Consequences of More Extreme Precipitation Regimes for Terrestrial Ecosystems

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Amplification of the hydrological cycle as a consequence of global warming is forecast to lead to more extreme intra-annual precipitation regimes characterized by larger rainfall events and longer intervals between events. We present a conceptual framework, based on past investigations and ecological theory, for predicting the consequences of this underappreciated aspect of climate change. We consider a broad range of terrestrial ecosystems that vary in their overall water balance. More extreme rainfall regimes are expected to increase the duration and severity of soil water stress in mesic ecosystems as intervals between rainfall events increase. In contrast, xeric ecosystems may exhibit the opposite response to extreme events. Larger but less frequent rainfall events may result in proportional reductions in evaporative losses in xeric systems, and thus may lead to greater soil water availability. Hydric (wetland) ecosystems are predicted to experience reduced periods of anoxia in response to prolonged intervals between rainfall events. Understanding these contingent effects of ecosystem water balance is necessary for predicting how more extreme precipitation regimes will modify ecosystem processes and alter interactions with related global change drivers.

Keywords: climate change, drought, ecosystems, precipitation, soil water

Human activities have caused dramatic and unprecedented changes in the global chemical and physical environment, including well-documented increases in atmospheric carbon dioxide (CO_2) concentration and mean annual temperature (Karl and Knight 1998, New et al. 2001, IPCC 2007). If greenhouse gas emissions continue to increase at present rates, atmospheric CO_2 concentrations will more than double preindustrial levels during the current century, and general circulation models (GCMs) predict additional increases in mean global temperature of between 1.1 and 6.4 degrees Celsius (IPCC 2007). Alterations in patterns of global atmospheric circulation and hydrologic processes are predicted to modify mean annual precipitation and to increase the inter- and intra-annual variability of precipitation (Easterling et al. 2000, Schär et al. 2004, Seneviratne et al. 2006, IPCC 2007). The combined effects of increased atmospheric CO_2, elevated global temperatures, and altered precipitation regimes represent a rapid and unprecedented change to the fundamental drivers of chemical and biological processes within ecosystems (Amundson and Jenny 1997). The complexity and pace of these global anthropogenic changes pose a major challenge for ecosystem scientists and managers (NRC 2001), particularly given their potential impact on the provisioning of ecosystem services (Bennett et al. 2005).

Amplification of the hydrological cycle, a consequence of global warming, has been expressed in the form of increased cloudiness, latent heat fluxes, and more frequent climate ex-

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tremes (Huntington 2006, IPCC 2007). Key predictions of hydrological amplification are an increased risk of drought and heat waves (recently exemplified by the extremely dry and hot summer of 2003 in Europe; Ciais et al. 2005, Reichstein et al. 2007) and an increased probability of intense precipitation events and flooding. The complexity, interactions, and scope of global-scale atmospheric processes have made potential changes in precipitation patterns difficult to predict, compared with the more consistent projections for increased atmospheric CO_2 and temperature. Thus, although most GCMs predict a modest increase in rainfall at the global scale, they often disagree on the magnitude and even the direction of change at regional and especially local scales (IPCC 2007, Zhang et al. 2007). In contrast, projections have been consistent for intensified intra-annual precipitation regimes (through larger individual precipitation events) with longer intervening dry periods than at present (Easterling et al. 2000, IPCC 2007). Less frequent but more intense precipitation events may increase the severity of within-season drought, significantly alter evapotranspiration, and generate greater runoff (Fay et al. 2003, MacCracken et al. 2003). These intra-annual modifications to the hydrological cycle are distinct from the better-known alterations in interannual precipitation variability associated with large-scale climate dynamics (e.g., the El Niño Southern and Pacific Decadal oscillations), although both intra- and interannual changes lie along a continuum of altered temporal patterns in hydrology. Our focus here is on increased intra-annual variability in precipitation (i.e., more extreme rainfall regimes), a more subtle but chronic and pervasive change in the way that precipitation is delivered to terrestrial ecosystems.

There is growing evidence at global, regional, and local scales that intra-annual precipitation regimes have already become more extreme. For example, global precipitation records show an average increase of only 9 millimeters (mm) of precipitation over land areas (excluding Antarctica) during the 20th century (figure 1). Regionally, however, these records show an increased frequency of wet days in portions of North America, Europe, and Southern Africa; an increased frequency and duration of dry periods in European-African, Australian, Mediterranean, and Asian monsoon regions; and an increased proportion of total precipitation originating from the largest precipitation events in several regions (figure 1; New et al. 2001, Groisman et al. 2005). Elevated temperatures have been associated with a 10% increase in annual precipitation in the contiguous United States over the past century; this increase is expressed primarily as an intensification of the largest precipitation events, particularly in the summer (Karl and Knight 1998). Thus, the link between higher temperatures and more extreme precipitation regimes has solid theoretical underpinnings and model validation (Karl and Trenberth 2003), as well as emerging empirical support from global climate data sets (Karl et al. 1995, Kunkel et al. 1999, Groisman et al. 2005).

Two examples further illustrate this predicted modification to intra-annual precipitation regimes. Across a precipitation gradient in the southern plains of the United States (440 to 1270 mm per year), a consistent trend of decadal increases in the mean size of individual rainfall events is evident from 1950 to 1990, with no corresponding increase in the amount of precipitation (figure 2a, 2b, 2c). Similarly, in southern Europe, the intensity of rainfall events has increased and the frequency of days with rainfall has decreased, with only a slight decrease in total precipitation (figure 2d, 2e). Both of these local records, spanning periods of 40 years or more, are consistent with a global trend of more extreme rainfall events in terrestrial ecosystems. These and other observations indicate that, globally, intra-annual precipitation patterns have already become more extreme and noticeably more variable in the second half of the 20th century.

