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PULSE EVENTS AND ARID ECOSYSTEMS

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Hierarchy of responses to resource pulses in arid and semi-arid ecosystems

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Abstract In arid/semi-arid ecosystems, biological resources, such as water, soil nutrients, and plant biomass, typically go through periods of high and low abundance. Short periods of high resource abundance are usually triggered by rainfall events, which, despite of the overall scarcity of rain, can saturate the resource demand of some biological processes for a time. This review develops the idea that there exists a hierarchy of soil moisture pulse events with a corresponding hierarchy of ecological responses, such that small pulses only trigger a small number of relatively minor ecological events, and larger pulses trigger a more inclusive set and some larger ecological events. This framework hinges on the observation that many biological state changes, where organisms transition from a state of lower to higher physiological activity, require a minimal triggering event size. Response thresholds are often determined by the ability of organisms to utilize soil moisture pulses of different infiltration depth or duration. For example, brief, shallow pulses can only affect surface dwelling organisms with fast response times and high tolerance for low resource levels, such as some species of the soil micro-fauna and -flora, while it takes more water and deeper infiltration to affect the physiology, growth or reproduction of higher plants. This review first discusses how precipitation, climate and site factors translate into soil moisture pulses of varying magnitude and duration. Next, the idea of the response hierarchy for ecosystem processes is developed, followed by an exploration of the possible evolutionary background for the existence of response thresholds to resource pulses. The review concludes with an outlook on global change: does the hierarchical view of precipitation effects in ecosystems provide new perspectives on the future of arid/semiarid lands?

Keywords Climate change · Ecosystem structure · Precipitation thresholds · Precipitation variability · Rainfall size

Introduction

In arid/semi-arid ecosystems, biological resources, such as water, soil nutrients, and plant biomass, typically go through periods of high and low abundance. Short periods of high resource abundance are triggered by rainfall events, which, despite of the overall scarcity of rain, can saturate the resource demand of some biological processes for some time. Rainfall input to a dry soil triggers a cascade of biogeochemical and biological transformations, which can range from the fast release of nitrogen by soil microbes residing at the soil surface within hours of the event (Cui and Caldwell 1997) to the demographic responses of primary producers and consumers that unfold over years (Ostfeld and Keesing 2000). This paper is aimed at developing a general framework for organizing the multiple responses of organisms and ecosystem processes in arid/semi-arid ecosystems to precipitation.

At the core of this review are two organizing principles; first, that precipitation pulses and their effects on ecosystems can be rationalized as discrete events. This idea goes back to Westoby (1972) and Noy-Meir (1973), who recognized the significance of discontinuous, highly variable and largely unpredictable rainfall inputs in arid ecosystems. Departing from the conventional approach of modeling ecosystem processes as continuous and regulated by smooth inflow/outflow relationships, the alternative model suggested a quasi-instantaneous recharge of ecosystem reserves followed by periods of slow resource drain. This "pulse-reserve" paradigm, revisited by Reynolds et al. (2004) in this issue, was intuitively appealing, because it explained to some extent the long-term stability

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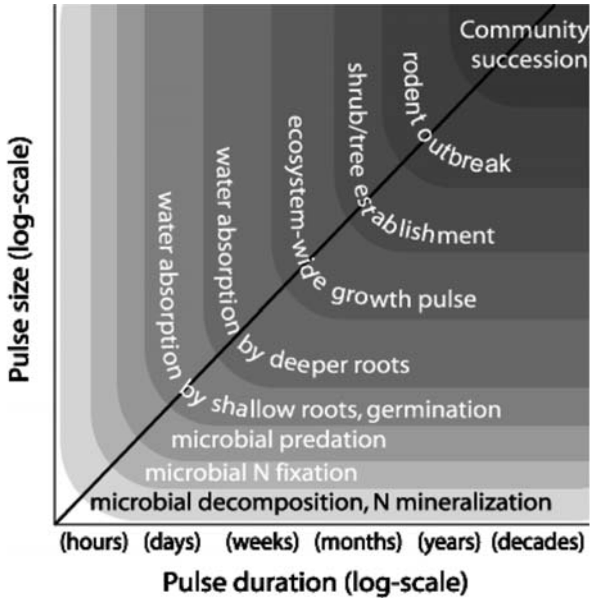

Fig. 1 An illustration of the ecological response hierarchy to soil moisture pulses of variable size and duration. An approximately linear relationship between size and duration on a log scale is indicated by the *solid line*. Small-short pulses can activate only the physiological rates of soil microbes that live at the soil surface. As pulse events become larger and longer, the physiological responses of larger organisms are also triggered, first of soil invertebrates, then of higher plants. Water absorption by shallow roots is triggered by smaller rainfall events than absorption by deeper roots. Similarly, germination will usually require a smaller minimal pulse size than establishment, especially of woody plants. Rainfall clusters, producing pulse events on the order of weeks to months add up to a wet season, which usually triggers ecosystem-wide vegetation growth. If the associated productivity peak is large enough, it can trigger an outbreak of herbivores or granivores, for example, small rodents. Wet periods spanning several years may trigger large-scale reorganizations of entire communities

of deserts in the face of extreme short-term variability of resource inputs.

