PULSE EVENTS AND ARID ECOSYSTEMS

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Precipitation pulses and carbon fluxes in semiarid and arid ecosystems

Abstract In the arid and semiarid regions of North America, discrete precipitation pulses are important triggers for biological activity. The timing and magnitude of these pulses may differentially affect the activity of plants and microbes, combining to influence the C balance of desert ecosystems. Here, we evaluate how a "pulse" of water influences physiological activity in plants, soils and ecosystems, and how characteristics, such as precipitation pulse size and frequency are important controllers of biological and physical processes in arid land ecosystems. We show that pulse size regulates C balance by determining the temporal duration of activity for different components of the biota. Microbial respiration responds to very small events, but the relationship between pulse size and duration of activity likely saturates at moderate event sizes. Photosynthetic activity of vascular plants generally increases following relatively larger pulses or a series of small pulses. In this case, the duration of physiological activity is an increasing function of pulse size up to events that are infrequent in these hydroclimatological regions. This differential responsiveness of photosynthesis and respiration results in arid ecosystems acting as immediate C sources to the atmosphere following rainfall, with subsequent periods of C accumulation should pulse size be sufficient to initiate vascular plant activity. Using the average pulse size distributions in the North American deserts, a simple modeling exercise shows that net ecosystem exchange of CO_2 is sensitive to changes in the event size distribution representative of wet and dry years. An important regulator of the pulse response is initial soil and canopy conditions and the physical structuring of bare soil and beneath canopy patches on the landscape. Initial condition influences responses to pulses of varying magnitude, while bare soil/beneath canopy patches interact to introduce nonlinearity in the relationship between pulse size and soil water response. Building on this conceptual framework and developing a greater understanding of the complexities of these eco-hydrologic systems may enhance our ability to describe the ecology of desert ecosystems and their sensitivity to global change.

Keywords Desert plants · Precipitation · Carbon · Photosynthesis · Respiration

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Introduction

The availability of water, like other resources limiting biological activity, is spatially and temporally heterogeneous on multiple scales (Lambers et al. 1998). Although water availability changes over short (hourly and daily) and long (seasonal and yearly) time scales, most studies have focused on the ecological implications of long-term

dynamics. Differences in plant functional type abundance and life history diversity across the four North American deserts is influenced by seasonal and annual water availability (Ehleringer 1985; Smith et al. 1997; Smith and Nobel 1986). Similarly, seasonal and annual precipitation inputs explain much of the variation in ecosystem processes, such as primary production (Webb et al. 1978; Gutierrez and Whitford 1987; Knapp and Smith 2001; Huxman et al. 2004a, b) .

Surprisingly, how short-term fluctuations in water availability influence ecological processes has not been evaluated to the same extent as other environmental variables. For example, the importance of light distribution has been critically evaluated across multiple temporal and spatial scales from the tropics to the tundra (Pearcy et al. 1985; Pearcy 1990; Smith and Knapp 1990). Similarly, seasonal, monthly and diurnal variations in temperature have been cited as important drivers of physiological processes in many biomes (Mooney and Billings 1961; Valentini et al. 2000; Huxman et al. 2003; Enquist et al. 2003). Infrequent, discrete, and largely unpredictable precipitation events (pulses; e.g., Schwinning and Sala 2004, this issue) have been suggested to be an important driver of arid land ecosystem structure and function (Noy-Meir 1973; Ehleringer et al. 1999), yet only now is a mechanistic understanding of their role in ecological processes emerging (Weltzin and Tissue 2003). The focus of this paper is to consider how variation in precipitation characteristics, such as pulse size or frequency, affects ecosystem C fluxes in semiarid and arid regions, and how those flux patterns may be influenced by variation in the edaphic, microbial and vegetation components of these ecosystems.

While we are beginning to understand how plant function and productivity are influenced by variation in episodic precipitation inputs (Osmond et al. 1987; Smith et al. 1997; Ehleringer et al. 1999; Schwinning and Ehleringer 2001; Whitford 2002; Huxman et al. 2004a, b), we still lack information on how the large-scale fluxes of CO_2 in arid lands are controlled by changes in water status. For example, Reynolds et al. (2004, this issue) suggest that our understanding of plant function in the North American deserts would be improved by considering multiple precipitation pulses (storms) as single, biologically relevant events. Additionally, Austin et al. (2004, this issue) point out that even fairly small rain events influence soil biogeochemical processes. It is the combination of these plant and microbial processes that combine to influence ecosystem C pools and fluxes; here such factors as seasonal rainfall event size distribution may be critical to ecosystem function. Understanding how precipitation events differentially influence these ecosystem components may shed light on the ecosystem CO_2 exchanges of arid ecosystems, and how these regions may respond to climate changes, which may include shifts in the magnitude, seasonal timing and event size pattern of precipitation pulses (Weltzin et al. 2003).