Although forecasts of more extreme rainfall regimes are now being corroborated, the ecological implications of greater intra-annual variability and extremes in precipitation have received minimal attention from the scientific community (Jentsch et al. 2007). This is surprising, given that the effects of increasingly variable precipitation patterns on terrestrial ecosystems have been predicted to rival the ecological impacts of other global-scale changes, including atmospheric warming and increased CO_2 concentrations (Easterling et al. 2000, Parmesan 2006, IPCC 2007). Most research to date has instead focused on the effects of changes in rainfall amount and seasonality (e.g., Beier et al. 2004), with recent emphasis on the role of pulsed events (Huxman et al. 2004a, Schwinning and Sala 2004).

In this article, we present a conceptual framework for improving our understanding of how terrestrial ecosystems that vary in their overall water balance may respond to more extreme precipitation regimes. We define an extreme precipitation regime strictly from an intra-annual perspective, as a shift from current rainfall patterns to a regime in which individual events are greater in magnitude and the intervening periods between events are longer. We begin by using modeled and empirical data to examine how such precipitation changes may affect soil water dynamics. Soil water availability is a critical variable for linking precipitation regimes with ecological responses (Kramer and Boyer 1995). Further, it provides a key point of intersection with other global change drivers, such as elevated atmospheric CO_2 and climate warming, which are also known to affect ecosystems through changes in the amount and dynamics of soil water (Hungate et al. 2002, Morgan et al. 2004, Luo 2007). We then develop a simple conceptual model focused on the interaction between increased precipitation variability and the water balance of terrestrial ecosystems. This model, in tandem with the extant literature, enables us to formulate hypotheses detailing how more extreme precipitation regimes will affect ecological processes in ecosystems that vary widely in their total precipitation inputs.

Projected changes in soil water dynamics: Theory, simulation, and experiments

Precipitation regimes are typically quite variable with regard to individual event size and event frequency. In general, inter-

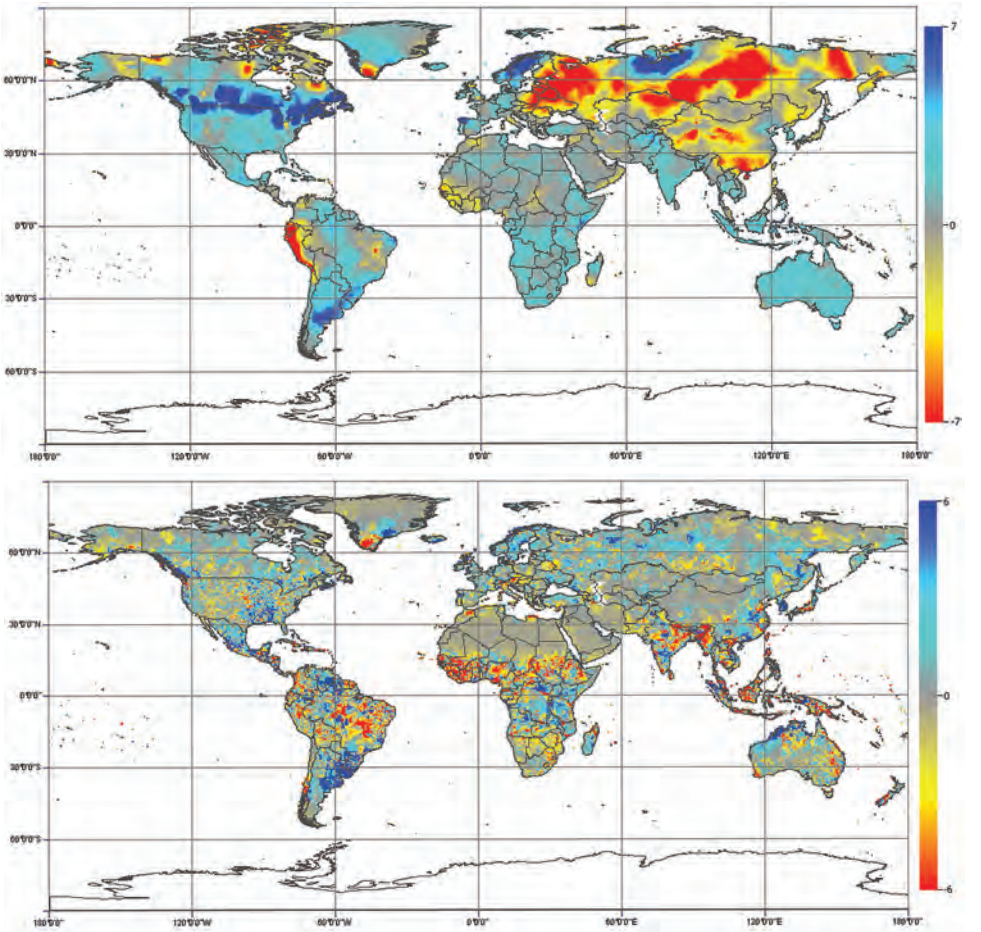

Figure 1. Trends in precipitation amount (upper panel, color scale from –6 [red] to 6 [blue] in millimeters per decade) and number of wet days (lower panel, color scale from –7 [red] to 7 [blue] in days per decade) according to the Climatic Research Unit global meteorology data set from 1900 through 2003. Note that there are distinct regional patterns of changes in rainfall frequency (number of wet days) that do not necessarily correspond to changes in total annual rainfall. For example, in parts of Eurasia, decreased rainfall frequency associated with increased annual rainfall is evident, indicating less frequent but more intense rainfall events than in the recent past. For a discussion of the limitations of this data set, see New and colleagues (2001).

annual variability is greater in xeric than in mesic systems (Knapp and Smith 2001, Davidowitz 2002), but much less is known about the intra-annual characteristics of event size and frequency among ecosystems. Soil water storage depends on vegetation type and cover, soil surface and subsurface characteristics (e.g., infiltration rate, slope, texture, depth, impermeable layers), and losses to deep drainage, lateral flow, and evaporation (Brady and Weil 2002). First we consider how extant rainfall patterns might be altered in ways that would lead to more extreme intra-annual precipitation regimes, then we assess the influence this change may have on the soil water dynamics of ecosystems.