The second, and more novel, organizing principle is that precipitation pulse patterns and their effects on ecosystems can be organized in a hierarchical manner. By this, we mean that there is a relationship between the magnitude of a pulse event, the magnitude and extent of the ecological responses it triggers, and the time scale over which these responses unfold (Fig. 1). This hierarchical view is intricately linked to the notion of response thresholds, defined as a minimal event size below which a specific ecological process is not triggered. A nested hierarchy will arise when small pulses only trigger a small number of relatively minor ecological events, and larger pulses trigger a more inclusive set and some larger ecological events. For example, a summer rain event of 2 mm may only stimulate the activity of soil microbes, leading to an increase in soil nitrate (Cui and Caldwell 1997), and a brief decomposition pulse (Austin et al. 2004). Summer rain events of at least 3 mm are usually necessary to elevate rates of carbon fixation in some higher plants (Schwinning et al. 2003), or for biological crusts to have a net carbon gain (Belnap et al. 2004, this issue) while events of at least 25 mm may be required to trigger the germination of many desert plants (Beatley 1974).

A central assumption throughout this review is the existence of a quantity we called "pulse size". This is not simply the equivalent of precipitation amount, but a complex composite of several environmental and ecological conditions accompanying precipitation. We begin our review by clarifying how precipitation, climate and site factors translate into soil moisture pulses of varying magnitudes. We then develop the idea of the response hierarchy for ecosystem processes and go on to explore the possible evolutionary background for the existence of response thresholds to resource pulses. We conclude with an outlook on climate change: does a hierarchical organization of ecosystem responses to pulse events help us develop new perspectives on the potential consequences of precipitation change in arid/semiarid ecosystems?

Characterization of soil moisture pulse events

Precipitation applied to a dry soil surface creates a pulse of soil moisture. From a biological point of view, the two most pertinent aspects of a soil moisture pulse are (a) the depth to which soil water potentials are elevated to levels that promote biological activities (pulse depth), and (b) the length of time over which water potentials remain at biologically relevant levels (pulse duration). Both characteristics describe the quantity "pulse size", i.e. larger pulse events usually affect greater soil volumes and last longer. This simple definition, however, already illustrates that precipitation amount is only one of many factors that can affect pulse characteristics. Soil type, climate, vegetation characteristics and the physiological and morphological characteristics of pulse users are also important.

Water applied to a dry soil infiltrates initially by saturating consecutive soil layers. Thus, for a given soil type, there is a nearly linear relationship between the initial infiltration depth and the amount of water applied to dry soil. Infiltration depth per unit of water applied varies with the saturated volumetric water content of soils, which ranges between 0.1 (sand) and 0.4 (clay) m^3m^{-3}, and the initial soil water content. Consequently, in a dry soil, initial infiltration ranges between 1 and 0.24 cm per mm of water applied. There are many mechanisms that can cause horizontal variation in infiltration depths, for example, runoff or run-on, which occur when the rate of water application exceeds infiltration capacity. Canopy interception and stem flow can also create spatial variation in infiltration depth. Once infiltrated, water continues to redistribute more slowly by diffusion or hydraulic redistribution. Both mechanisms involve the movement of along water potential gradients, smoothening steep vertical and horizontal gradients in soil water potential and increasing pulse depth (Ryel et al. 2004, this issue).

Pulse depth is ecologically important in a number of ways, including the partitioning of precipitation between transpiration and soil evaporation. Small rainfall events wet only the uppermost cm of the soil, where a large fraction of soil moisture is lost by direct evaporation, due to high temperatures and low root densities. With increasing soil depth, evaporation and vapor diffusion rates decline while rates of plant water uptake increase. Thus, the deeper the pulse depth, the larger the fraction of precipitation leaving the soil via transpiration and contributing to the primary productivity of higher plants.

While pulse depth is strongly controlled by the interactions of soil characteristics and precipitation amount, pulse duration also depends on climate and vegetation characteristics. In a given climate and vegetation type, the more water applied and the greater the pulse depth, the longer the pulse duration. For example, on a sandy surface on the Colorado Plateau, every millimeter applied approximately added another day to pulse duration for infiltration amounts between 2 and 20 mm (Schwinning et al. 2003). In an example from the North American shortgrass steppe, a 5-mm event in mid-summer, which is close to the median event size for many dry regions, increased soil water potential in the upper 5 cm of the profile for a 2-day period (Sala and Lauenroth 1982). At the other end of the spectrum, a very large experimental rainfall event wetted the profile to 100 cm depth and raised the soil water status for several weeks (Sala et al. 1981). These quantitative relationships vary greatly with season. Since evaporative demand is much lower under cooler and often more humid winter conditions, soil moisture pulses in winter last much longer than in summer. In addition, variation in vegetation type or density, giving rise to different rates of evapotranspiration, will affect pulse length.

The beginning and end of a pulse event is ultimately defined by the ability of pulse users to initiate and maintain higher metabolic rates. Therefore, pulse events are likely to have different durations for different users. For surface dwelling organisms, pulse events will usually be short, limited by the water status of the immediate soil surface, while for higher plants, a pulse event ends when soil water potentials throughout the rooted portion of the infiltration depth drop below some plant-extractable level. Even the onset of the pulse event may be different for different organisms, as the availability of water is only a necessary but not sufficient prerequisite of physiological activity. For example, photoperiod or temperature, rather than water availability, are likely to constrain the onset of physiological activity in a cold desert spring.

So far we assumed that pulse events are neatly separated in time. However, when rainfall events are frequent or evapotranspiration rates are low, soil moisture can accumulate between precipitation events leading to greater infiltration depths than could be generated by any isolated precipitation event.

