of soil moisture conditions (generalists) cannot outcompete those that specialize at high soil moisture levels (specialists). For both scenarios, the resulting equilibrium composition for a given resource amount is obtained from a Lotka-Volterra competition model with a total of N species (see supplementary methods at the end of this chapter; Figure 7.3). By modulating the local composition with regional resource distribution according to equation (7.1), we can plot the modeled regional species richness again as a function of resource mean and variance, shown in Figure 7.4. When all species equivalently dominate their own niches (case 1), the regional diversity increases with both increasing mean and variance of soil moisture. In contrast, when species overlap variably along the soil moisture gradient (case 2), the highest diversity is found at intermediate soil moisture mean and variance. The latter is much more consistent with the empirical patterns observed in Figure 7.2.

7.4 Discussions and conclusions

The above expositions lend strong support to the idea that dryland plant diversity is controlled by the hydrological distribution of available soil moisture. Whereas previous studies have shown linear correlations between species richness and a range of climatic variables such as potential or actual evapotranspiration, rainfall, or the

81
Figure 7.4: Contour plots for modeled species richness against the mean and variance of soil moisture. The left plot shows the equivalently niched case (Figure 2, left), while the right plot shows the saturating case (Figure 2, right). Hotter color indicates areas of high richness.

number of wet days per year (Kreft and Jetz, 2007; Currie, 1991), here we have consolidated these disparate influences into the dominant driver of biological activities in water-limited ecosystems, namely soil moisture. Furthermore, the use of the soil moisture pdf gives a simple physical justification to why resource heterogeneity may be maximized at intermediate mean quantities, and allows us to reconcile the effects of both the resource mean and variability. For example, in Figure 7.4a, biodiversity is shown to be much more dependent on mean resource at high variance levels, and conversely more dependent on variance at high mean resource levels, giving us a way to potentially disentangle when either the effect of resource quantity or resource heterogeneity might dominate (Lundholm, 2009; Reynolds et al., 2007; Stevens and Carson, 2002). In addition, whether biodiversity increases monotonically along the mean resource gradient (Figure 7.4a) or reaches a maximum (Figure 7.4b) can result from the type of species interactions taking place at the local scale. Since the exact form of the diversity-productivity relationship—whether it is monotonically increasing or humped—as well as its underlying mechanisms are still largely con-
tested (Waide et al., 1999; Adler et al., 2011), this provides a framework within which the effects of multiple statistical attributes of the resource, as well as local interactions mediated by species sorting over the regional scale, can be simultaneously analyzed. This can in turn shed more light on the influence of ongoing climate change to regional species composition and biodiversity.

Supplementary methods

Datasets

Rainfall and potential evapotranspiration are obtained from the Climate Research Unit 0.5 by 0.5 degree gridded monthly time series, and soil water storage from the International Satellite Land-Surface Climatology Project (ISLSCP II) Total Plant-Available Soil Water Storage Capacity of the Rooting Zone dataset with 1 by 1 degree resolution. The vascular plant species richness data, from Kreft and Jetz (2007) are projected onto hexagonal grid cells of median area of 7792 square kilometers. The climatic data corresponding to each species richness grid cell is taken from the nearest grid point. Each location is characterized as arid or semiarid if they belong to one of the following Olson Biome Classes (Olson et al., 2001): (1) Tropical and subtropical moist broadleaf forests, (2) Tropical and subtropical dry broadleaf forests, (3) Tropical and subtropical grasslands, savannas and shrublands, (4) Mediterranean forests, woodlands and shrublands, and (5) Deserts and xeric shrublands.

Local community composition

The equilibrium composition at the local scale for a given resource amount is obtained from a Lotka-Volterra competition model with a total of $N = 100$ species. The interspecific competition rates are set to 1 and intraspecific competition rates are set to less than 1, resulting in a community matrix that is symmetric and positive definite, which ensures the existence and uniqueness of the equilibrium solution.
The growth rates are dependent on the resource level at a local community and are defined using the competition scenarios described below. The equilibrium solution of the system can be solved as a linear complementarity problem using the Python package openopt.

Local competition scenarios

Two types of local competition scenarios are adopted in Figure 7.3 and 7.4. In the first case, species are separated in their niches, containing no overlap in the range of soil moisture levels that sustain their growths. They are also completely equivalent in terms of the span of the soil moisture values within which they dominate as well as their growth rates within those regions. In the second case, species decrease their saturated growth rates as soil moisture become increasingly limiting. Each species uses different strategies involving tradeoff between the soil moisture threshold at which their growths are decreased and the rate they decrease to zero. Such tradeoffs are achieved by setting the area under each curve to a constant value while varying the stress threshold.

Regional resource distribution

Four physical variables are needed to describe the regional soil moisture distribution: the long term mean frequency and depth of daily rainfall $\lambda$ (e.g., 1/day) and $\alpha$ (e.g., mm), the effective soil water storage capacity $w_0$ (e.g., mm), and the potential evapotranspiration $E_{max}$ (e.g., mm/day). These are derived from the climatic and soil dataset described earlier. For rainfall, we assume a constant rainfall depth of $\alpha = 10$ mm and uniform distribution of rainfall over the year and calculate the mean frequency of daily rainfall as $\lambda = R/(\alpha 365)$. Defining two dimensionless parameters as $\gamma = w_0/\alpha$ and $D = E_{max}/(\lambda \alpha)$, the mean and the variance of the soil moisture
distribution can be derived as:

\[
\langle x \rangle = \frac{1}{\bar{\gamma}} \frac{\Gamma\left(\frac{\gamma}{D} + 1, 0, \gamma\right)}{\Gamma\left(\frac{\gamma}{D}, 0, \gamma\right)},
\]  

(7.2)

\[
\langle x \rangle^2 = \frac{1}{\bar{\gamma}^2} \frac{\Gamma\left(\frac{\gamma}{D}, 0, \gamma\right) \Gamma\left(\frac{\gamma}{D} + 2, 0, \gamma\right) - \Gamma\left(\frac{\gamma}{D} + 1, 0, \gamma\right)^2}{\Gamma\left(\frac{\gamma}{D}, 0, \gamma\right)^2}.
\]

(7.3)

These values are plotted in the contours of Figure 7.2 and 7.4.
Conclusions and future developments

The series of studies presented in this dissertation are motivated by the need to understand the impacts of a rainfall regime that is projected to change in its seasonal distribution and interannual variability. They are focused on seasonally dry ecosystems, which may be historically overlooked yet are nevertheless socially important and ecologically vulnerable. An appropriate set of theoretical tools have been developed to study the nonstationary drivers of ecohydrological processes. In what follows, the main contributions in each chapter are summarized and situated within a broader scientific context. Some remaining issues and potential future developments are also discussed.