We evaluated the impacts of three scenarios—one scenario of ambient precipitation event size and frequency, and two scenarios of increasing extremes in precipitation—on soil water dynamics, using a general soil water model (TECO [terrestrial ecosystem] model; Luo and Reynolds 1999, Weng and Luo 2008). We focused on growing-season precipitation, because in most ecosystems, this should have the largest direct impact on ecological processes.

1. *Ambient event size and frequency.* Our starting point was an average precipitation regime imposed on a mesic grassland ecosystem with representative soil characteristics for the central United States (eastern Oklahoma; annual precipitation = 970 mm). This regime incorporated the known distribution of event sizes and frequencies from recent climatic records (1950–1990).

2. *Extreme (larger) event size with no change in ambient frequency.* In this modification of the ambient regime, we increased the size of large precipitation events by combining them with a constant portion of smaller events that occurred adjacent to them in time (figure 3). This changed the size distribution of events (i.e.,

more large and small events, and fewer of intermediate size) but not the event frequency or temporal distribution.

3. *Extreme event size with reduced frequency.* In this scenario, we further increased the size of large events by combining entire adjacent events. This increased the size of the largest events and the mean event size, decreased the number of events, and lengthened the dry intervals between events.

The two modified scenarios (2 and 3) result in more extreme precipitation regimes in three key ways: maximum event size is increased (both scenarios), event frequency is decreased (scenario 3), and intraseasonal dry periods are lengthened (scenario 3, figure 3). In all scenarios, the total amount of precipitation remained constant, enabling us to focus on the consequences of more extreme rainfall regimes without the additional effect of altered precipitation amount.

Model simulations suggest that these more extreme precipitation scenarios will have significant consequences for soil water dynamics at both shallow and deep soil depths. Modeled soil water responses for scenarios 2 and 3 (figure 3a) indicated that periods of reduced soil water were more pronounced and frequent in the upper soil layers relative to those of the ambient precipitation regime. Thus, soil water (0 to 50 centimeters [cm] depth) in this mesic ecosystem was reduced to levels that are lower on average than occur with extant precipitation regimes. This is likely to have important ecological implications, because the majority of root mass, and most biogeochemical activity, occur within 50 cm of the soil surface in ecosystems characteristic of this region (e.g., Knapp et al. 2002). In addition, periods of reduced water availability were of longer duration in scenario 3 even in the absence of a change in total precipitation (Porporato et al. 2006). A similar response has been experimentally documented in mesic grassland (Knapp et al. 2002). Model output also suggests that larger rain events recharged deeper soil layers more effectively (figure 3b, 3c).

Ecohydrological theory predicts that ecosystems will respond to any change in precipitation regime through the integrated effect of key hydrological components on overall system water balance (Rodríguez-Iturbe 2000). The modeling exercise described above was based on a relatively mesic ecosystem, but it can be extended to other ecosystems with very different water balances. First, we focus on xeric versus mesic ecosystems. Xeric ecosystems with a precipitation-to-potential-evapotranspiration ratio (P/E) of much less than 1 consistently experience very low levels of soil water availability because of low annual precipitation or high rates of evapotranspiration, or both. This produces chronic and often intense periods of water stress that are only intermittently alleviated. Mesic ecosystems are defined by relatively abundant soil water availability (relative to demand; P/E > 1) and minimal water stress for substantial portions of the growing season.

These contrasting ecosystem types are expected to have both common and unique responses to more extreme rainfall regimes. In most ecosystems, larger individual rainfall events are likely to result in a loss of soil water if surface runoff increases. Conversely, proportional losses of precipitation to canopy interception and evaporation will be reduced as the event size increases. The greatest expected distinction in response between mesic and xeric ecosystems may be related to differences in their sensitivity to event size and event frequency. In xeric ecosystems characterized by small rainfall events, soils are typically already dry between events, and evaporation from upper soil layers (the rooting zone) rapidly leads to significant reductions in soil water availability (Fischer and Turner 1978). We anticipate that this loss would be substantially reduced if a greater proportion of rain fell in larger events, allowing water to move to deeper soil layers less affected by evaporation. Thus, soil water available to the biota may be increased with fewer, larger events in xeric