This paper addresses two fundamental questions about CO_2 exchange dynamics: (1) how does a "pulse" of water availability influence C metabolism from microbes and leaves to whole ecosystem and (2) how do pulse characteristics, such as size and frequency, control C dynamics in arid lands?

Ecosystem component responses to precipitation pulses

As with all other biological activities, the ability of organisms to acquire and utilize C depends on the presence of sufficient water. Since the organisms facilitating different components of the C cycle are partially separated in space, the physical distribution of soil water following rainfall links ecosystem C exchanges to precipitation patterns. The vertical distribution of soil moisture likely exerts overwhelming control on patterns of ecosystem C exchange. For example, as several contributions in this issue have pointed out (e.g., Austin et al. 2004; Schwinning and Sala 2004), microbes located on or just beneath the soil surface are hydrated most frequently, and even minute rainfall events may enhance the microbial contribution to ecosystem activity, while being ineffective for triggering the autotrophic processes of vascular plants. Even biological soil crusts require fairly large-sized events to achieve net C gain (Belnap et al. 2004a, b; Cable and Huxman 2004, this issue). Often overlooked, the horizontal distribution of soil moisture may be equally important in determining ecosystem C fluxes. Runoff and runon patterns redistribute precipitation from the plot to the landscape level (Loik et al. 2004, this issue) and, other processes, such as canopy interception may significantly interfere with ecosystem water use, particularly of small rainfall events. Both the vertical and horizontal distributions of precipitation-derived water in the soil are strongly influenced by edaphic factors; however, our understanding of these complexities are still quite limited.

Below, we briefly review both the microbial and higher plant responses to soil moisture pulses. Both phenomena are covered in depth by other contributions in this special issue (e.g., Austin et al. 2004; Belnap et al. 2004; Cable and Huxman 2004; Huxman et al. 2004b; Ogle and Reynolds 2004; Schwinning and Sala 2004; Snyder et al. 2004). Here, we expand on the question how precipitation pulse patterns, interacting with physical and edaphic site factors, impact the balance of respiration and assimilation in arid/semiarid ecosystems. We also present a simple model to conceptualize the role of precipitation patterns in influencing ecosystem C cycling, using the example of the three North American warm deserts.

Microbial response to precipitation pulse

In arid ecosystems, a precipitation pulse into dry soil immediately alters the C balance of the system in several ways. First, high concentrations of CO_2, built up from inorganic C sources and soil microbial activity during the

previous dry period (interpulse), are physically displaced as percolating water fills soil pore spaces. The amount of CO_2 efflux is a function of soil texture and soil macropore structure. Second, precipitation pulses can liberate C held in large soil pools of inorganic carbonates (Schlesinger 1985; Monger and Gallegos 2000). Third, by increasing access to substrate, soil re-wetting can rapidly increase decomposition, N mineralization, and microbial activity (Austin et al. 2004). Thus, high respiration rates from biological processes can occur quickly following a precipitation pulse resulting in substantial CO_2 release to the atmosphere (Kessavalou et al. 1998; Tang et al. 2003; Huxman et al. 2004b; Scott et al. 2004). Together these CO_2 effluxes may outweigh the subsequent photosynthetic CO_2 accumulation, so that a precipitation pulse, or indeed an entire rainy season, may result in a net loss of C from an ecosystem (Emmerich 2003).

Heterotrophic activity of microbial communities can make up a substantial portion of respiration activity in many ecosystems (Law et al. 2002) and probably responds most rapidly to moisture input of all the different biotic components of an ecosystem. However, intervals of high microbial respiration are typically of short duration, as the near-surface soil microbial environment also tends to dry out quickly. As a consequence, measuring the microbial contribution to ecosystem C exchange is difficult. The few data that describe the ecosystem C flux dynamics following precipitation pulses in arid zones show that large effluxes of CO_2 occur within hours of rainfall. The contribution of physically displaced CO_2 versus microbe-respired CO_2 to these effluxes is currently unknown as long interpulse periods associated with these events allow for the accumulation of a high CO_2 concentration in soil pore space (Frank and Dugas 2001; Emmerich 2003; Huxman et al. 2004b; Scott et al. 2004).

Leaf and whole-plant responses to precipitation pulses

Arid and semiarid ecosystems commonly contain a large fraction of species that are dormant during the drier parts of the year, and which become active with the first rain events of the growing season. Thus, seasonal trends in leaf area development are critical to controlling the magnitude of C fixation (Flanagan et al. 2002). A precipitation pulse when functional leaf area is low can only be converted into positive C accumulation after substantial canopy development. For example, early growing season precipitation pulses may trigger germination of annual plants (e.g., Death Valley in the Mojave Desert), but may not translate into ecosystem C accumulation, unless subsequent rain events allow seedlings to survive and grow or significant water is stored in the soil. Similarly, in a semiarid grassland and shrubland, the greatest net CO_2 accumulation was observed in the middle of the rainy season, at peak leaf area index (Emmerich 2003).