In effect, the accumulation of water between precipitation events leads to the creation of “higher-order” pulse events, with greater infiltration depth and longer duration. The most common higher order pulse event is the seasonal pulse, often generated by a winter rainy season, or a particularly intense summer rainy season. Either way, higher order pulses are generated when during some period of time water inputs exceed evapotranspiration. How long can such time periods last? Due to feedbacks between vegetation growth and precipitation inputs, we would expect soil moisture in arid and semiarid regions to be depleted completely at least once a year. However, it is theoretically possible that soil moisture at depth is carried over from one year to the next, for example after a strong El Niño year or after fire, both situations where annual water input may exceed the vegetation’s annual uptake capacity. This would give rise to pulses of at least annual length. For shallow-rooted plants, this pulse may be indistinguishable from a seasonal pulse, but deeper-rooted plants may benefit from continually elevated soil water potentials at depth. Similarly, a run of wet years could cause pulses of decadal duration, recharging even deeper soil layers and potentially affecting patterns of deep root proliferation.

Because soil moisture pulses can span vastly different time scales, potentially from minutes to decades, various sorts of pulses usually overlap. For example, the tail end of a winter recharge pulse, characterized by dry shallow soil, but residual soil water at depth, may coincide with a short-lived, shallow spring pulse. A shallow rooted plant species may respond only to the short-lived, shallow pulse, while an exclusively deep-rooted species may respond only to the seasonal pulse. In all likelihood, there will be species responding to pulses at both time scales, and the spring pulse could be said to end when water use drops back to pre- (spring) pulse levels.

The precipitation regimes of arid and semiarid regions

Relatively small rainfall events between 2 and 5 mm are the most common rainfall events in arid/semiarid ecosystems (Loik et al. 2004, this issue), suggesting that most summer pulse events are brief, and that seasonal pulses are most likely to be generated in regions with cold wet winters.

In the North American shortgrass steppe, a region receiving predominantly summer rain, precipitation events of 5 mm or less accounted for 25% of total rainfall and 70% of the events (Sala and Lauenroth 1982). Events of 10 mm or less comprised 41% of growing season precipitation and 83% of the events. Similar patterns occur in quite different arid and semiarid regions across the globe, from the cold and warm deserts of Utah and Arizona to the cold deserts of Patagonia (Smith and Schreiber 1974; Golluscio et al. 1998; Schwinning et al. 2002).

Small rainfall events are not only quite frequent in arid and semiarid ecosystems but their contribution to total precipitation tends to be quite constant among years. The amount of water received in the form of small events varies very little, whereas the amount of water in large events varies markedly among years. For example, in the cold Patagonian steppe, the amount of water received in events of 5 mm or less remained practically constant

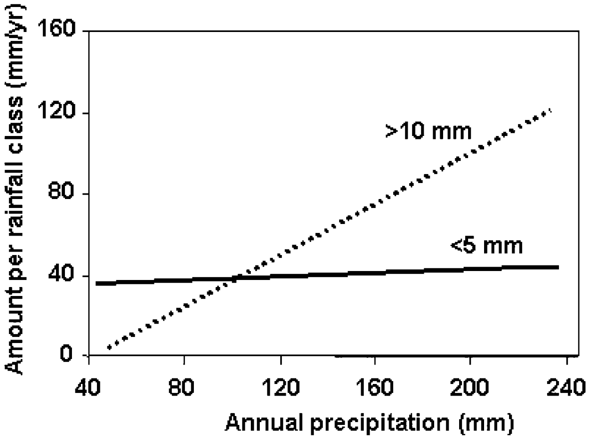

Fig. 2 The contribution of small rainfall events to total precipitation shows very little variability across years in contrast with large events that account for most of the interannual variability in total precipitation. The amount of water received in rainfall events of 5 mm or less (*solid line*) and the amount of water received in events of 10 mm or more (*dashed line*) as a function of annual total precipitation for different years during a 22-year period in the Patagonian steppe where annual average precipitation is 137 mm (redrawn from Golluscio et al. 1998)

throughout a 22-year period (Fig. 2; Golluscio et al. 1998). In contrast, the amount of water in events of 10 mm or more ranged from 20 to 170 mm per year for this site where annual mean precipitation is 137 mm. Similar relationships were found in comparable ecosystems in other parts of the world (e.g. see Loik et al. 2004, this issue; Fravolini et al. 2003). This suggests that dry and wet years are characterized by different event size distributions with potential effects, as we will show later, not just on the overall rates of ecosystem fluxes, but also in the relative magnitudes of different ecosystem component rates. Since the occurrence of large rainfall events is quite variable among years, this could be a major source of among-year variability in ecosystem functioning.

Ecological pulse responses

We suggest that the hierarchy of pulse events, ranging from brief pulses that only wet the immediate soil surface to pulses of potentially decadal length carried over in the moisture status of deeper soil regions, has a corresponding hierarchy of ecological responses that is determined by the ability of organisms to utilize soil moisture pulses of different durations, infiltration depths, and soil water potentials.

In matching pulse events with ecosystem responses, a few general criteria may apply. Species probably have restricted sensitivities for pulse size and duration, in essence, they filter the pulse signals in different ways. Brief pulses of a few hours probably only affect organisms with fast response times, such as species of the surface dwelling soil micro-fauna, while it takes longer pulse periods and more water to affect the physiology, growth or reproduction of larger, slower growing organisms, such as higher plants or small mammals (Fig. 1). Within higher plants, rooting depth may further constrain species responses. For example, shallow-rooted plant species may not respond differentially to large and small rainfall pulses because it tracks only the soil moisture dynamics in the shallow soil, which would be approximately the same for the two pulses. In contrast, species with deep and shallow roots would distinguish between a small and large pulse event because the species would continue to take up water from the deeper soil after the large event, at a time when shallow soil water is already depleted. Variation in tolerance to soil water potentials may additionally modify the perceived pulse duration among morphologically similar species. Species differences in sensitivity to factors other than water, for example to temperature, or the duration of the preceding drought period, can create additional “signal-filtering” mechanisms that make species more or less likely to respond to a soil moisture pulse at a given time (see also Chesson et al. 2004, this issue). In summary, precipitation packaging and timing may be of the utmost importance in determining the relationship between precipitation and ecosystem functioning. Below, we elaborate on these ideas through some specific examples.