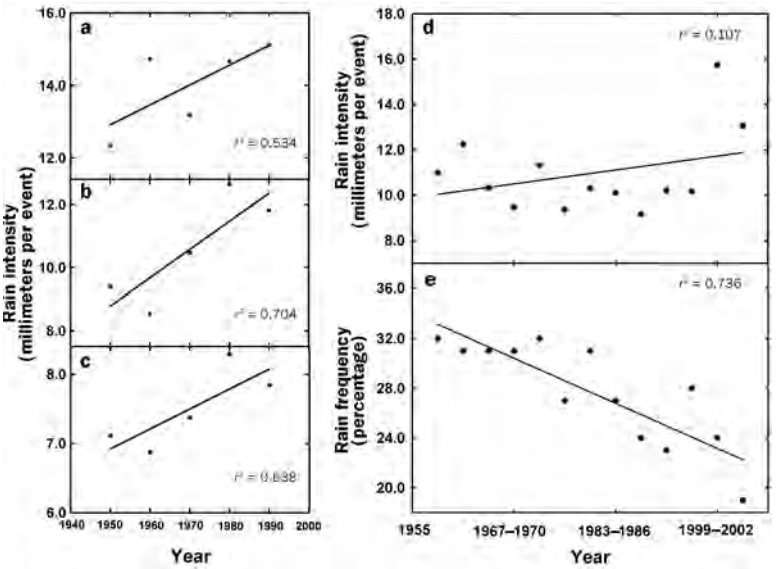

Figure 2. (a–c) Ten-year averages of rainfall intensity from 1950 through 2000 across a precipitation gradient encompassing much of the state of Oklahoma. (a) East-central Oklahoma, where the average yearly rainfall was 1270 millimeters (mm). (b) Central Oklahoma, where the average yearly rainfall was 970 mm. (c) Western panhandle of Oklahoma, where the average yearly rainfall was 480 mm. (d and e) Four-year averages from 1955 through 2006 of (d) rainfall event intensity and (e) frequency of days with rain for Corfu, Greece, where the average yearly rainfall was 1100 mm (Klein-Tank et al. 2002; data and metadata are available at **http://eca.knmi.nl***). Note that while the frequency of days with rain has consistently and strongly decreased, the intensity of individual rain events has increased sharply over the last eight years at Corfu. These recent precipitation records illustrate similar changes in rainfall regimes in climates as different as midcontinental, temperate, and coastal Mediterranean.***

ecosystems. In mesic ecosystems with soils that are usually moist, larger events would most likely increase the proportion of water that percolates to deep soil layers or is lost to groundwater. More important, the longer periods between rainfall events would lead to greater drying of the soil than is currently experienced.

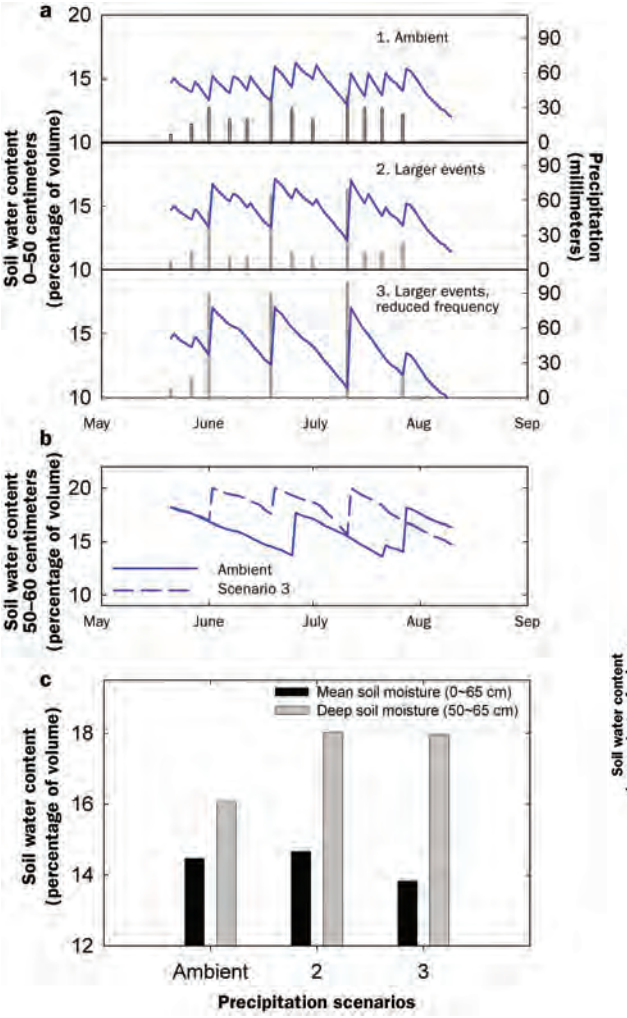

Figure 3. (a) Three precipitation scenarios with identical total precipitation amounts but different distribution patterns (bars): (1) ambient event size and frequency, (2) increased event size with ambient frequency, and (3) increased event size with reduced event frequency. Also shown are the consequences of these scenarios for soil water dynamics simulated by a TECO (terrestrial ecosystem) model (see Weng and Luo 2008) in the upper soil layers (lines in [a], 0–50 centimeters [cm]) and in a deeper soil layer ([b], 50–65 cm). Seasonal mean soil water dynamics in the upper and lower soil layers are shown in (c). Simulations were based on climate and soils data from Washington County, Oklahoma, where a warming experiment is being conducted (Luo et al. 2001). Soil water-holding capacity was set at 20% in this simulation, and a portion of rainfall water was allowed to run off during extreme precipitation events.

This contingent effect of precipitation amount and mean soil water content is illustrated by experimental data from grassland mesocosms (figure 4) showing that regardless of total precipitation amount (high versus low), decreases in event frequency with concomitant increases in event size amplified soil water fluctuations in shallow soil layers. This resulted in soil water stress thresholds (dashed lines in figure 4) being exceeded more often in the mesic system, whereas soil water stress is alleviated more often in the xeric system.