Ecosystem leaf area has a large and immediate effect on ecosystem C exchange, however, leaf-level photosynthetic capacity also commonly varies during the season. For example, while leaves developed early in the growing season are often retained until late in the season, they typically have lower photosynthetic capacity than younger leaves (Mooney 1972; Chabot and Hicks 1982). Thus, though leaf area on a landscape may change little, a late precipitation event may result in a smaller proportional increase in gross photosynthetic activity of the ecosystem compared to an early precipitation event, constraining the net response of CO_2 exchange to late season rainfall events.

A more complex and largely unknown factor is the degree to which the photosynthetic capacity of leaves covaries with leaf area production, and how this might affect the magnitude and sign of landscape-scale C exchange (Baldocchi et al. 2002). Plants may increase photosynthetic rates in response to precipitation through an increase in leaf-level CO_2 exchange or through the incremental addition of more leaf area, or both. While the effect on gross photosynthetic fluxes may be largely indistinguishable, there may nevertheless be quite different outcomes for net exchange of ecosystem C over the course of a season.

In addition to the annual cycle of leaf area development and physiological activity, plants in arid and semiarid systems are regularly exposed to short-term fluctuations in water availability within the growing season. Under these conditions, the severity of the water stress experienced during interpulse periods, and the speed of recovery after rain should have major effects on the average response of plants to water inputs. Interpulse duration and stress severity determine the physiological status of a plant at the onset of rain, which in turn determines its rate of recovery of photosynthesis and transpiration (Yan et al. 2000; Schwinning et al. 2002). Plant water status can exert an overriding effect on photosynthesis through its influence on stomatal conductance (Boyer 1985; Passioura 1988; Zhang and Davies 1990; Nobel 1994; Kozlowski and Pallardy 1997; Lambers et al. 1998). With increasing interpulse length, photosynthesis is progressively constrained as stomatal closure influences not only CO_2 diffusion into chloroplasts (Kaiser 1987; Mansfield et al. 1990) but also key photosynthetic pathways, such as photophosphorylation and ribulose 1,5-biphosphate regeneration (Kozlowski and Pallardy 1997). Belowground, progressive soil drying reduces active absorbing root area due to cavitation (Alder et al. 1996; Sperry et al. 1998), abscission and suberization (North and Nobel 1991). Such belowground effects, particularly dieback of woody roots, may limit plant C assimilation during times of intermittent water supply by diminishing water transport capacity.

Although occasional pulses during severe drought may not elicit net C gain, they may nevertheless alleviate stress, foster tissue repair and rehydration and maintain limited plant activity under water-limited conditions (Sala and Lauenroth 1982). Thus, small pulses may help plants survive or maintain leaf area, which increases their capacity to respond to larger events, as was shown for *Larrea tridentata* (Yan et al. 2000). In addition, plant C gain after a pulse may depend on the way that previous

pulse history has influenced other elements of the ecosystem (Austin et al. 2004), such as fungal and bacterial activities that influence nutrient availability and plant water status (Yan et al. 2000). Through these mechanisms, even subtle differences in the timing and amount of rain, may produce interannual variation in the rain response of vascular plants (Leffler et al. 2002). For example, *Juniperus osteosperma* (Utah juniper) responds to summer precipitation during some years but not others (Flanagan et al. 1992; Donovan and Ehleringer 1994). Variation in pulse response has also been observed across gradients in summer precipitation (e.g., Williams and Ehleringer 2000), suggesting that the long-term exposure to summer rain events can affect the ability to respond to summer rain, either through evolutionary mechanisms or the acclimation of individuals to the predominant precipitation regime.

Plant functional types and precipitation pulses

So far, we have discussed plant responses to rain only in general terms. However, several contributions in this issue have highlighted how the precipitation responses of various species or plant functional types might differ (e.g., Ogle and Reynolds 2004; Chesson et al. 2004). We need not repeat these insights here, other than to discuss how these species-specific differences, and by extension, differences in the functional composition of dryland communities, may influence the impact of precipitation on ecosystem C exchanges.

Photosynthesis in shallow-rooted species (e.g., herbs, grasses, and succulents) is known to recover rapidly after rain and grasses have been found to respond to rainfall events as small as 5 mm (Sala and Lauenroth 1982; Sala et al. 1982). Likewise, succulents quickly produce new rain roots (Nobel and Sanderson 1984; Nobel 1988) and increase stomatal conductance (Szarek and Ting 1975; Nobel 1976; Green and Williams 1982) and stem water storage after small pulse events (Nobel 1988; Dougherty et al. 1996). These characteristics would confer a relatively high rain use efficiency to these classes of plants by minimizing delay times during which water would only be lost by evaporation, and by utilizing a greater portion of the rainfall size distribution. However, interpulse photosynthetic rates would be quite low, due to lack of access to soil moisture stored in deeper soil layers.