We begin the discussion with an example that highlights how pulses of soil moisture may interact with soil food webs. Since the short-term responses of soil organisms to rainfall events have not been studied in vivo, we can only infer the likely responses based on known soil drying patterns, in this example, associated with a large recharge event observed in the shortgrass steppe (Fig. 3A) and the known responses of microorganisms to soil water potentials (Fig. 3B). The result is an estimate of relative changes in the activities of the different soil microorganisms during a drying cycle (Fig. 3C). Freckman (1986) described the response of a group of four soil microorganisms to changes in soil water potential. In this comparison, a fungivorous nematode was most sensitive to water potential. Its growth activity was halted at a soil water potential as high as −1 MPa (Fig. 3B). In contrast, the fungus *Fusarium roseum* was the most resistant microorganism and still showed 80% of maximum growth activity at −2 MPa of soil water potential. Given the soil drying dynamics depicted in Fig. 3A, activity of all four studied microorganisms would be sustained for the first 12 days of the drying cycle. After day 12, the activity of the fungivorous nematode would collapse while the activity of the fungi and bacteria would continue at a level higher than 50% of maximum growth rate. At day 20 of the drying cycle, the activity of bacteria would stop, while fungi would maintain a high level of activity. The activity of *G. graminis* would collapse on day 25 while *F. roseum* would still be active on day 30.

Superimposed on these responses of relative activity to soil water potential would be the feedback responses to changing levels of substrate and prey availability, which would potentially lead to quite complex trophic web dynamics, associated with just one pulse of soil moisture. In this example, the top levels of the trophic pyramid

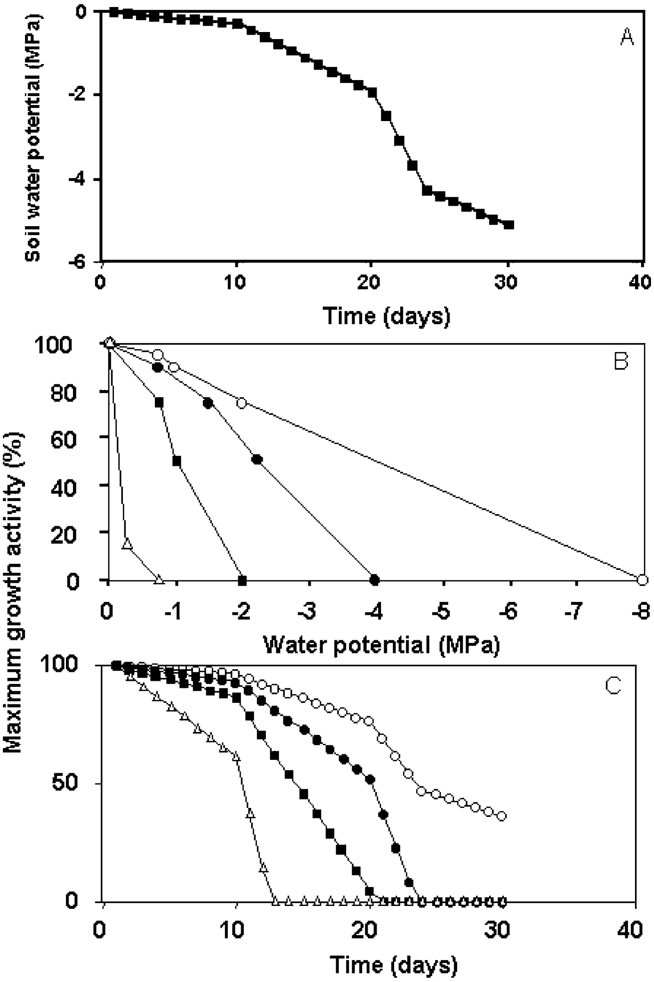

Fig. 3A–C Changes in soil water potential and the consequences on the activity of different soil microorganisms. **A** Changes in soil water potential in the 0–5 cm layer throughout a drying cycle that started with the entire profile wet, in the North American shortgrass steppe (Sala et al. 1981). **B** Effects of soil water potential on the activity of different soil microorganisms expressed as percentage of maximum growth activity, for fungivorous nematode (*triangles*), gram-bacteria (*squares*), *G. graminis* (*filled circles*), *F. roseum* (*open circles*). Redrawn from Freckman (1986). **C** Changes in growth activity of the same four soil microorganisms of *panel B* throughout the drying cycle depicted in *panel A*

halted their activities first while lower levels remained active for weeks, suggesting that lower trophic levels might recover from initially high levels of predation. However, the net result of such trophic interactions on carbon and nitrogen fluxes and stores may be quite sensitive to the exact course of soil water recharge and depletion (see also Austin et al. 2004, this issue). The implication is that changes in the patterns of rainfall variability, which would modify the frequency of time spent at various levels of soil water potentials, could alter the very structure of the soil trophic web, leading to profound changes in overall ecosystem functioning.