Chapter 2 lends support to the premise that rainfall seasonality has indeed changed (along with its interannual variability) in many parts of the world over the last century and underscores the importance of examining its ramifications. This is done through the development and use of a threshold-independent, objective index of seasonality—based on the measure of relative entropy in information theory—on global datasets, subsuming a variety of seasonal climate types which are otherwise classified as tropical dry, monsoon, or Mediterranean. This seasonality index has a
few more advantages that follow from established information theory: (1) in seasonal climates, the relative entropy of rainfall can be directly related to the duration of the wet season based on the support of the intra-annual rainfall distribution function, and (2) the relative entropy vary predictably as a function of the time resolution of the precipitation dataset, facilitating model intercomparison and ranking. This seasonality index has now been applied to a set of state-of-the-art climate models in the Coupled Model Intercomparison Project Phase 5 (CMIP5) in a series of papers (Pascale et al., 2014, 2015), on both past and future climate change. They have served to diagnose regions with substantial anomalies in their local representation of seasonality and where more scientific efforts are needed to resolve the physical mechanisms used to generate rainfall seasonality in climate models.

The results on the effects of climate seasonality on soil water partitioning presented in Chapters 3 and 4 can be consolidated within a wider literature on systematic deviations from Budyko’s curve, whether they be attributed to climate variability, vegetation, or anthropogenic influences (Donohue et al., 2007; Williams et al., 2012; Gentine et al., 2012; Chen et al., 2013). Of particular note are the extensions made in Chapter 4 to stochastic soil moisture models to account for time-dependence in parameters. This allows for the adoption of climate inputs that vary explicitly in their seasonal amplitude and phase, quantitatively differentiating between climate types in which potential evapotranspiration may or may not be synchronized with rainfall. Another significant revelation is the seasonal hysteresis in the soil hydrological response moderated by soil water storage. This means that quantifying intra-annual hydrological fluxes would require not only knowledge of instantaneous climate conditions but also consideration of the history of the soil moisture trajectory; the soil water storage now retains a memory of whether it’s on the dry down or the re-wetting part of the seasonal cycle.

Chapter 5 first introduces the idea that plant productivity can be maximized per
given amount of annual rainfall based on how it is distributed between the wet and the dry season. For a fixed annual rainfall, initial increase in the rainy season increases plant water use efficiency due to a reduction in losses through runoff. As the rainy season keeps increasing, however, the same rainfall amount is stretched over a longer period during which the plant is chronically stressed, resulting in suboptimal conditions for growth. In addition, such optimality in plant productivity has been shown to carry over into soil carbon sequestration in seasonally dry forests, in a follow up study by Rohr et al. (2013). Seasonal variations in soil moisture increases both primary productivity and soil microbial respiration, resulting in a delicate balance between soil carbon deposition through litterfall and soil carbon loss through heterotrophic respiration. Using a minimalist model that couples the dynamics of soil moisture, plant productivity, and soil carbon dynamics, and parametrized using data from a drought-deciduous forest in northeast Brazil, soil carbon storage is also shown to be maximized for a fixed annual rainfall as a function of rainy season length. Such first order hydrological controls on productivity and soil carbon storage can of course be complemented by other factors, such as feedback from physiological and phenological adaptations of species in these seasonally dry ecosystems, as synthesized by Vico et al. (2014).

The implications of this “optimal” use of rainfall at intermediate rainy season length becomes immediately apparent when we consider that rainfall is projected to change not only in magnitude but also in its spatial and seasonal distribution (as discussed in Chapter 2 and elsewhere). Guan et al. (2014) provided a continental-scale support for the importance of such “optimal rainy season length” when satellite remote sensing records over Africa were examined. Tree fraction cover in African savannas and woodlands, over an intermediate range of annual rainfall amount, is shown to initially increase with lengthening of the rainy season until it reaches a maximum, then decreases. This means that, even for regions of similar rainfall totals,
if the duration of the rainy season changes, then predicting concomitant changes in their tree fraction covers would need to account for the direction from which they are initially situated with regards to this maximum.

Chapter 6 and 7 delves into topics relevant to making management decisions in seasonally dry ecosystems, with regards to controlling secondary salinization and maintaining plant biodiversity. While they are key considerations in seasonally dry ecosystems, they also serve as natural applications of the stochastic models previously developed. This is because, similarly to the case of soil water partitioning (Chapter 3 and 4) and plant growth (Chapter 5), the coupled dynamics of soil water and soil solutes as well as the formation of hydrologic niches are strongly determined by the variability of rainfall. The parsimonious approaches adopted here bypass the use of computationally intensive numerical methods and offer insights on the first order impacts of climate variabilities and potential human interventions. They can also readily accommodate changes in the statistical properties of climate forcings that shift beyond the scope of historical records, as the climate system increasingly venture into regimes previously unseen.

While a focus of this dissertation has been on the seasonal rainfall with embedded short term (e.g., daily) variabilities, it is important to recognize that the seasonal interplay between water and energy inputs (e.g., through solar radiation, temperature) can also play a pivotal role in regulating many ecohydrological processes of interest. The work here lays the foundation for characterizing deviations of the seasonal rainfall signal from the observed seasonal temperature signal, which can serve as a measure of the potential “utility” of synchronized water and energy sources for ecological and societal use. Another promising direction for future development is in the use of macroscopic equations to capture low frequency variations in the governing parameters. The transient, bulk behavior of the nonlinear leakage term has been thoroughly analyzed in Chapter 4. However, more systematic closure methods may
be needed to properly scale other ecohydrological variables from their microscopic fluctuations (see Appendix E for a more thorough discussion on scaling).