An integrative conceptual framework

Given that soil water is a primary regulator of most ecosystem processes, we used principles from a "soil water bucket" model (Gordon and Famiglietti 2004) to further assess changes in soil water dynamics and responses of ecosystem functions to altered rainfall regimes (figure 5). In this conceptual model, the upper soil compartment (with assumed maximum root

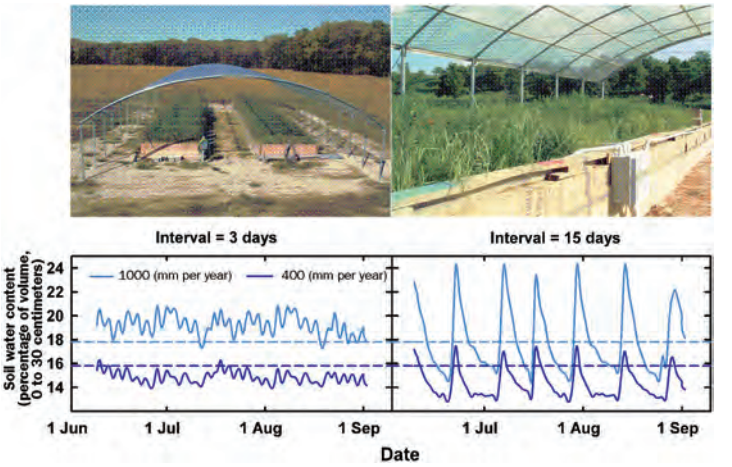

Figure 4. Seasonal dynamics of soil water content from four experimental soil mesocosms within a rainfall manipulation facility (top photographs) at the Konza Prairie Biological Station in northeast Kansas. These mesocosms were planted with native mesic grassland species (top right) and supplied with either high (1000 millimeters [mm]) or low (400 mm) precipitation amounts, with individual rain events occurring regularly at either 3- or 15-day intervals. Dashed lines represent putative soil water stress thresholds for illustrative purposes only. These data demonstrate the greater amplitude in soil water dynamics that occurs when the same amount of rainfall is delivered in larger but less frequent events. As a result of greater soil water variability, we predict that in ecosystems with sufficient precipitation to maintain soil moisture at nonlimiting levels, periods of even higher soil water content caused by larger precipitation events are likely to have little impact on ecosystem processes. Longer intervals between events may lead to greater water stress. The opposite is predicted for ecosystems where soil water is typically limiting. Here, periods of high soil water content caused by larger rain events are likely to be more important for ecosystem processes. Photographs: Philip A. Fay.

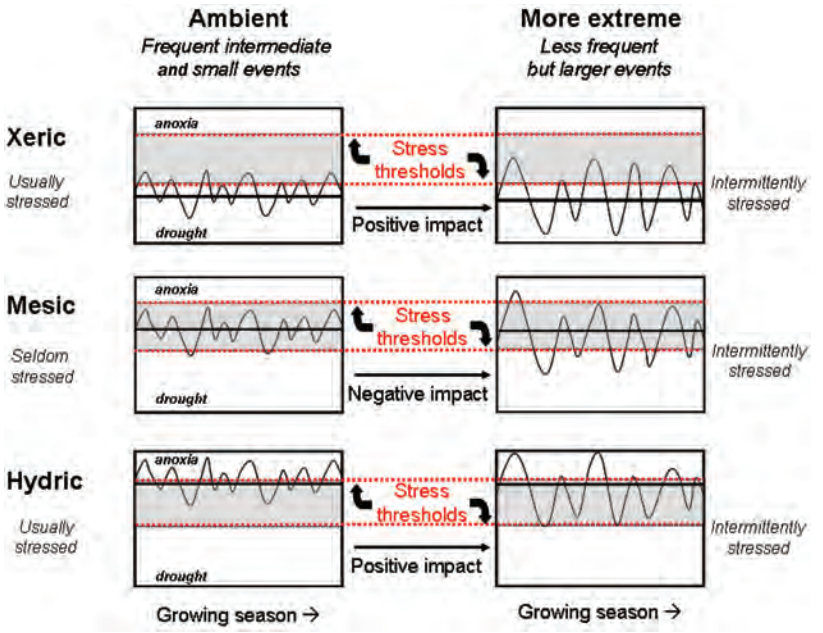

Figure 5. Conceptual depiction of the contingent responses of ecosystems to alterations in soil water dynamics resulting from more extreme precipitation regimes (larger but fewer events). The rectangles represent a single "soil water bucket" in xeric (top), mesic (middle), and hydric (bottom) ecosystems. Within these soil compartments, the solid, heavy black lines represent soil water; the solid, thin black lines represent temporal fluctuations in soil water; the dashed lines represent stress thresholds for water limitation (lower) and anoxia (upper); and the gray shaded area between them denotes soil water levels that do not strongly limit ecological processes. In this idealized comparison, ecosystems exposed to present-day (ambient) precipitation regimes consisting of relatively frequent intermediate and small events experience moderate fluctuations in soil water levels. Thus, mesic systems are seldom stressed, whereas xeric and hydric systems are water stressed much of the time. Soil water fluctuations are amplified by more extreme precipitation patterns (right panels) and are predicted to have opposing effects in mesic systems versus xeric and hydric systems. Larger but fewer precipitation events lead to more frequent and greater water stress in mesic systems, as longer dry intervals decrease soil water levels below stress thresholds more often. In contrast, longer dry intervals reduce stress in typically anoxic hydric systems. Xeric systems may experience less seasonal water stress because large rain events more completely recharge the water bucket, increasing the amount of time when soil water content is above stress thresholds.

density) is represented as a single bucket that varies in the quantity of water held, but has both upper and lower water stress thresholds for ecological processes (Porporato et al. 2004). We define water stress as a significant reduction in the rate of a process (e.g., photosynthesis, growth, nitrogen [N] mineralization, etc.) due to either limited or excess water availability (Osmond et al. 1987, Kramer and Boyer 1995). The general relationship between water content and process rates could take many forms (e.g. linear, quadratic, or sigmoidal; Domec and Gartner 2003), but in general very high and very low levels of soil water will result in minimal process rates, because of either direct water limitation or anoxia (lower and upper dashed lines in figure 5). However, at intermediate soil water levels, there will be a strong relationship between changes in soil water content and rates of plant or ecosystem processes, with pronounced thresholds separating the stressed and unstressed states as soil water content varies (Kramer and Boyer 1995).