In contrast, deep-rooted plants often experience less water stress during dry interpulse periods than shallow-rooted plants, because of their ability to draw on deep water reserves left over from previous rainy seasons, but may also respond more slowly and less extensively to present precipitation pulses (Davis and Mooney 1985; Schwinning et al. 2002; Ogle and Reynolds 2004, this issue). For example, the relatively shallow-rooted *L. tridentata* (creosote bush) responded more rapidly to rainfall than the deeper-rooted *Prosopis glandulosa* (mesquite; BassiriRad et al. 1999). As compared to the shallow-rooted species, photosynthetic and respiratory activity are expected to be greater during interpulse periods in this functional type.

How important is community composition to ecosystem rain use? These functional type differences in precipitation pulse use would suggest that communities with large differences in plant functional type composition use precipitation in quite different ways, with consequences for the effects of precipitation on the dynamics of ecosystem C cycles. However, water-limited ecosystems as a whole have a remarkably conservative relationship between rainfall input and primary production (Le Houerou et al. 1998). Most recently, Huxman et al. (2004b) showed that a wide range of biomes, receiving precipitation of between 50 and 3,000 mm year^{-1}, converge on the same maximal rain use efficiency during the driest years experienced at each. It is possible that differences in functional type composition between ecosystems show compensatory rain-use responses through the trade-off between interpulse activity level and pulse responsiveness. Thus, while the temporal dynamics of water use may differ between communities, cumulative annual water consumption and its use efficiency could be similar. However, while net production by plants may have similar dependencies on rainfall inputs across communities with different plant functional type compositions, net ecosystem production may not be the same if there are characteristic differences in heterotrophic activity.

What is the influence of precipitation patterns on ecosystem C fluxes?

In recent years, there has been a renewed interest in the question of how precipitation patterns, rather than just total seasonal or annual precipitation, may influence ecosystem processes in arid and semiarid systems. Groundbreaking experiments such as by Knapp and co-workers (e.g., Knapp et al. 2002; Fay et al. 2003) have provided solid evidence that differences in precipitation patterns alone, independent of rainfall amount, can have a large impact on community composition and possibly ecosystem structure and function. However, there have been few experimental evaluations of this question in the context of ecosystem C cycling. Where experiments have considered C exchange, they have not specifically measured each ecosystem component through time in correlation with changes in water status. There are of course considerable logistical challenges associated with an approach where precipitation is controlled on a scale that represents an entire ecosystem, and also the capacity to measure ecosystem C fluxes year-round and with high enough resolution to capture rapid respiratory bursts associated with the end of the dry and beginning of the growing season. An alternative to this direct experimental approach is the comparison of rainfall effects on ecosystems across regions with different natural precipitation patterns (see also Weltzin et al. 2003; Huxman et al. 2004b; Loik et al. 2004).

A third alternative is the development of models. Although several biogeochemical ecosystem models are currently in use and development, none of them are yet capable of addressing the question of precipitation pattern effects in a satisfactory manner (see Weltzin et al. 2003 for review). A major weakness across models is the representation of rainfall size effects that, as suggested above, should affect the balance between gross photosynthetic activity in the ecosystem by vascular plants (gross ecosystem exchange, GEE) and ecosystem respiratory activity (R_e), which consists of both autotrophic (R_a) and microbial heterotrophic (R_h) sources. Here, we construct a simple working hypothesis to address the question of rainfall size effects on C exchange components. Our purpose is to explore the plausible consequences of shifts in rainfall patterns for ecosystem C exchange, and perhaps most importantly, identify the major gaps in our knowledge, along with important directions for future ecosystem experiments.