Plants respond differently than microorganisms to changes in soil water availability in part because they integrate available water resources over larger fractions of the soil profile. Rooting depth determines the portion of the soil profile from which plants absorb water and it varies among plant species and plant functional groups (Jackson et al. 1996; Schenk and Jackson 2002). For the pulse event described in Fig. 3, the dominant grass species *Bouteloua gracilis*, which absorbed water down to 90 cm in the soil profile, showed ecophysiological changes that were in sharp contrast with those of most soil microorganisms (Sala et al. 1982; compare Figs. 3C, 4). Leaf water potential and leaf conductance, both major factors in determining plant carbon fixation and growth rates, showed that the activity of the dominant plant species remained at the maximum rate longer than any of the soil microorganisms described in Fig. 3C. Such extended periods of activity are not expected of soil microorganisms, because they are concentrated in the upper soil layers, which dry out first. *B. gracilis* also experienced lags in response to the soil moisture pulse (Fig. 4), which greatly exceed the lag times expected for soil microorganisms. In this example, where rainfall followed a prolonged drought, leaf conductance reached maximum only after 10 days. Single rainfall events can trigger increases in photosynthetic rates in some, but not all plant species. While Sala and Lauenroth (1982) observed that the C_4 grass *B. gracilis* increased leaf water status within hours of a 5 mm rain event, deeper-rooted plants may not have been significantly affected by this event. On the Colorado Plateau, the C_4 grass *Hilaria jamesii* was also found to be very responsive to small rainfall events, while it took larger events to produce a slight physiological effect in a root-dimorphic shrub species. In the same study, a long-lived deep-rooted shrub showed no significant physiological responses to summer rainfall events of up to 20 mm (Schwinning et al. 2003).

One would expect that elevated rates of carbon assimilation in plants eventually translate into growth, either of new vegetative structural biomass, or of flowers and seeds. However, not all episodes of elevated carbon gain trigger new growth. Most desert plants have distinct periods of active growth, coinciding with the season of

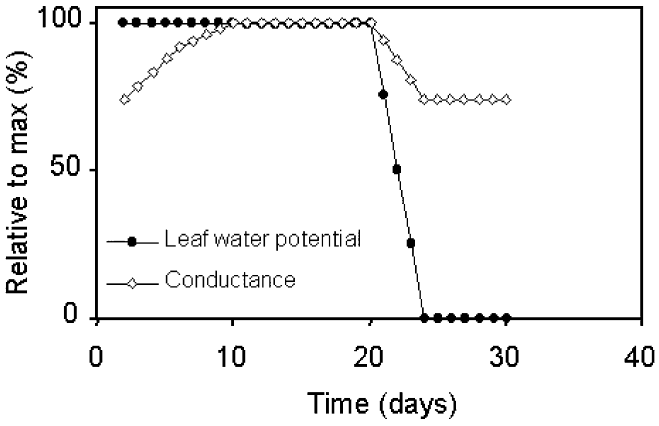

Fig. 4 Relative changes in leaf water potential (*circles*) and leaf conductance (*squares*) for the dominant grass species of North American shortgrass steppe, *Bouteloua gracilis* throughout the drying cycle described in (Sala et al. 1981) and Fig. 2. Observed plant responses as reported by Sala et al. (1982)

predictably greatest soil water recharge. For example, many shrubs and grasses of the Colorado Plateau cold desert do not grow in summer, apparently independently of the amount of summer rain received. In one experiment, a difference of 170 mm in precipitation between plants growing in the open or under rainout shelters did not produce a significant difference in vegetative growth either during summer or the following spring (Schwinning, personal observation). In contrast, drought-deciduous shrubs of warm deserts are often capable of producing two leaf cohorts, in spring and summer, in response to rain (Smith et al. 1997), and some shrubs, both evergreen (e.g., *Larrea tridendata*) and drought-deciduous (e.g., *Encelia farinosa*) can produce a flush of leaf and root growth at nearly any time of year, provided adequate soil moisture (Comstock and Ehleringer 1986; Reynolds et al. 1999). In every case, a minimal pulse size may be required to trigger growth responses, and these would typically exceed the precipitation pulse size required to elevate rates of photosynthesis and may require multiple rain events in short succession (see also Ogle and Reynolds 2004, this issue). However, the comparison between the summer rain response of species from the Colorado Plateau cold desert and the North American warm deserts suggest that there may be very large species differences in exactly how much rain is needed to trigger growth at a given time of year.

As with the production of leaves, roots, flowers, and seeds, seed germination is typically triggered by rainfall events that must exceed a minimal size. Triggering rainfall events have been reported between <10 mm to >25 mm for particular species (Beatley 1974; Bowers 1996). However, additional temperature or scarification requirements, seed age, or other environmental cues are often required, so that precipitation can trigger the germination of different sets of species in any given year.

Animals, perhaps more so than plants, have distinct requirements for meeting reproductive thresholds (Silvertown 1991). Especially if reproduction requires significant accessory expenditures, such as brooding, some animals in the population may forfeit reproduction in a year with low resource availability (Bull and Shine 1977). Primary consumers that reproduce once a year, i.e. most vertebrates in arid/semiarid regions may be particularly sensitive to seasonal soil moisture pulses, which strongly affect annual primary productivity and/or seed output. Reviewed in detail by Ostfeld and Keesing (2000), a year of very high leaf or seed production often has positive effects on the birth rates of primary consumers, such as granivorous rodents, which then may peak in population density several months to one year after the pulse in plant biomass. The link between rodent outbreaks and particularly long and wet rainy seasons is well documented (Madsen and Shine 1999), and rodent population cycles have been linked to the ENSO phenomenon (Jaksic and Lima 2003). In turn, a rodent outbreak can increase the birth rates of rodent consumers, such as owls and foxes, with their population densities reaching a peak 2 years after the original soil moisture pulse event. Two years after the event, however, the original pulse of plant biomass would be largely depleted, and mortality rates among primary consumers would be high due to the now high rates of predation. As a consequence, primary consumer densities would crash, followed eventually by a crash in the secondary consumers, which would die of starvation.