In mesic ecosystems, where the soil water bucket is usually moderately full, ambient rainfall regimes characterized by numerous intermediate and small rain inputs will keep soil water levels above drought stress levels much of the time, maintaining most ecosystem processes in an unstressed state (figure 5, middle example). However, in xeric ecosystems in which soil water content is usually low (i.e., a nearly empty bucket system with low precipitation inputs and high evaporative demand), small and intermediate rain events tend to be of insufficient size to increase soil water above stress levels for substantial periods of time, creating conditions of chronic stress for plant and microbial activity (figure 5, upper example).

How might more extreme precipitation regimes influence the proportion of time that ecosystems are in either stressed or unstressed states? Precipitation regimes with fewer but larger events would be expected to amplify fluctuations in soil water content, with the most important consequences in mesic ecosystems being prolonged dry periods between events and an increase in the length and occurrence of drought stress (Porporato et al. 2006). A similar amplification of soil water dynamics would occur in xeric ecosystems, but here larger events would more fully recharge soil water levels by reducing the proportion of water lost to evaporation and permitting soil water to be maintained above drought stress thresholds for longer periods (figure 5). Of course, stress levels in ecosystems vary widely from system to system and process to process, but the general prediction is that an intensification of rainfall regimes will result in xeric ecosystems experiencing more frequent (and potentially longer) periods when plant and soil processes are less stressed, whereas mesic ecosystems may be subject to more frequent and longer periods of soil and plant water stress.

Characterizing ecosystems as mesic or xeric belies the range and complexity of ecosystems and their potential responses to altered precipitation regimes (e.g., Fang et al. 2005). Of particular interest are hydric (wetland) ecosystems that cover vast areas of Earth, particularly at high latitudes.

Here, the more relevant water stress thresholds are due to anoxia rather than low soil water content. In these ecosystems, more extreme rainfall regimes, characterized by larger events and longer intervals between precipitation events, may lead to a reduction in the number of days when soils are anoxic and therefore may increase the rates of some aerobic ecosystem processes (figure 5; Jensen et al. 2003, Emmett et al. 2004). In this case, "drier" conditions may accelerate rather than slow many ecosystem functions, particularly when combined with warmer temperatures. Indeed, the most complex responses will be in those ecosystems in which multiple stress thresholds exist for key processes. This underscores the need to model and conduct coordinated experiments to assess the role of various ecosystem attributes (e.g., soil texture, topography, anoxic soils) in determining the ecological consequences of altered rainfall regimes.

These arguments invoke nonlinear stress responses, with distinct thresholds, to changes in resource (soil water) availability. This assumption has precedent in recent modeling studies that have addressed precipitation controls on soil erosion and ecosystem degradation (Porporato et al. 2004, Williams and Albertson 2006). These models support the idea that increases in precipitation variability can have either positive or negative effects, contingent on the system's typical state above or below critical thresholds. Thus, terrestrial ecosystem responses to increased variability in precipitation inputs are posited to interact with ambient soil water levels (i.e., how much water is typically in the soil moisture "bucket") along precipitation gradients in complex ways.

The conceptual model developed above is heuristic by design and focuses on altered soil water dynamics, and we recognize that many additional factors may mediate ecosystem responses to more extreme precipitation events. For example, soil texture can potentially modify the effect of precipitation patterns on ecosystem water balance, as described by the well-known inverse texture hypothesis (Noy-Meir 1973). In mesic ecosystems, fine-textured soils would be expected to dampen variation in soil water content in response to large rainfall events because of increased water-holding capacity and reduced losses to groundwater. In contrast, fine-textured soils in xeric ecosystems may magnify variation in soil water fluctuations in response to large rainfall events through increased evaporation (due to shallower wetting fronts), which would partially offset greater water-holding capacity. Coarse-textured soils would have the opposite effect in these two systems, potentially increasing soil water availability in xeric systems but decreasing it in mesic systems. The overall effect on soil water content would depend on the balance between these responses and the potential for alterations in runoff if infiltration rates are affected. Root-system morphology may also modify responses to altered soil water dynamics. Ecosystems dominated by plants with deeper roots, or by species that can alter rooting depth in response to precipitation changes, may dampen or partly offset the ecological responses to soil water fluctuations. Although the degree and duration of soil water stress may be modified by variations in soil texture, in other hydrological characteristics (particularly infiltration rate), and in rooting depth, these modifications should not substantively alter the basic principles and conclusions stated above.

Ecological consequences of extreme precipitation patterns

Because more extreme precipitation patterns represent permanent, as opposed to transient, changes in terrestrial ecosystems (e.g., those related to disturbances), resource levels will also be chronically altered—either directly, through soil water dynamics, or indirectly, through the effects of soil water on the availability of other resources, such as N (see below). These chronic alterations in resources—affecting their availability or temporal variability, or both—may change ecosystems over time in a hierarchical manner through physiological responses of the extant biota (particularly the dominant species), population-level adaptation, and altered community structure. For example, modification of resource availability associated with extreme precipitation events may contribute to the alteration of community structure and composition by promoting exotic species invasions. Indeed, one proposed mechanism by which exotic species may invade communities is predicated on resource availability being altered and the native dominant species suppressed (Buckland et al. 2001, Thompson et al. 2001). This combination is more likely to occur in those ecosystems experiencing more extreme precipitation regimes.