Conceptual response of ecosystem components to a pulse

The conceptually strongest link between ecosystem C fluxes and precipitation patterns, in our view, is based on the relationship between precipitation amount, infiltration depth, the location of the soil microbial fauna and plant roots in the soil, and the response time differences of microbes and plants to wetting events: we would expect shallowly located soil microbial communities to be highly responsive to even small rainfall events [down to 2 mm (Austin et al. 2004, this issue)], while larger events ($\geq$5 mm) should be required to infiltrate to a depth where it becomes plant-available and can trigger assimilation processes (Reynolds et al. 2004, this issue). Furthermore, we would expect some delay between the arrival of water at a given soil depth and peak photosynthetic rates, due to physiological acclimation and the growth of new roots and leaves (Ogle and Reynolds 2004, this issue). As a
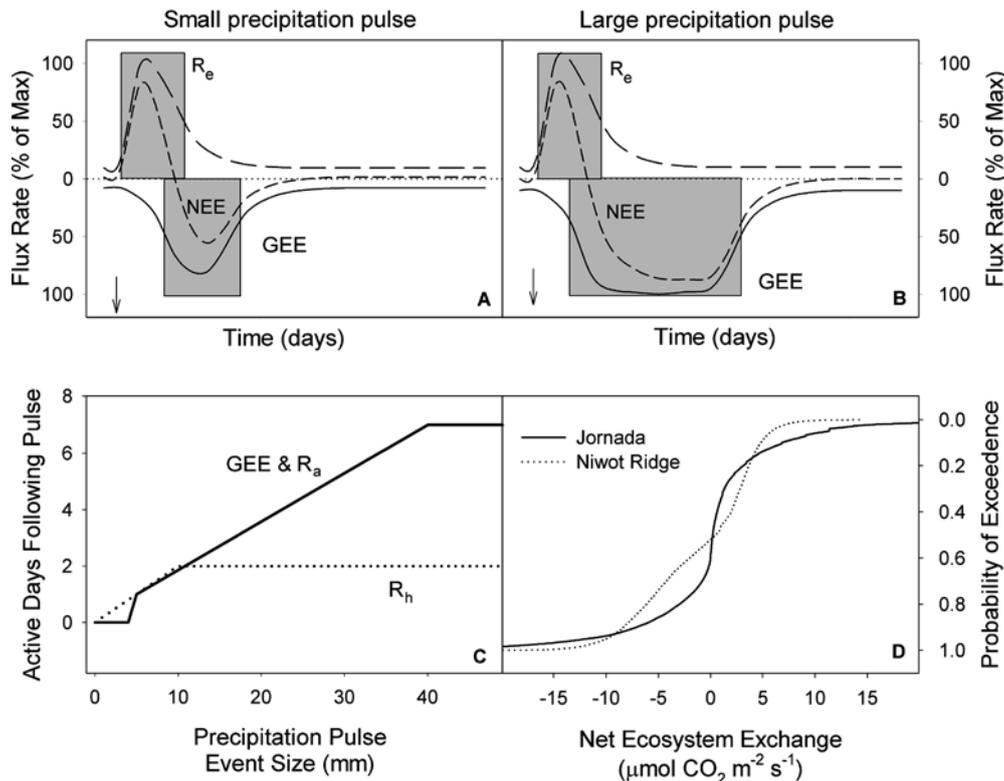
Fig. 1a–d Ecosystem CO_2 exchange [ecosystem respiration (R_e); gross ecosystem exchange (*GEE*); net ecosystem exchange (*NEE*)] following a pulse through time. **a** R_e, GEE and NEE as a percentage of maximum achievable rates (*Max*) following a small hypothetical precipitation pulse (at *arrow* and of sufficient size to stimulate autotrophic activity). **b** Similar to panel **a**, this figure illustrates the response expected with an increase in pulse size. The primary driver of differences in cumulative flux rates is the extended period of high GEE activity as a result of greater infiltration with a larger rainfall event rather than changes in instantaneous flux rates. **c** The activity period for GEE, heterotrophic respiration (R_h) and autotrophic respiration (R_a) following precipitation events of different sizes. R_h increases up to a maximum duration of activity of 2 days from very small pulses to 10 mm (duration=event size×0.2). R_a and GEE have a small pulse size threshold of 5 mm which activates each for a period of 1 day, up to a maximum of 7 days at a very large pulse size (40 mm; duration=event size×0.17+0.14), when processes such as overland flow dominate the hydrologic cycle. These functions relate pulse size to duration of activity in our simple model for a seasonal distribution of event sizes. **d** Composite functions of NEE for the primary growing season (June, July and August) for two different ecosystem types; a coniferous forest [Niwot Ridge (see Monson et al. 2002)] and a desert grassland [Jornada Experimental Range (see Mielnick et al., in press)]. Composite functions are constructed from the probability distribution of fluxes for multiple years (Niwot Ridge, 4 years; Jornada, 4 years), and plotted as a function of the probability in time that a flux value will be exceeded (see Appendix). In **a, b** and **d**, rates are plotted such that negative values represent flux into the ecosystem and positive values represent efflux to the atmosphere

consequence, the cumulative fluxes of CO_2 attributed to either R_e or GEE measured over a pulse interval would have different functional responses to rainfall size, with small events favoring ecosystem C loss chiefly through microbial respiration, and larger events being necessary to elicit net C gain through autotrophic components in the ecosystem. As pulse size and infiltration depth increase, we expect a close positive relationship between GEE and pulse duration, i.e., the time that water remains biologically available to plants (see also Schwinning and Sala 2004), but R_e should be independent of pulse duration because the microbial community's environment at the soil surface dries relatively quickly and is fairly independent of pulse size.