In addition, the emphasis on transient characterization of system states rather than equilibrium projections can be transferred towards a framework for predicting threshold ecosystem responses under evolving drought stress. While there have been much improvements in recent years in monitoring and modeling short timescale fluxes in carbon, energy, and water, the mechanisms that trigger ecosystem threshold events (e.g., mass tree mortality) remain unresolved. With projected changes in the climate, these threshold events are likely going to be induced through a series of punctuated seasonal and interannual climate extremes, and cannot be predicted by imposing future conditions onto the present. Progressive changes in plant water status over the course of a drought as well as the history of exposure to stress need to be considered. As such, the transient characterization of probabilistic soil moisture and other ecohydrological variables given here can be used to address the likelihood of physiological damage that may ultimately lead to death.
Appendix A

Analysis of the Seasonality Index, changes in seasonality components and their interannual variability

A.1 Seasonality Index

The monthly rainfall data from the Global Historical Climatology Network (GHCN-Monthly) (Vose et al., 1992) were downloaded from the IRI/LDEO Climate Data Library. To construct the seasonality indices (equation (2.1)), stations with at least 20 years of data from 1970-1990 (including gaps) were selected (2715 total) to obtain first their monthly rainfall climatology, calculated by averaging the monthly rainfall over all available years in each station. The hydrological year $k$ is then defined starting on the first month after that of minimum mean rainfall and proceeds for 12 months, indexed by $m \in [1, 12]$. The monthly rainfall distribution is denoted for each hydrological year as $r_{k,m}$, and the monthly rainfall climatology is $\tau_m = (1/k) \sum_k r_{k,m}$ averaged over all available years $k$.

The mean annual rainfall for each stations is $\overline{R} = \sum_{m=1}^{12} \tau_m$, and its monthly probability distributions is $\overline{p}_m = \tau_m / \overline{R}$. To present each station in the context of
the global range, we normalize $R$ by the maximum $\overline{R}$ of the entire GHCN-Monthly dataset ($\overline{R}_{\text{max}} = 7932$ mm/year in Tabubil, Papua New Guinea).

The relative entropy for each station can be calculated as $D = \sum_{m=1}^{12} p_m \log_2 (\overline{p}_m / q_m)$, where $q_m$ is the uniform distribution, for which each month has a value of $1/12$. This is a positive semi-definite measure for the distance between the observed monthly rainfall distribution $\overline{p}_m$ and the uniform distribution $q_m$. For our purposes, the relative entropy is a good description of the concentration of rainfall around the wet season and is then combined with $\overline{R}$ to define the long-term seasonality index as in equation (2.1).

The identification of seasonality hotspots using the GHCN-Monthly station data is corroborated by replicating the derivation of $\overline{S}$ using the CRU TS 2.1 gridded dataset (Figure 2.2), which has complete coverage from 1901-2002 over the tropics. Though the data at individual gridpoints are not suitable for seasonality decomposition due to the extent of their spatial and temporal interpolation, it is nevertheless helpful to use this gridded dataset for a first estimation of regions that are undergoing marked changes in seasonality. This is done by finding for each hydrologic year $k$ its corresponding annual rainfall $R_k = \sum_{m=1}^{12} r_{k,m}$ (and associated distribution, $p_{k,m} = r_{k,m}/R_k$), relative entropy $D_k = \sum_{m=1}^{12} p_{k,m} \log_2 (p_{k,m} / q_m)$, and seasonality index $S_k = D_k \cdot R_k / \overline{R}_{\text{max}}$, and then applying linear regressions over their changes from 1930-2002.

A.2 Magnitude, timing, and duration of seasonality

The rainfall seasonality hotspots from the GHCN-Monthly dataset were visually identified as regions with high seasonality ($\overline{S}$) stations. Among those, we focused on northeastern Brazil, western and central Africa, and northern Australia for further analysis of specific seasonality components. To minimize the effect of missing data, only stations with 2 or less consecutively missing monthly data between 1930-1990
were admitted for analysis from each region, reducing the total number of eligible stations to \( n = 30, 51, 35, 38 \) for northeast Brazil, western Africa, central Africa, and northern Australia, respectively. Missing data were then filled by linearly interpolating between the bounding months if they occur in the middle of the time series, or substituted with the corresponding mean monthly value if they occur at either ends. For every station, yearly indicator series for the magnitude, timing, and duration of rainfall were obtained. For each hydrological year \( k \), the annual rainfall (magnitude) is \( R_k = \sum_{m=1}^{12} r_{k,m} \). The centroid \( C_k \) (timing) and the spread \( Z_k \) (duration) are found using the first and the second moments of \( r_{k,m} \), specifically,

\[
C_k = \frac{1}{R_k} \sum_{m=1}^{12} mr_{k,m},
\]

\[
Z_k = \sqrt{\frac{1}{R_k} \sum_{m=1}^{12} |m - C_k|^2 r_{k,m}^2}.
\]

### A.3 Regional trends and variabilities

For all eligible rainfall series, regression was applied to each of the indicator series for the magnitude, timing, and duration of seasonality. For the timing series (centroid and phase), circular-linear regression was performed with the \textit{circular} package in R, while linear regression was performed on all other series using the \textit{scipy} package in Python. Slopes from the regressions, for each indicator series in each region, were then assembled and presented in boxplot forms in Figure 2.4, top row.

To find their variability over time, we passed a 12-year moving standard deviation window through the residuals of the series (circular standard deviation was used for phase and centroid). The slopes from the linear regression of all resulting variability series in each region were then similarly compiled into boxplot form and presented in Figure 2.4, bottom row. The significance of the spatial ensembles was tested using
the Wilcoxon signed-rank test, which compares against the null hypothesis that the mean value of the ensemble is zero. Those with p-values greater 0.05 were considered inconclusive and grayed on the plots.
Appendix B

Analytical seasonal soil moisture models

B.1 The minimalist model

A minimalist approach to the description of the soil water balance is to assume that soil moisture is instantaneously brought to a stochastic steady state at the beginning of the wet season. Thus for the wet season the stochastic steady state solution for the soil moisture model of Porporato et al. (2004) is adopted, resulting in the following average effective soil moisture

\[
\langle x^w \rangle_{ss} = \frac{1}{D^w} - \frac{\gamma^{\frac{w}{\gamma}}^{-1}}{\Gamma \left( \frac{w}{\gamma}, \frac{w}{\gamma}, \gamma \right)} e^{-\gamma},
\]

where \( \Gamma(\cdot) \) is the gamma function and \( \Gamma(\cdot, \cdot) \) is the incomplete gamma function (Abramowitz and Stegun, 1964).

Conversely, during the dry season, the soil moisture cannot realistically be considered at stochastic steady state. Nevertheless, the analytical description can be simplified by noticing that the infrequent rainfall events typical of the dry season result in infrequent runoff and deep percolation events. At a first approximation, it is thus possible to neglect the upper bound on \( x \) without introducing significant errors.
(see, e.g., Viola et al. (2008)). Thus, setting \( \langle LQ(x,t) \rangle \) to zero in equation (3.14), the temporal evolution of the ensemble average \( \langle x(t) \rangle \) can be obtained by solving the macroscopic equation (4.3) with the initial condition \( \langle x^d(t = T^w) \rangle = \langle x^w \rangle_{ss} \) (equation (B.1)), to obtain for \( T^w \leq t < T^{yr} \)

\[
\langle x^d(t) \rangle = \frac{1}{D^d} + \left[ \langle x^w \rangle_{ss} - \frac{1}{D^d} \right] e^{-\left( \frac{ET_{max}^s}{w_0^s} \right) t}, \tag{B.2}
\]

where \( D^d = \frac{D^w}{\rho^s} \) is the dryness index in the dry season. This ensemble mean soil moisture decays exponentially from the mean value found at the end of the wet season.