In the next sections, we provide some additional predictions focusing on ecosystem and community responses, discussing in greater detail how key ecological processes are likely to be affected by more variable precipitation regimes.

Ecosystem responses

Modifications to the overall water balance and soil water dynamics of ecosystems are anticipated to affect most major ecosystem processes (figure 6). This can occur directly, or indirectly through modifications in community structure. We begin by focusing on carbon (C) dynamics in general and on net primary production (NPP) in particular, given the well-known links between precipitation and this primary driver of ecosystem function (Knapp and Smith 2001). We hypothesize that the occurrence of fewer, larger rainfall events will reduce NPP and respiration (plant and microbial) in more mesic systems (Knapp et al. 2002, Harper et al. 2005) as a result of prolonged periods of low soil water content in the upper soil profile (figure 5). Leaching of dissolved organic C is anticipated to increase in response to greater vertical water movement through the profile. In contrast, intensified rainfall events may increase NPP and respiration in xeric systems compared with ambient precipitation regimes. However, the effect on net ecosystem exchange (NEE) will depend on the relative change in the magnitude of these opposing C fluxes, and would most likely vary in direction as well as magnitude among mesic and xeric ecosystems, making it difficult to predict. Hydric ecosystems are likely to show increases in

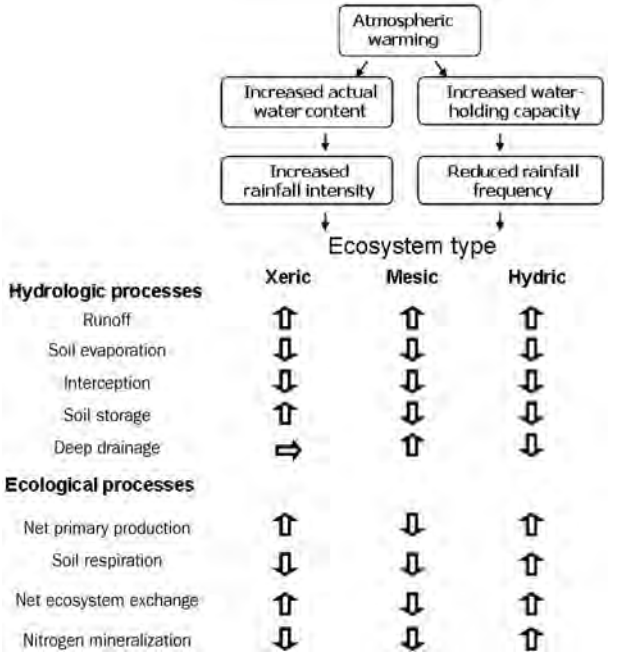

Figure 6. Hypothesized responses of mesic, xeric, and hydric ecosystems to extreme rainfall patterns characterized by fewer, but larger, individual events. We anticipate that extreme rainfall patterns will uniquely modify hydrological and ecological processes contingent on the ambient rainfall regimes of these systems. More extreme rainfall regimes are hypothesized to reduce soil water in mesic systems by increasing runoff and deep drainage, but increase it in xeric systems by increasing percolation depth and decreasing evaporative losses. The responses of hydric systems are predicted to be more similar to those of xeric ecosystems, because stress (anoxic) conditions will be alleviated more frequently. Increased (upward-pointing arrow), decreased (downward-pointing arrow), or neutral (right-pointing arrow) responses relative to ambient rainfall regimes represent hypotheses, because few empirical studies have focused on this aspect of climate change.

ecosystem processes similar to those of xeric ecosystems in response to the occurrence of less frequent rainfall events that alleviate anoxic conditions, although potentially rapid rates of organic matter decomposition, and thus increased respiration, are likely to dominate changes in NEE.

If resource inputs do not change but NPP is altered as predicted, existing spatial patterns in NPP and ecosystem resource-use efficiency may also be altered. For example, present-day geographic and topographic gradients in precipitation amounts, corresponding ecosystem water balance, and NPP have been well documented. But the forecasted increase in intra-annual variability of precipitation may decrease spatial gradients in NPP because of opposing responses in drier (increased NPP) versus wetter (decreased NPP) ecosystems. This may be particularly striking if species composition is altered or if dominant life forms are replaced, further affecting NPP. Similarly, it has recently been established that ecosystem rain-use efficiency (RUE, defined as the ratio of annual NPP to annual precipitation) is determined by differences in the strength of abiotic-biotic interactions in mesic and xeric ecosystems (Huxman et al. 2004b). Our model suggests that RUE may decrease with higher rainfall variability in mesic ecosystems because less soil water will be available to support primary production, resulting in less water loss through plant transpiration. Conversely, RUE should be higher with increased rainfall variability in xeric ecosystems, because deeper percolation of soil water will reduce soil evaporation as the major pathway of water loss and increase the amount of water available for biotic activity.