Empirical evidence, as far as it has been measured, supports this scenario. We generalize the response of ecosystem CO_2 exchange to a precipitation pulse in Fig. 1a, that is relatively small, but of sufficient size to stimulate autotrophic activity (ca. 5 mm). This is based on measured patterns from a number of different ecosystem types [semiarid grasslands (Emmerich 2003; Huxman et al. 2004b; Mielnick et al., in press), coniferous forests (Monson et al. 2002; Huxman et al. 2003), temperate grasslands (Flanagan et al. 2002), semiarid shrublands (Emmerich 2003), and a Mediterranean grassland (Xu and Baldocchi 2004)]. In a system that has not experienced rainfall for some time, where physiological activity is very low (essentially zero), rainfall first triggers a burst of positive CO_2 flux, caused by the mixture of mechanisms discussed above, including the physical displacement of CO_2-rich soil air and microbial respiration.

If water infiltrates to such a depth and persists for sufficient time to stimulate plant water uptake (possibly requiring root and leaf growth), ecosystem photosynthesis eventually increases, lagging by several days behind the respiration response. At some point following a pulse, a period of net ecosystem accumulation of CO_2 should occur, in part because of increasing rates of ecosystem photosynthesis (through plant acclimation and/or leaf growth), and because the declining water potential in shallow layers will begin to restrict microbial activity. Both semiarid grasslands and semiarid shrublands appear to exhibit this behavior following rainfall events that are isolated in time (Emmerich 2003).

It is more difficult to deduce how rainfall event size is likely to modify these dynamic patterns in ecosystem C exchange. We are suggesting a tentative working hypothesis in Fig. 1b, where we make the simple assumption that increases in rainfall event size beyond the threshold for plants (ca. 5 mm) increases the duration of peak photosynthetic fluxes, but not necessarily microbial respiration. Fig. 1c describes how these assumptions would affect the duration of activity of R_h, R_a and GEE, integrated over the entire pulse period, as pulse size increases. Note that the R_a response parallels that of the GEE response, since both depend on the activity of vascular plants.

We make several assumptions in formulating this conceptual model. First, we assume that the duration of physiological activity is proportional to pulse size (e.g., as depicted by the width of the gray boxes in Fig. 1a, b). Second, total flux associated with a pulse is given by the duration of activity×the peak flux rate (as depicted by the area of the gray boxes), where duration of activity has an overwhelming effect on cumulative flux values. Third, there is a lower threshold on pulse size such that R_e and GEE do not substantially respond to the precipitation event. Fourth, the lower threshold differs for R_e (insignificant below 2 mm) and GEE ($\cong$5 mm). Fifth, likewise, there is an upper threshold on pulse size where R_e and GEE are at their maximal flux rates and large pulses do not increase R_e and GEE beyond their maximum rates. Finally, the upper pulse threshold also differs for R_e and GEE such that the threshold for R_e is less than that for GEE. Together, these assumptions result in a linear relationship between pulse size and cumulative GEE and R_e for pulse sizes between the lower and upper thresholds. Though these assumptions minimize complexity, they are in fact quite robust in the light of observation. For example, Schwinning et al. (2002) observed just such a linear threshold response for three species of the Colorado Plateau desert for infiltration amounts of 2–20 mm. Furthermore, the generally linear relationship between seasonal rainfall input and primary production at the ecosystem scale (e.g., Huxman et al. 2004a, b) is consistent with a first pass linear relationship between single event precipitation inputs and the production attributed to them.

We can extend this conceptual framework to a simple quantitative model to estimate the cumulative fluxes of C into and out of an ecosystem for a fixed season, given maximum and reference state flux values for GEE, autotrophic respiration and heterotrophic respiration, along with a precipitation pulse size distribution. The size distribution of pulses determines the duration of maximum activity of GEE, R_h, and R_a (specific relationships between pulse size and duration given in Fig. 1c), summed across all events of all sizes throughout a season. The season length (in this case 100 days) minus the duration of maximal activity gives the duration of reference state activity. The seasonal sum of GEE, R_a, R_h (combining both maximal and reference periods) combine to produce a season-specific value of net ecosystem CO_2 exchange (NEE).

The model takes the point of view that deserts tend to be in only three activity states: a low activity reference state reflecting the availability of only the ecosystem reserve pools, e.g., water stored in plants or deeper soil layers, a high activity state for respiration, triggered by small rainfall events, and a high activity state for GEE, triggered by larger rainfall events. Though this assumption is extreme, it does capture a characteristic feature of water-limited ecosystems. Data from long-term assessments of CO_2 fluxes from the Jornada Experimental Range support this notion when compared to an ecosystem that experiences relative steady-state declines in soil water availability through time [a coniferous forest (Niwot Ridge AMERIFLUX site)]. Peak growing-season (June–August)

values of NEE observed over 4 years have different frequency distributions that illustrate these three states and that differ between the two sites (Fig. 1d, Appendix). At the desert grassland site, long interpulse periods with limited ecosystem activity (NEE values near zero) are punctuated by infrequent episodes of high rates of ecosystem activity (large NEE values, both positive and negative). The resulting composite flux duration curve is steep around NEE near zero and relatively flat through its extremes. In contrast, the Niwot Ridge curve has a gentle slope near zero, which reflects an ecosystem experiencing a steady-state decline in soil water conditions through the growing season (a high frequency of mid-range NEE values), where ecosystem processes are also controlled by seasonality in temperature and light (Huxman et al. 2003).