With the above approximations, the time averaged evapotranspiration during a single season can be calculated using \( \langle ET^s \rangle = \frac{1}{T^s} \int_{t_0}^{t_0 + T^s} ET_{max}^s \langle x^s(t) \rangle \, du \) (where \( t_0 = 0 \) for the wet season, \( t_0 = T^w \) for the dry season, and the superscript \( s \) is used to denote a single season), and with equations (3.6), (3.15), and the dimensionless groups defined in Section 3.3, the annual water balance can be recast into equation (3.16).

Figure 3.1a shows the evolution of soil moisture generated by the minimalist model (dashed line) compared to that generated by a numerical simulation using the same parameters (dotted line). The minimalist seasonal model provides a good approximation for soil moisture in water-limited ecosystems where leakage and runoff are negligible compared to other terms during the dry season and soil moisture quickly reaches stochastic steady state after the beginning of the wet season. In the presence of a marked dry season, with PET high relative to rainfall, leakage and runoff tends to be negligible when the ratio of effective soil water storage to rainfall depth, \( \gamma \), is relatively large or the frequency of rainfall \( \lambda^d \) is relatively small. However, during the wet season, the same conditions (large \( \gamma \), small \( \lambda^w \)) increase the inertia of soil moisture response to rainfall forcing, resulting in a substantial time lag
between the start of the rainy season and when the soil moisture reaches stochastic steady state (see Figure 3.1a). Consequently, the minimalist seasonal model can occasionally lead to unsuitable overestimates of soil moisture, especially when $\gamma$ is large. In summary, the minimalist seasonal model cannot be applied to climates lacking a prominent dry season, including tropical rainforest, humid subtropical, and maritime climates, or when the inertia of the soil moisture process (as defined by $\gamma$) is high and the stochastic steady state is not readily reached at the beginning of the wet season.

B.2 The linear LQ model

To improve the description of the mean water balance when the minimalist model is not a good approximation, we introduce a linear approximation for the leakage and runoff ensemble averages in equation (3.14). Since $\langle LQ(x, t) \rangle$ is state dependent and requires the full determination of the time-dependent soil moisture pdf, it is extremely difficult to find it apriori. A satisfactory approximation, however, can be obtained noting that $\langle LQ(x, t) \rangle$ is known in two special cases: if the soil moisture pdf is deterministic (i.e., the pdf of soil moisture is concentrated at a point) and at stochastic steady state.

Assuming that at the beginning of each season the soil moisture pdf is concentrated around a soil moisture level $x_0^s$, where the superscript $s$ stands for either season, the pdf is a Dirac delta function $\delta(x - x_0^s)$, which, when substituted into the runoff term (3.14), gives

$$\frac{\langle LQ^s \rangle_0}{w_0} = \frac{\lambda^s}{\gamma} e^{-\gamma x_0^s}. \tag{B.3}$$

Moreover, the mean soil moisture will be $x_0^s$ at the beginning of the season.

Furthermore, the macroscopic equation (4.3) can be linearized by linearizing both the ET and the LQ terms, resulting in exponential dependence in time of $\langle x^s(t) \rangle$ to-
wards the stochastic steady state value $\langle x^s \rangle_{ss}$. Using $\langle ET^s \rangle_{ss} = ET_{max}^s \langle x^s \rangle_{ss}$, the dryness index $D^s$, and equation (B.1) for $\langle x^s \rangle_{ss}$, we obtain for each seasonal partitioning

$$\langle LQ^s \rangle_{ss} = \langle R^s \rangle - \langle ET^s \rangle_{ss} = \alpha \lambda^s \frac{D^s \gamma \beta^{-1}}{\Gamma \left( \frac{\gamma}{\beta} \right) - \Gamma \left( \frac{\gamma}{\beta}, \gamma \right)} e^{-\gamma}. \quad (B.4)$$

Combining these approximations, the linearization of $\langle LQ^s(x, t) \rangle$ for each season is then given by

$$\langle LQ^s(x, t) \rangle = \frac{\langle LQ^s \rangle_{ss} - \langle LQ^s \rangle_0}{\langle x^s \rangle_{ss} - x^s_0} \left( \langle x(t) \rangle - x^s_0 \right) + \langle LQ^s \rangle_0. \quad (B.5)$$

Substituting equation (B.5) into (3.14) and solving the macroscopic equation (4.3), we obtain the temporal evolution of the soil moisture ensemble during one season

$$\langle x^s(t) \rangle = \langle x^s \rangle_{ss} + [x^s_0 - \langle x^s \rangle_{ss}] e^{-(\frac{ET_{max}^s \alpha^s \theta^s}{u_0})t}, \quad (B.6)$$

where the effect of leakage is introduced in the exponential decay coefficient $\theta^s = \frac{\langle LQ^s \rangle_{ss} - \langle LQ^s \rangle_0}{\langle x^s \rangle_{ss} - x^s_0}$ (using (B.3) and (B.4)) and $x^s_0$ must be found by the continuity condition between the two seasons by imposing $x^d_0 = \langle x^w(T^w) \rangle$ and $x^w_0 = \langle x^d(T^d) \rangle$.