Microbially mediated processes, including C and N mineralization, gaseous N fluxes, and soil (heterotrophic) CO_2 flux, can respond quickly even to very small rainfall events (e.g., 5 mm; Austin et al. 2004). This responsiveness is a product of the shallow soil depth in which most microbial activity takes place. However, potential evaporation is also very high from shallow soil layers, so the duration of microbial and other biotic activity in response to small events is short-lived as soils rapidly dry (Belnap et al. 2004). Further, C and N mineralization can be enhanced as a result of repeated drying and rewetting cycles (Fierer and Schimel 2002, Miller et al. 2005). Therefore, reductions in the frequency of rainfall events could decrease microbial activity and biogeochemical cycling in the upper soil profile, independent of any effects on NPP, potentially decoupling water and nutrient availability in both mesic and xeric ecosystems (e.g., Seastedt and Knapp 1993, Knapp et al. 2002). Conversely, in hydric ecosystems, extended dry periods may increase microbial activity, leading to increased soil respiration (Jensen et al. 2003) and N mineralization (Emmett et al. 2004). Of course, microbial-mediated transformations that require anoxic conditions (e.g., denitrification, methanogenesis) would decrease concurrently.

Plant and community responses

Individual plant species and functional groups have many adaptive avenues to cope with varied amounts of and temporal fluctuations in water availability, as evidenced by the occurrence of distinct life-history strategies and patterns of species replacement along precipitation gradients (e.g., Noy-Meir 1973). Adaptation to water limitation frequently involves a trade-off with plant productivity, as plant stature and canopy leaf area are minimized to reduce transpirational loss and plant water stress (Kramer and Boyer 1995). Such adaptations to prevailing precipitation regimes establish the potential for intensified precipitation regimes to alter patterns of resource availability and acquisition, influence competitive interactions, and lead to community change.

This is especially relevant to the architecture, distribution, and persistence of root systems, because these sytems determine the ability of plants to mediate variations in soil water availability. Root systems generally become shallower, but more laterally extensive, in hot, dry climates compared with

wet, cool climates (Schenk and Jackson 2002). Consequently, maximum rooting depth generally decreases with increasing aridity, and a greater proportion of the total root system occurs in shallower soil layers. On the basis of these broadscale rooting patterns, we predict that an increase in large rainfall events would favor the growth of more deeply rooted species in both mesic and xeric ecosystems, but for different reasons. In xeric ecosystems, greater soil water storage at depths where evaporation is less likely would promote deeper rooting strategies, whereas in mesic ecosystems, frequent drying of upper soil layers would negatively affect shallow-rooted herbaceous species that currently depend on a greater frequency of smaller rainfall events (Schwinning and Ehleringer 2001, Huxman et al. 2004a).

More severe drought intervals interspersed between infrequent, large rainfall events may produce pulses in soil nutrient availability, because available soil N increases during drought periods, when plant absorption is suppressed to a greater extent than N mineralization (Seastedt and Knapp 1993, Augustine and McNaughton 2006, Yahdjian et al. 2006). Consequently, the availability of soil water will coincide with high N levels during subsequent rainfall events, resulting in altered patterns of resource availability, with plant access determined by the species that can recover most rapidly from drought (Gebauer and Ehleringer 2000). The ability to adjust to these potential modifications in spatial and temporal patterns of resource availability may vary among species, potentially altering competitive interactions and the conditions that determine recruitment, plant establishment, and invasion (Lloret et al. 2004, Peñuelas et al. 2004). This could be particularly dramatic in those wetlands that may become vulnerable to invasion by "upland" species. As noted above, alterations in competitive outcomes and susceptibility to invasion are predicted to lead to shifts in community composition and concurrent impacts on ecosystem processes.

Summary, research needs, and future perspectives

Our intent in this article has been to provide testable predictions of how ecological systems may be affected by forecasted modifications to intra-annual precipitation patterns arising from the amplification of the global hydrological cycle. Despite the global-scale forecast of increases in precipitation extremes and variability, the potential ecological consequences of these changes have received minor attention compared with other changes, notably elevated atmospheric CO_2 and global warming. The key finding of our assessment is that ecological responses to more extreme precipitation regimes will be contingent on ambient precipitation amounts, so that important ecological processes in xeric, mesic, and hydric ecosystems can be expected to respond uniquely (figure 6) to this pervasive aspect of climate change. This, in turn, will lead to unique and perhaps surprising interactions with associated global change drivers (Fang et al. 2005, Porporato et al. 2006), with cascading effects through all hierarchical levels of ecological processes.

Additional research is needed to test these predictions and fill critical knowledge gaps in our understanding of ecological responses to more extreme rainfall regimes. We suggest that research programs focus on the need for (a) enhanced documentation and projection of intra-annual precipitation patterns at local, regional, and global scales; (b) greater insight into the direct effects of these modified rainfall delivery patterns on ecosystem structure and function, as well as interactions with other global change drivers; and (c) greater understanding of how modifying the dynamics of the ecosystem water balance may influence various biotic groups, with special emphasis on their responses to increased variability in soil water availability and stress levels. There is a clear need for field experimentation combined with systems modeling to address this understudied component of climate change (Weltzin et al. 2003, Jentsch et al. 2007). Key to these experiments is greater knowledge of exactly how precipitation regimes are changing and how much they can be expected to change in the future. The potential exists to rapidly implement altered rainfall regime experiments in a variety of ecosystems, using infrastructure that has been recently developed for rainfall manipulation experiments (Fay et al. 2003, Beier et al. 2004). These types of studies will be critical for assessing the impacts of climate change on the provisioning of key ecosystem services (Weltzin et al. 2003).

Finally, a deeper understanding of the ecological consequences of more extreme intra-annual precipitation patterns will also strengthen our knowledge of vegetation-climate relationships and feedbacks, and will inform emerging Earth system models so that they can more effectively assess this component of climate change (Cox et al. 2000, Betts et al. 2004). The importance of more extreme precipitation patterns relative to other global change drivers, such as elevated atmospheric CO_2 and warming, is unknown; but through comparisons of GCM-based predictions of vegetation responses with these drivers independently and interactively, we can improve forecasts of the future of ecological systems.

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