Simulated NEE-precipitation relationships for the three North American warm deserts

We use three long-term (85 year) precipitation records for the Mojave, the Sonoran and the Chihuahua Deserts to simulate the components of C flux using our model (summarized in Fig. 1a–c). These data sets were the same as used by Reynolds et al. (2004), kindly provided by the authors, and are based on analyses of data obtained from: http://www.wrh.noaa.gov/lasvegas/lasvegas_records.htm (Mojave); http://www.wrh.noaa.gov/Tucson/climate/climate.html (Sonoran); http://jornada-www.nmsu.edu/ (Chihuahuan) (Fig. 2). We focused our analysis only on daily precipitation between July and September, an interval characterized by brief convective, monsoonal storms. Consistent with rainfall patterns typical for summer events, we equate an "event" with any day in which rain was recorded.

These three deserts differ not only in total summer precipitation, but also in event size distribution for summer [see also Reynolds et al. (2004) for distributions

Fig. 2 The cumulative size distribution of daily precipitation events for July through September (*Sept*) from an 85-year data set from the Sonoran, Mojave and Chihuahuan Deserts. Data were provided by Reynolds et al. (2004, this issue), and based on analyses of data obtained from http://www.wrh.noaa.gov/lasvegas/lasvegas_records.htm (Mojave); http://www.wrh.noaa.gov/Tucson/climate/climate.html (Sonoran); http://jornada-www.nmsu.edu/ (Chihuahuan). Plotted here is the average size distribution for the driest 25% of years, middle 25% (*mid*) of years and wettest 25% of years. These size distributions are used with the functions given in Fig. 2c to determine periods of high ecosystem activity (GEE$_{max}$, $R_{h, max}$, $R_{a, max}$, see Table 1) and periods of reference state activity (GEE$_{ref}$, $R_{h, ref}$, $R_{a,ref}$, see Table 1) in order to calculate seasonal NEE. For other abbreviations, see Fig. 1
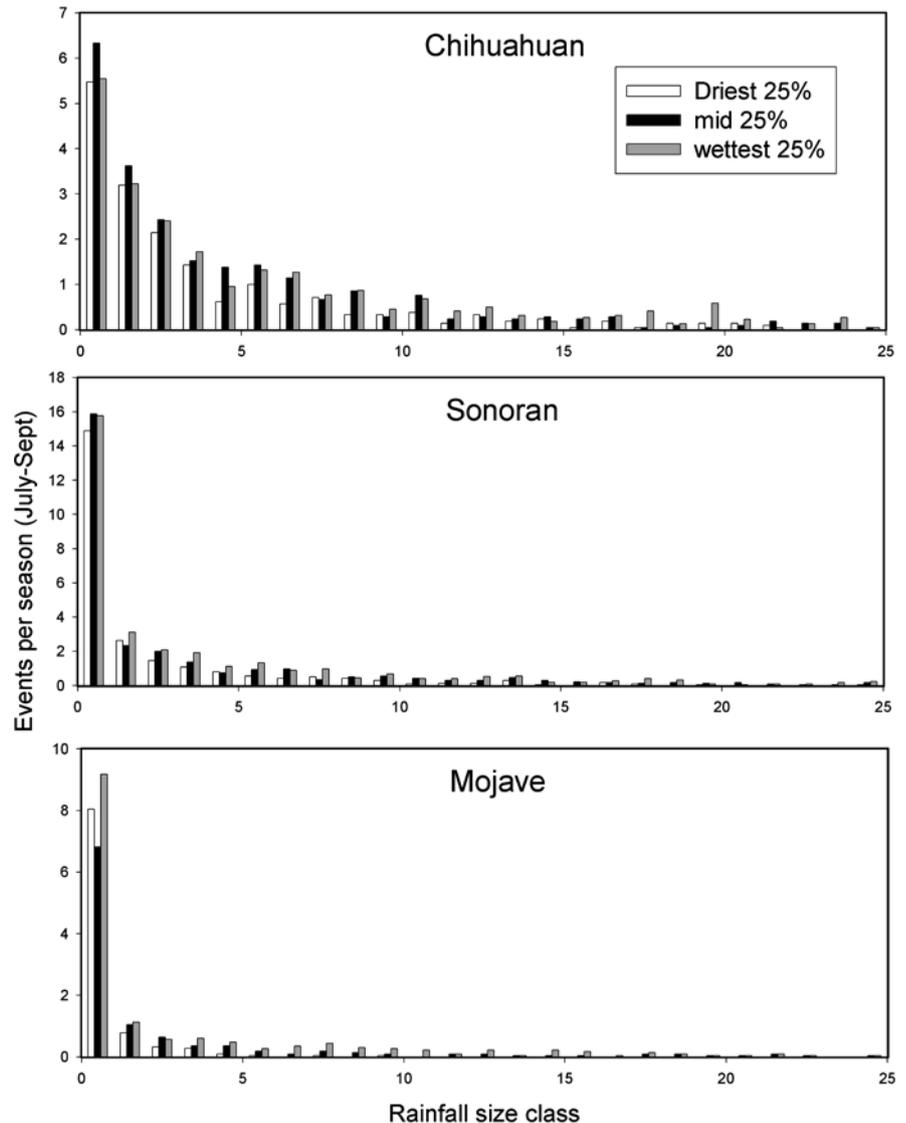
of alternative event classifications]. In all three deserts, total seasonal precipitation is strongly, and for the most part, linearly, correlated with the total number of events >5 mm, i.e., those event classes that we expect to affect both microbial dynamics *and* vascular plant activity (Fig. 3a). Furthermore, the relationships between total precipitation and the number of events >5 mm are almost indistinguishable between the three deserts, except for small differences in the average size of events >5 mm (Chihuahua, 13.3; Sonoran Desert, 14.2; Mojave, 14.0). By contrast, there is no statistically significant relationship between total precipitation and the number of events ≤5 mm (Fig. 3b). However, the average number of events ≤5 mm declines in the order Sonoran Desert (22) >Chihuahua (14)>Mojave (ten). The question is, can these differences in precipitation patterns be expected to affect the C exchange patterns of the different deserts?