As is the case for the minimalist model, once the ensemble soil moisture evolution for each season is found, the time averaged evapotranspiration can be calculated as $\langle ET^s \rangle = \frac{1}{T^s} \int_{t_0}^{t_0 + T^s} ET_{max}^s \langle x^s(t) \rangle \, du$, and the annual water balance (3.18) can then be derived from equations (3.6) and (4.4) and the dimensionless groups.
Appendix C

Performance assessment of numerical models

The accuracy of the three new models introduced in Chapter 4 is checked against simulation results under more general climate conditions. Figure C.1 shows differences in the annual evapotranspiration ratio $\langle ET \rangle / \langle R \rangle$ as calculated from model results versus simulations. Three climatic conditions are considered, using the standard sinusoidal form in equation (4.15): (1) dry, $(\mu, A) = (0.2, 0.1)$; (2) seasonal, $(\mu, A) = (0.5, 0.5)$; and (3) wet, $(\mu, A) = (0.9, 0.1)$, with three constant soil storage index $\gamma = 3, 5.5, 30$, and five phase difference regimes between rainfall and potential evapotranspiration (while potential evapotranspiration itself remains the same at $(\mu_k, A_k) = (0.03, 0.01)$ for all cases). The three clustered bars represent results from each model, with the leftmost for the quasi steady state approximation, the middle for the negligible fluctuations approximation, and the rightmost for the self-consistent truncated gamma approximation. As can be seen, all models are able to capture simulation results for $\langle ET \rangle / \langle R \rangle$ to within a conservative 0.05 threshold, with the self-consistent truncated gamma approximation (right) performing the best overall, as expected. The negligible fluctuations approximation (middle) does not do
Figure C.1: Difference in the annual evapotranspiration ratio \( \langle ET \rangle / \langle R \rangle \) as calculated between each of the three new models in Chapter 4 and simulation. The potential evapotranspiration parameters are the same for all cases \( (\mu_k, A_k) = (0.03, 0.01) \), while three rainfall conditions are considered: (1) dry, \( (\mu_\lambda, A_\lambda) = (0.2, 0.1) \), (2) highly seasonal, \( (\mu_\lambda, A_\lambda) = (0.5, 0.5) \), and (3) wet, \( (\mu_\lambda, A_\lambda) = (0.9, 0.1) \), with the phase difference between rainfall and evapotranspiration \( \Delta \phi \) ranging from 0\(^\circ\) to 180\(^\circ\) in 45\(^\circ\) increments, and soil storage indices \( \gamma_t = 3 \) (left panel), \( \gamma_t = 5.5 \) (middle panel), and \( \gamma_t = 30 \) (right panel). The three solid bars in each cluster (from left to right) represents the difference between simulation and the quasi steady state model (left), the negligible fluctuations model (middle), and the self-consistent truncated gamma model (right). Scale bars indicate that all differences considered are within a threshold of 0.05.

as well in some cases, while the quasi steady state model (left) has a weakness under seasonal climates with deeper soils. Nevertheless, for \( \gamma_t = 5.5 \), which is adopted for our tropical dry and Mediterranean examples, the quasi steady state model can capture \( \langle ET \rangle / \langle R \rangle \) very accurately under broad rainfall conditions, justifying its use for the results shown in the annually averaged values (for example, in Figure 4.6).

We also evaluate the ability of the models to follow intra-annual variations in mean soil moisture, which influences their ability to reproduce the transient trajectories of Figure 4.5. The modeled values are evaluated using their pattern correlation \((PC)\) and centered root mean square error \((RMSE)\) over an annual cycle as compared to simulated values. These measures are related to each other through \( RMSE = \sigma_f^2 + \sigma_r^2 - 2\sigma_f\sigma_rPC \), where \( \sigma_f \) and \( \sigma_r \) are the standard deviations re-
respectively of the modeled and simulated values. This relationship can be concisely summarized in the Taylor diagrams (Taylor, 2001) of Figure C.2. The triangle, diamond, and circular markers now represent respectively the quasi steady state model, the negligible fluctuations model, and the self-consistent truncated gamma model. Each is subjected to the same climate and soil conditions as in Figure C.1, except the phase difference between rainfall and potential evapotranspiration is restricted to 0° (in-phase) and 180° (out-of-phase).

We find in Figure C.2 that the self-consistent truncated gamma model vastly outperforms the other two models, especially in highly seasonal climates. In the Taylor diagrams at the top, the self-consistent truncated gamma model markers (circles) have the shortest distance to the simulation marker (star), which indicates the lowest values of $RMSE$. Here all values are normalized with respect to the standard deviation of the simulation (Taylor, 2001). The bottom panels show the $RMSE$ for all models using non-normalized results; thus the values represent how much modeled mean soil moisture deviates from the simulated results in absolute terms. The self-consistent truncated gamma model shows a remarkable level of fidelity to simulation results under all conditions considered. The $RMSE$s for the other two models tend to grow with increasing soil depth, with especially large errors in highly seasonal climates due to their tendency to exaggerate the variations in mean soil moisture over each season, resulting in a larger standard deviation compared to simulations. These plots collectively show that we can be confident in our use of the self-consistent truncated gamma model to produce transient trajectories in Figure 4.5.
Figure C.2: Comparison of the intra-annual results for $\langle x_t \rangle$ for each model against simulation results. The dry, highly seasonal, and wet conditions correspond to those described in Figure C.1, with each model shown with triangles (model 1: quasi steady state), diamonds (model 2: negligible fluctuations), and circles (model 3: self-consistent truncated gamma). The results are shown in filled markers for when rainfall and potential evapotranspiration are in-phase, and in open markers for when they are out of phase, for three different soil depths of $\gamma_t = 3, 5.5, 30$. The Taylor diagrams (Taylor, 2001) in the top panels show the modeled standard deviation and correlation coefficient relative to simulation results; the distance between the model marker and the simulation marker (star) indicates the centered root mean square error $RMSE$ of the normalized model result (relative to the standard deviation of each simulation). The bottom panels show the absolute $RMSE$ using non-normalized model results.
Appendix D

Nonlinear effects of climate seasonality

Failure to consider seasonal variations in the climate can lead to significant underestimation of the proportion of the annual rainfall lost through leakage/runoff, and thus an overestimation in the annual evapotranspiration ratio. We illustrate this point by comparing $\langle ET \rangle / \langle R \rangle$ calculated from seasonally-varying climate parameters with the same ratio calculated from annually averaged climatic parameters. Both sets of climatic parameters have the same annual mean, which is often used as a first point of reference when making comparisons between regions of different climates. However, climate averages, while maybe acceptable for an order-of-magnitude approximation, can often obscure the large effects of the inherent nonlinearities in the soil system (Katul et al., 2007).

Figure D.1 considers the effects of nonlinearity in the soil moisture model resulting from explicitly considering seasonal rainfall parameters. The standard sinusoidal form (4.15) is used for both rainfall and potential evapotranspiration, with $(\mu_k, A_k) = (0.03, 0.01)$. The amplitude of rainfall seasonality, $A_\lambda$, varies along with the phase shift $\Delta \phi = \phi_k - \phi_\lambda$, which changes from $0^\circ$ (in-phase) to $180^\circ$ (out-of-phase). The
grey and black meshes show the results respectively for a deeper soil of $\gamma_t = 30$ and an typical soil depth of $\gamma_t = 5.5$. It is worthwhile to stress that the results are shown in each panel for a constant mean annual rainfall $\langle R \rangle$.