Prolonged wet periods of very low frequency, such as those resulting from decadal weather anomalies (see review by Loik et al. 2004, this volume) may result not only in transient changes in the abundances of plant species and their consumers, but may have long-lasting effects on community structure. In this context, one could envision the “structure” of a community as an entity with longer response times than any of its member species, prone to respond only to multi-annual weather trends rather than to year-to-year variability, and also prone to threshold responses (Vandermeer and Yodzis 1999). An example of structural change in communities and ecosystem function has been observed in the southwestern United States, where a multi-decadal increase in winter precipitation has resulted in a 3-fold increase in shrub density (Brown et al. 1997). These changes in the abundance of different plant species rippled throughout most of the food web affecting the species composition of many groups of primary consumers from rodents to ants. Several major species of rodents and ants went locally extinct while other rare species increased their presence and some previously absent species colonized. Together with possible biogeochemical threshold effects (Schlesinger and Pilmanis 1998), or the interference by exotic invaders (Chapin et al. 1998), a return to average climate conditions may in this case not be followed by quick return to the previous community structure.

Following through these examples of ecosystems and ecological pulse responses from the smallest to the largest pulse events, it becomes clear that pulse-response relationships may seldom be smooth, and that response thresholds and triggering event sizes are a recurrent theme across species and levels of ecological organization. In the next section we offer an explanation of why response thresholds may be common in species dependent on fluctuating resource supply, based on evolutionary considerations, involving adaptations to minimize the cost to benefit ratio of resource pulse utilization.

Evolutionary aspects of pulse utilization in plants

We discuss evolutionary aspects of pulse utilization, using the example of higher plants. We note however, that the approach we take here can be generalized to any consumer of pulsed resource, and could in principle apply to organisms both faster in exploiting resource pulses (such as soil microorganisms) and slower (such as vertebrate consumers).

Small to large rainfall events, event clusters, rainy seasons or rainy decades all contribute water to different locations in the soil profile, where water is removed at different rates and returns in different intervals. These differences in precipitation patterns may result in different selection pressures for different species, and tradeoffs associated with the utilization of water at different depths, average soil water potentials, and recharge frequencies may lead to the establishment of distinct niches, such that a plant specialized on the use of one kind of precipitation pattern may be less capable of utilizing another. Functionally, these strategies are in many ways equivalent to the foraging strategies of predators (e.g. Krebs and Davies 1993). For example, predators may be faced with a choice between abundant prey species with low nutritional value and rare prey species of high value. Co-evolution between predators is thought to generate divergent foraging strategies, so that eventually one predator species adapts to maximize the reward-to-effort ratio for the low-value prey type, while the other species develops adaptations to maximize use of the high value prey type. By analogy, desert plants can also be expected to maximize the effort (e.g. allocation to non-photosynthetic tissues) to reward (carbon assimilation rate) ratio of pulse use, with different species potentially specializing on different types of pulse events (Schwinning and Ehleringer 2001). The ways in which differences in gross morphology, physiology and phenology can give rise to contrasting overall pulse use strategies is reviewed elsewhere (e.g. Ogle and Reynolds 2004; Reynolds et al. 2004; Chesson et al. 2004, this issue).

Plant adaptations to low water availability have been investigated for nearly 100 years. However, separate from the question of how plants adapt to different average water availability is the question of how plants adapt to variability and uncertainty in pulse size and timing. Desert plants are quite capable of responding to single rain events with a range of physiological and phenological activities, but not all plants do so under all circumstances. To explain this diversity of threshold responses, we develop here the framework for a cost-benefit analysis for pulse responses. The approach was first considered by Lauenroth et al. (1987) and recently elaborated upon by Schwinning et al. (2003). The underlying idea is that morphological and physiological tradeoffs prevent plants from being optimally adapted to both dry and wet conditions (Schwinning and Ehleringer 2001). Thus, when a dry period is interrupted by a sudden rainfall event, plants are usually not in an optimal state to utilize the pulse of soil moisture. Modification of their physiological state, for example, the synthesis of more photosynthetic enzyme, or the growth of new leaves or roots, could however improve their pulse use. The question is, what type of physiological or morphological adjustments would maximize net carbon gain in a given situation?

We present a conceptual model that is built upon the simple premise that the net carbon gain attributable to a pulse, i.e. the difference in the carbon gain of plants with and without pulse exposure during the same interval, is positively correlated with pulse duration, thus pulse size (Fig. 5). Different line styles indicate the relationships between net carbon gain and pulse duration for plants that adjust to pulse events in different ways. For example, at response level 0, the plant does not modify any physiological function after the initial rainfall event. While this plant still has some small carbon gain due to the pulse event, its potential carbon gain could be greater, as shown by the broken lines. For example, the plant could synthesize photosynthetic enzymes to increase photosynthetic efficiency, grow rain roots to support higher rates of gas exchange, or grow more leaves to increase whole plant photosynthetic rates. All of these responses would eventually increase pulse use efficiency, i.e. the slope of the net carbon gain versus pulse duration function. However, these responses first result in carbon losses associated with the respiratory cost of enzyme synthesis or growth. These "layout costs", which are the larger the more elaborate the response, are expressed by downward shifts in the y-intercept in the net carbon gain function. Additionally, we assume that more elaborate responses take increasingly more time to express; while the synthesis of more enzyme may take a few hours, the growth of new roots could take a day, and the growth of new leaves several days. These "lag-times" are expressed in the distance on the x-axis between the origin and when the net carbon gain function changes slope. Both layout costs and lag times may result in a negative carbon balance if pulse duration is short, but if pulse duration crosses a certain threshold, more carbon can be gained than if plants had done nothing to adjust to the soil moisture pulse.