Errors in $\langle ET \rangle / \langle R \rangle$ generally grows with increasing climate phase shift and increasing rainfall seasonal amplitude. In the case of a wet location with high seasonal rainfall and deep soil, error can grow to as much as 0.30 when rainfall and potential evapotranspiration are out-of-phase, as in Mediterranean climates. For low rainfall of $\mu_\lambda = 0.3$, errors in $\langle ET \rangle / \langle R \rangle$ is more pronounced for shallower soil depth of $\gamma_t = 5.5$. This is probably due to the generation of a substantial amount of leakage due to a relative lack of soil water storage. On the other hand, for high rainfall of $\mu_\lambda = 0.7$, increasing rainfall amplitude $A_\lambda$ may actually decrease the calculated error, especially for deeper soils when the climate inputs are in-phase. However, this trend quickly reverses, with the errors increasing again once rainfall amplitude increases
past a certain level.

Altogether, these observations show that assessing hydrological variables containing inherently nonlinear behavior, such as the case with $\langle ET \rangle/\langle R \rangle$, in the presence of climate seasonality can produce a range of unexpected behaviors, and that their approximation using annually averaged inputs can often lead to misleading results.
Appendix E

Linking discrete and continuous stochastic population models across scales

This appendix is adapted from Feng, X. and A. Porporato, Discrete and continuous models of community distributions and related measures of biodiversity, in preparation. Here, we show within a coherent mathematical framework how deterministic descriptions of populations follow naturally from stochastic descriptions with increasing system size. This is done by tracing the effects of stochastic population dynamics from the scale of the individuals to the community and showing how bulk behavior of large populations can be approximated using a deterministic process. These considerations are important not only for population dynamics but also for understanding the linkage between microscopic processes in high dimensional, complex systems and their macroscopic behavior. The limitations of system size expansion and other scaling formulas have to be carefully applied under certain conditions, as will be discussed.

Birth and death processes provide a natural framework for modeling the dynamics of populations in systems consisting of discrete units. Their extensive applications
Figure E.1: Schematics extending from the microscopic to macroscopic view, from stochastic to deterministic descriptions of system dynamics. The approximations made at each step are shown next to arrows, and models and theories are situated with their associated toolsets. Stochastic differential equations are abbreviated as SDE.

Cover the study of spin states in quantum mechanics, molecules in biochemical reactions, cell and virus populations in immunology, human populations in epidemiology and demography, biological populations in ecology, and other fundamental units in queuing theory and communications (Bailey, 1964; Gardiner, 2009; Gillespie, 2000; Liggett, 2005).

Mathematically, birth and death processes are a special class of continuous-time Markov processes whose range is discrete and whose state transitions consist of jumps between immediately adjacent states (they are sometimes called one-step processes or generation-recombination processes (Van Kampen, 1992)). In such models, the state of the system evolving over continuous time is described using the total number of units (e.g., individuals) belonging to one of \( S \) fixed groups (e.g., species). This is expressed by the multivariate random vector \( \mathbf{X} = X_1, ..., X_k, ..., X_S \), whose \( k \)-th component denotes the number of individuals in species \( k \). The population of each
species, $X_k$, is considered as a discrete random variable and allowed to take any integer value between 0 and $\infty$. The probability of $X_k$ taking a specific value $x_k$ is indicated as $p[X_k = x_k]$, following notations from Priestley (1981). A fixed number of $S$ species implies that species evolution is considered to be constrained in such a way that any extinction of a species is exactly balanced by the introduction of a new species.

Changes in the population of each species, $X_k$, are caused by an instantaneous jump of a type belonging to one of $j = 1, \ldots, M$ processes (for example $M = 2$ for a birth and death process) which are characterized by a transition probability per unit time of moving between two allowable states. Two key ingredients describe such jump events: (1) a state-change vector $\nu_j = \nu_{j1}, \ldots, \nu_{jS}$ where $\nu_{jk}$ denotes the transition in the state of $X_k$ resulting from process $j$, and (2) a transition probability per unit time, $a_j$, between allowable states for each process $j$. Specifically, $a_j$ is defined following Gillespie (2000) as

$$a_j(x)dt \equiv \text{the probability that process } j \text{ will occur during } [t, t + dt) \text{ given current state } X(t) = x.$$  

If the value of $a_j(x)dt$ remains essentially constant over a small interval $dt$, the occurrence of a jump can be thought of as a random event with exponentially distributed waiting times (Gillespie, 2000), with the system state approximated by

$$X(t + dt) = X(t) + \sum_{j=1}^{M} P_j(a_j(X(t))dt)\nu_j + O(dt), \quad (E.1)$$

where $P_j(\lambda)$ is a statistical independent Poisson random variable with mean and variance $\lambda$. Ultimately, the practical interest in the problem lies in tracing the evolution of the vector $X = X_1, \ldots, X_S$ from some initial state.

The discrete population dynamics of a system as modeled by general stochastic birth and death processes have an analogous representation as biochemical reactions,
which draws from a rich literature on nonlinear, stochastic biochemical dynamics (Qian, 2011; Gillespie, 2007; McQuarrie, 1967). Here, each type of jumps can be thought of as a biochemical reaction, with transition probabilities termed “propensity functions” (Gillespie, 2000). While these propensity functions can be constructed based on the details of each reaction, a simple, realistic form is given by the law of mass action, which constrains the functions to be proportional to the product of the reactant concentrations (Murray, 2002). This law is commonly applied in reaction kinetics and other models involving the transformation of material or population densities (Murray, 2002; Qian, 2011); in fact, it has been the basis of Lotka’s seminal work on predator-prey population dynamics (Lotka, 1925).

E.1 The master equation

The master equation is an exact consequence of the discrete birth and death process (Van Kampen, 1992; Gardiner, 2009) and provides a probabilistic description of $x$ as a balance equation of probabilities governed by $M$ processes,

$$\frac{\partial p[x, t|x_0, t_0]}{\partial t} = \sum_{j=1}^{M} (a_j(x - \nu_j)p[x - \nu_j, t|x_0, t_0] - a_j(x)p[x, t|x_0, t_0]). \quad (E.2)$$

This is a differential equation for the joint distribution of the $S$-dimensional variable $p[x, t|x_0, t_0]$ (see Figure E.1). It can be solved analytically for only a very few cases, one of which we will consider in Section E.4.

E.2 From discrete to continuous: Fokker-Planck and Langevin equations

The Fokker-Planck and the Langevin equations are two equivalent forms of an approximation that exist in the limit of a scaling parameter applied to the master equation (E.2). The most salient effect of using these scaling parameters is that it
allows us to replace each jump processes with a diffusion process and to approximate the discrete random variable $X$ with a continuous random variable (whose probability density we now denote with $f(X)$). Physically, the rescaling is analogous to assuming an appropriate “macroscopic infinitesimal timescale” (which, incidentally, can be more easily realized for larger populations; see Gillespie (2000) and the rescaling method in Gardiner (2009)).

When the conditions related to rescaling are satisfied, the Fokker-Planck equation can be directly derived from the master equation, retaining the first two moments after the master equation is expanded in terms of its power series (via the Kramers-Moyal expansion),

$$
\frac{\partial f(x,t)}{\partial t} = -\sum_{k=1}^{S} \frac{\partial}{\partial x_k} A_k(x)f(x,t) + \frac{1}{2} \sum_{k,m=1}^{S} \frac{\partial^2}{\partial x_k \partial x_m} D_{km}(x)f(x,t),
$$

(E.3)

where

$$
A_k(x) = \sum_{j=1}^{M} \nu_{jk} a_j(x), \quad D_{km}(x) = \sum_{j=1}^{M} \nu_{jk} \nu_{jm} a_j(x).
$$

The coefficients $A_k$ and $D_{km}$ are terms respectively from a differentiable $1 \times S$ drift vector $A$ and a symmetric $S \times S$ diffusion matrix $D$.

Likewise, in the limit of a large population, the Poisson random variable in equation (E.1) is replaced with a normal random variable, resulting in the Itô interpretation of the Langevin equation,

$$
\frac{dX(t)}{dt} = \sum_{j=1}^{M} \nu_j a_j(X(t)) + \sum_{j=1}^{M} \nu_j \sqrt{a_j(X(t))} W(t),
$$

(E.4)

where $W(t)$ is a column vector of $M$ independent Gaussian white-noise processes.

The population dynamics is outwardly separated into a deterministic (first term) and a stochastic (second term) component; these terms also appear in the Fokker-Planck equation as drift and diffusion. While the Fokker-Planck equation and the Langevin
equation can be used interchangeably for the same process, the former describes its ensembles while the latter its trajectories (Figure E.1).

There are several advantages of using these approximated forms over the master equation (E.2) or the discrete stochastic equation (E.1). First, they are more amenable to analysis, making available an extensive set of tools for analyzing partial differential equations and stochastic differential equations. Second, since these equations delineate a clear separation between drift and diffusion, the bulk behavior of the system, in some cases, can be used in their construction, generating links to observable macroscopic dynamics. While the Fokker-Planck and Langevin equations are the most frequently used forms of approximations, some types of problems call for other approaches to the master equation; these may involve the use of the generating function (Gardiner, 2009) or the Wentzel-Kramers-Brillouin (WKB) approximation (Bender and Orszag, 1978).

E.3 The macroscopic equation and the role of nonlinearity and noise

The bulk behavior of the system resulting from averaging the microscopic fluctuations can be described by the macroscopic equation for the mean of $X$. It can be found by averaging the Fokker-Planck equation (E.3) or the Langevin equation (E.4) as

$$\frac{d\langle X(t) \rangle}{dt} = \sum_{j=1}^{M} \nu_j \langle a_j(X(t)) \rangle, \quad \text{(E.5)}$$

where the mean of the diffusion term is zero (in the Itô interpretation). Its resemblance to the deterministic component of the Langevin equation (E.4) is not a coincidence, because in the large population limit for which the Langevin equation is constructed, the random fluctuations around the ensemble mean grow at a slower rate compared to the mean itself, resulting in an overwhelming majority of the in-
individuals becoming concentrated around the mean. In the thermodynamic limit (where system size is taken to infinity while species concentrations are kept constant), the contribution of the stochastic terms in the Langevin equation becomes negligible compared to that of the mean. A snapshot of this procedure is illustrated in Figure E.2: the relative size of the variance of the pdf (which results from fluctuations) to its mean is much less for a larger population. Under these conditions, the Langevin equation is sometimes replaced with yet another set of deterministic ordinary differential equations,

$$\frac{dx(t)}{dt} = \sum_{j=1}^{M} \nu_j a_j(x(t)).$$

(E.6)

This heuristic construction, sometimes called a “phenomenological equation,” is often taken to represent the bulk behavior of the system when the effect of fluctuations are small (Van Kampen, 1992). It is a deterministic population model typified by the Lotka-Volterra type equations in ecology, the SIR models in epidemiology, the Michaelis-Menten reaction kinetics, amongst others (see for example Murray (2002)).

Several caveats, however, apply to the interpretation of the phenomenological equation (E.6). Equation (E.6) is an approximation to the exact macroscopic equation (E.5) and only becomes mathematical equivalent to (E.5) when $a_j(\langle X \rangle) = \langle a_j(X) \rangle$, that is, when the functional form of $a_j(x)$ is linear for all $j$ (Figure E.1). Thus, for linear processes with natural boundaries, the expected value of the stochastic process will be exactly equal to its corresponding phenomenological values. For nonlinear processes this is emphatically not the case; their moment equations (starting with (E.5)) cannot be closed. Only the large size approximation allows the pdf of $X$ to become concentrated around $\langle X \rangle$ and thus for $a_j(\langle X \rangle)$ to approach $\langle a_j(X) \rangle$, effectively rendering the trajectory of $\langle X \rangle$ deterministic.

In addition, it is important to distinguish whether the stochasticity in the orig-
Figure E.2: Simulated trajectories and exact steady state solutions are shown based on the linear birth and death model of Section E.4. The trajectories are simulated based on the exact kinetic reactions using Gillespie's algorithm (black lines) and based on the Langevin equations using Milstein's method (grey lines), and the pdfs are exact solutions from the master equation (E.9) (discrete) and the Fokker-Planck equation (E.10) (continuous). The top panels (a,c) are for a process with $b_1 = 0.99$ and the bottom panels (b,d) are for $b_1 = 0.50$. Both processes use $d_1 = 1.0$.

inal birth and death model originates from “internal” or “external” sources (Van Kampen, 1992). The limiting procedure of Section E.2 only applies in case of internal noise (sometimes referred to also as demographic stochasticity (May, 1973; Lande, 1993)) by increasing system size. However, the existence of external noise (or environmental stochasticity) can also change the limiting equations, since in general such extrinsic factors cannot be reduced with increasing system size (Lande, 1993).