This conceptual model suggests that, in optimally adapted organisms, different event sizes should trigger different pulse responses. More elaborate actions should be taken by plants to improve carbon gain, as pulses

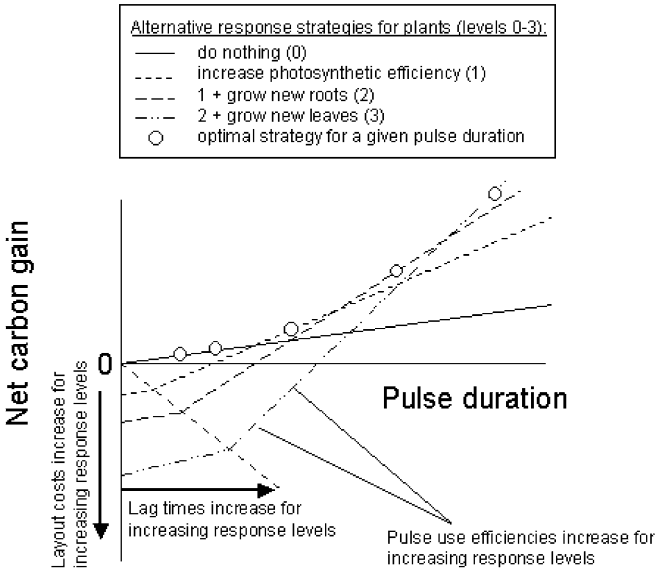

Fig. 5 A graphical model to explain when optimally adapted plants should trigger physiological responses to pulse events. The x-axis is a measure of pulse size, expressed as pulse duration, which may span from single small rainfall event to large event clusters. The y-axis is a measure of carbon gain due to the use of pulse water. The *solid line* represents plants whose response to pulse is entirely passive. The *broken lines* give several alternatives for plant response to a pulse of resource availability. These alternatives are associated with variable lay-out carbon costs and lag times. The optimal pulse response is indicated by the *circles*. For more detail, see text

become longer. Thus, the model predicts a hierarchy of pulse responses, where larger, longer pulse events would trigger more sweeping, more costly and more delayed adjustments in plant function.

This model also suggests a possible relationship between triggering event size and plant functional type, as some data suggest. Plant types that are structurally better adapted for small pulse use (e.g. shallow-rooted C_4 grasses) probably require smaller triggers. This idea, developed in more detail elsewhere (Schwinning et al. 2003) is based on the premise that while the layout costs and lag times associated with a certain type of physiological or morphological response may be similar between species, e.g. between a C_4 grass and a C_3 shrub, the resulting increase in pulse use efficiency may be higher for one of the species (the C_4 grass), which would lower the response threshold for that species.

There is one complication that we have not yet addressed. The problem lies in the assumption that plants can accurately predict the length of the pulse event shortly after it occurred. In some instances, this is feasible. For example, larger rainfall events usually have greater effects on plant water potentials, which the plant can potentially sense and respond to appropriately. In addition, the longer plant water potentials remain elevated, the more responses may eventually be triggered. However, there may often be circumstances in which the magnitude or duration of the initial change in plant water potential contains no information about the likelihood of continued high water potentials, for example by follow-up rain events. Thus, the optimal response function in Fig. 5 is based on the inaccurate assumption of "perfect prior knowledge".

We relax the perfect prior knowledge assumption in Fig. 6 by incorporating two alternative functions to describe the likely pulse responses of plants adapted to different environments. "Optimistic" plants are adapted to an environment where multiple rain events and long pulse duration are common. Carbon gain approaches the perfect knowledge function when a pulse event turns out to be long, but they lose carbon when it happens to be short. "Pessimistic" plants are adapted to an environment where rain events are usually isolated and pulse duration is short. These plants perform best when pulse events turn out to be short, but lose out on potential carbon gain when events are long.

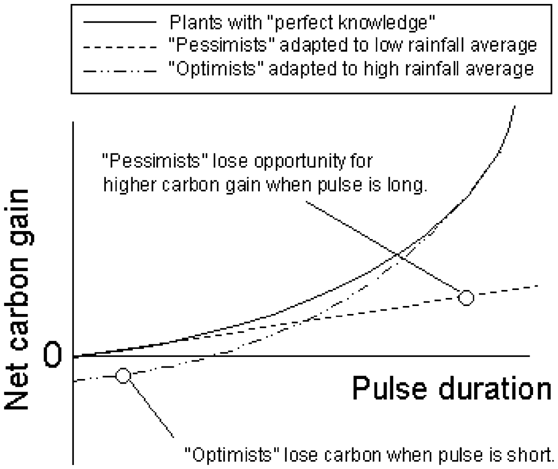

Fig. 6 A comparison of pulse response strategies based on expectations of pulse duration. The *solid line* represents the ideal response and is identical to the *dotted line* from Fig. 5. The two *alternative lines* represent plants adapted to stochastically different precipitation patterns. *Pessimists* are better adapted to use pulses of short duration, requiring few, if any, pulse-triggered physiological responses. *Optimists* are better adapted to pulses of long duration, requiring extensive physiological adjustments to improve pulse use. For more detail, see text