At the microscopic scale, the inclusion of sudden jumps (for example, via rare but catastrophic events), time dependencies in $a_j$ and $\nu_j$ (due to fluctuating resource levels), discontinuities, or artificial boundary conditions can alter the dynamics of the original birth and death process. In the thermodynamic limit, these modifications can result in adjustments to the drift and diffusion terms.
E.4 Application to a single-species population

To discuss the previous limiting procedures in the ecological context, we use the one-dimensional birth and death process to model the population of a single isolated species. The progression from its reaction kinetic formulation to full stationary solution serves to establish the connection between its rules of microscopic fluctuations and the ensuing macroscopic description. We examine through these models the validity of approximating stochastic jumps with a diffusion process and the interpretation of mean trajectories. We discuss implications of the discrepancies in the model dynamics and steady state solutions.

For each one-dimensional birth and death process, we define a generalized linear form for the birth and death rates to account for constant population fluxes and density dependent mechanisms, e.g.,

\[ b(x) = b_0 + b_1 x, \quad d(x) = d_0 + d_1 x. \]

These rates are valid for \( x > 0 \), with \( b_0, b_1, d_0, d_1 \) as constants. In the reaction kinetics context, this birth and death process can be translated to a set of \( M = 2 \) reactions involving a single species,

\[ X \xrightarrow{b} 2X, \quad X \xrightarrow{d} \emptyset, \]

where each reaction corresponds to a simple birth \((j = 1)\) and death \((j = 2)\) process and increases or decreases the reactant \( X \) by 1, with \( \nu_1 = 1 \) and \( \nu_2 = -1 \). Each reaction proceeds according to their prescribed rates given by \( b(x) \) and \( d(x) \). The master equation according to (E.2) now looks like

\[
\frac{dp[x,t|x_0,t_0]}{dt} = (b_0 + b_1(x - 1)) p[x - 1, t|x_0, t_0] + (d_0 + d_1(x + 1)) p[x + 1, t|x_0, t_0] - (b_0 + b_1 x + d_0 + d_1 x) p[x, t|x_0, t_0]. \tag{E.7}
\]
In the large populations limit, the corresponding Fokker-Planck equation is

\[
\frac{\partial f(x,t)}{\partial t} = -\frac{\partial}{\partial x} \left[ (b_0 + d_0 - (b_1 + d_1)x)f(x,t) \right] + \frac{1}{2} \frac{\partial^2}{\partial x^2} \left[ (b_0 + d_0 + (b_1 + d_1)x)f(x,t) \right].
\] (E.8)

We now consider a special case where both growths and deaths are density dependent, i.e., \( b(x) = b_1 x \) and \( d(x) = d_1 x \). To maintain a finite population and to prevent total extinction when \( b_1 < d_1 \), the lower boundary at \( x = 1 \) is modified to a reflecting boundary, which allows an artificial process to inject new individuals at \( x = 1 \) when the original process reaches \( x = 0 \), ensuring that a new individual can arise from extinction. In general, artificial boundaries can create considerable difficulties for solving the master equation (van Kampen, 1976; Montroll and Shuler, 1958). Thus, the full solution is not available in this case (although Azaele et al. (2006) have obtained its spectral resolutions for both absorbing and reflecting boundaries).

Here, we focus on the steady state solution to the master equation (E.7) under a reflecting boundary, which can still be found using detailed balance as a logarithmic (or log-series) distribution,

\[
p_{st}[x] = N_p \frac{(b_1/d_1)^x}{x},
\] (E.9)

where the normalizing constant is \( N_p = -1/\ln \left( 1 - \frac{b_1}{d_1} \right) \) for \( x = 1, 2, \ldots, \infty \).

The solution to the associated Fokker-Planck equation for a large population is

\[
f_{st}(x) = N_f \frac{e^{\frac{b_1-d_1}{d_1+b_1}x}}{x}.
\] (E.10)

This is an approximation to equation (E.9) for \( x \geq 1 \) with \( N_f = 1/\Gamma \left( 0, 2\frac{d_1-b_1}{d_1+b_1} \right) \), where \( \Gamma(\cdot, \cdot) \) is the incomplete gamma function (Abramowitz and Stegun, 1964). The modified reflecting boundary is applied again at \( x = 1 \).
Trajectories from the reaction kinetics and from the stochastic differential equations are plotted in Figure E.2a and E.2b. At larger population sizes, they have excellent agreement. Only at smaller population sizes do the traces begin to differ qualitatively: the discrete jumps are larger and occur less frequently compared to its diffusion counterpart. This leads to the diffusion process spending more time close to the reflecting barrier, leading to considerably higher probabilities of lower values (Figure E.2c and E.2d).

Another difference between the discrete and continuous representations of the process can be framed in terms of extinction probabilities under natural boundary conditions (Ovaskainen and Meerson, 2010; Doering et al., 2005). The macroscopic equation for (E.7) under natural boundary conditions is

$$\frac{d\langle X(t) \rangle}{dt} = (b_0 - d_0) + (b_1 - d_1)\langle X(t) \rangle,$$

(E.11)

which is also the phenomenological equation since both $b(x)$ and $d(x)$ are linear. Note that the macroscopic equation maybe very different with different boundary conditions for the original stochastic process. Equation (E.11) results in either exponential growth or decay depending on the ratio of $b_1$ to $d_1$ (Murray, 2002). Notably, it never goes to extinction in finite time. The corresponding stochastic process, however, always has a non-zero extinction probability when $b_1 > d_1$ and will certainly go to extinction when $b_1 \leq d_1$. Even when $b_1 = d_1$ and the deterministic mean trajectory remains indefinitely at the initial condition, the chance of extinction as predicted by the stochastic process is still unity. This is because the high values attained during some realizations will be offset by the extinction of many others, such that the mean will remain constant. Thus, Bailey (1964) warns of “attaching too much importance to stochastic mean values, even when these are exactly equal to the corresponding deterministic quantities.”
Bibliography


Biography

Xue Feng was born in Dujiangyan, China in April 1988. She earned a Bachelor of Science degree in Mechanical Engineering and a minor in Biology from Stanford University in June 2010. In August 2010 she started work on her Ph.D. degree at Duke University, in Civil and Environmental Engineering, to study the effects of climate variability on the ecohydrology of seasonally dry ecosystems. In 2012 she was awarded a U.S. National Science Foundation (NSF) Graduate Research Fellowship for funding towards her thesis. Starting in August 2015 she will be working as visiting scientist under an National Oceanic and Atmospheric Administration (NOAA) Climate and Global Change Postdoctoral Fellowship, at University of California, Berkeley.

List of publications


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