The question of the costs and benefits associated with deploying new tissue in response to a resource pulse was tackled with a combination of controlled experiments and simulation modeling (Lauenroth et al. 1987). The specific questions were whether drought-stressed *B. gracilis* deployed new roots as a response to a simulated small rainfall event (5 mm), and to investigate the role of these new roots and the costs and benefits for the entire plants in carbon terms. *B. gracilis* did produce new roots 40 h after the small rainfall event, accounting for up to 15% of total root length. Nevertheless, their presence was apparently not necessary to restore a non-stressed leaf water status, as water status recovered ahead of root growth. Based on the 5-mm event size, the carbon gain resulting from the new roots exceeded the estimated carbon cost but the largest payoff occurred when experimental plants received 15 mm of rainfall. The observed deployment of new roots only 40 h after a rainfall and the fact that this response had higher pay-off when the rainfall events were larger than smaller suggests that this species would be optimally adapted to an environment dominated by relatively large events. On the contrary, *B. gracilis* is native of the shortgrass steppe, which has a precipitation regime dominated by small rainfall events. We must conclude that either *B. gracilis* is not optimally adapted to the shortgrass steppe or alternatively that it is optimally adapted to the shortgrass steppe environment and that this is dominated by frequent but clustered small rainfall events. Indeed, a Markov analysis of daily precipitation events in the shortgrass steppe showed that rainfall events are not randomly distributed in time but they tend to occur in clusters (Bertolin and Rasmussen 1969).

The present analysis (Fig. 6) predicts that morphologically similar species or conspecifics from different rainfall regions could evolve different requirements for triggering event sizes. Williams and Ehleringer (2000) similarly predicted a relationship between the capacity for summer rain use and the location of populations with respect to the Arizona Monsoon boundary, expecting populations inside the monsoon boundary to have a greater capacity for summer rain use. Supporting this prediction they found, among trees of the pinyon pine-juniper assemblage, that the capacity of trees to take up moisture from summer rain events drops off sharply along the summer rainfall gradient from Northern Arizona into Utah. Though the study could not ascertain whether this apparent difference in the responsiveness of trees was due to local acclimation or had a genetic basis, it does suggest that response thresholds depend on the long-term means of pulse duration.

How does a hierarchy of pulse responses affect our views on the effects of precipitation change in arid/semi-arid ecosystems?

We summarized the evidence suggesting that adaptations to pulsed resource supply, as well as the species interactions and community characteristics that result from these adaptations, may be quite specific to the stochastic characteristics of precipitation, as reflected in the timing, magnitude and uncertainty of soil moisture pulse events. Consequently, long-term changes in one or all of these pulse characteristics could have complex effects on virtually all ecosystem and population processes, as well as on food web dynamics and structure.

If ecosystems respond, as we argue here, discontinuously and non-linearly to soil moisture pulses of increasing magnitude due to the existence of response thresholds, we would certainly not expect a simple scaling relationship for the effects of average precipitation amount on the average process rates in arid and semi-arid ecosystems. With average precipitation amounts, event size distributions also change (Fig. 2), representing a different set of triggers for the various ecosystem processes.

Atmospheric scientists speculate that climate change may result in changes in the low-frequency pulse component of precipitation such as the one resulting from El Niño/Southern Oscillation phenomenon (Tudhope et al. 2001). Frequency and intensity of El Niño events are expected to increase as a result of anthropogenic climate change. Since the mid 1970s, the warm phases of El Niño have been more frequent or persistent than the opposite phase of the phenomenon, La Niño (Nicholls et al. 1996). Recent models also suggest that global warming could increase evaporative demand, so that, despite of increases in total precipitation, average pulse duration may become shorter, and soil moisture variation therefore more extreme (Gregory et al. 1997; Daly et al. 2000). Other changes in climate that may result in changes in pulse characteristics are less certain. For example, evidence to support the hypothesis of increased extreme events and storm intensity is not yet available (Nicholls et al. 1996).

A shift to larger, and possibly longer pulse events is likely to disproportionately increase the primary productivity of higher plants, compared to the activities of microbial decomposers or biological crusts. This might increase the capacity for carbon sequestration in arid/semi-arid regions. Furthermore, a strengthening of the seasonal to inter-annual component of the pulse pattern would disproportionately promote the growth of deeper-rooted plant species. Therefore, the continuing expansion of deep-rooted woody shrubs and trees into arid and semiarid grasslands, and associated effects on animal diversity, is a likely outcome of increased inter-annual rainfall variability.

Global change is expected to alter biodiversity in arid and semi-arid regions not just through climate change, but also through changes in land use and biotic exchange (Sala et al. 2000). These changes will occur simultaneously with changes in nitrogen deposition, and atmospheric CO_2 concentrations. Human activity in arid and semi-arid regions in particular often results in overgrazing, overexploitation, and the introduction of alien species. The sum of these phenomena would reduce the abundance of some native species adapted to the local pulse regime, with some of them driven to local extinction, and would increase the abundance of non-native species, less well adapted to long-term precipitation patterns. The new selection pressures, resulting from increased grazing intensity, altered disturbance regimes, and recently introduced species, may result in the formation of novel communities.

Simultaneous rapid changes in climate and biodiversity may lead to profound mismatches between resource pulse characteristics and resource pulse consumers that may decrease the efficiency of ecosystem-wide resource utilization and the rates of several ecosystem processes. In the short to mid term, this mismatch could render the ecosystem more vulnerable to disturbances, increase the likelihood of "surprise", and result in a reduction in its ability to provide goods and services to humans.

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