As discussed before, a major unknown for any simulation of ecosystem C balance is the question of how much leaf area is triggered at the onset of the growing season and how much of the respiratory efflux of CO_2 is attributable to the growth of new leaves and roots. We
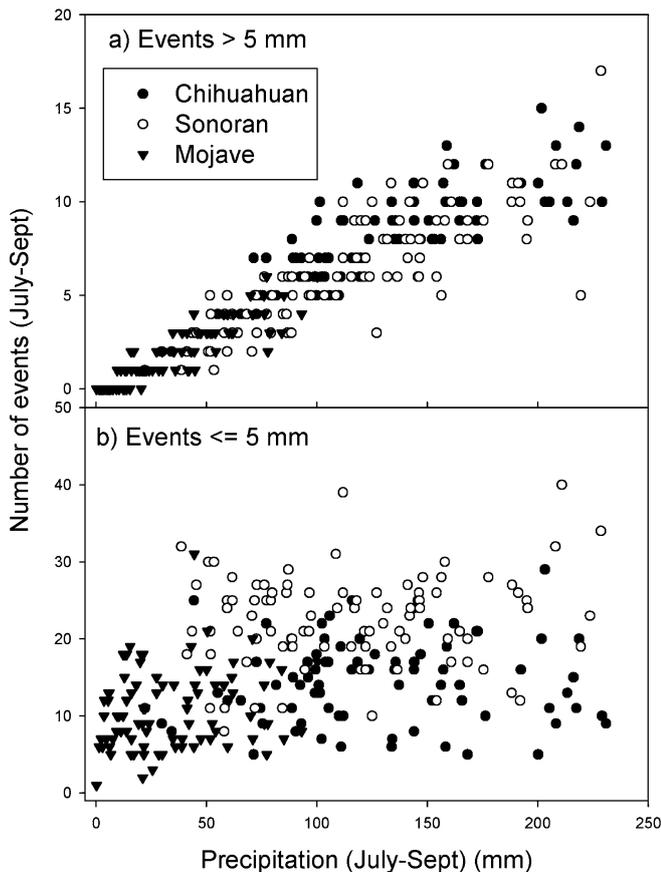
sidestep this and other unknowns by assuming a fully developed canopy at peak potential photosynthetic capacity, therefore focusing on the more limited question of how precipitation patterns may affect mid-season NEE. We further assume that each ecosystem can be characterized by minimum [reference state (interpulse values)] and maximum (pulse) flux rates for respiration (R_a and R_h) and GEE. The values used here were taken from the literature (Sonoran and Chihuahuan Deserts) or, where unavailable, estimated by scaling known canopy and bare soil C exchange rates by plant cover (Mojave Desert). Table 1 summarizes the estimates used. To evaluate the influence of total seasonal precipitation for the three locations, we divided the rainfall data set into three classes representing dry (lower quartile), average (mid quartile) and wet (upper quartile) seasons, and calculated an average event size distribution for each quartile, as well as an average event number and size (Table 2). These distributions were used to estimate the duration of maximal and reference activity of GEE, R_a and R_h (as in Fig. 1c) to produce seasonal totals allowing for a calculation of NEE.

The analysis shows that the three deserts have a coherent relationship between NEE and seasonal precipitation, although the component fluxes were more similar for the Sonoran and Chihuahuan Deserts than for the Mojave (Fig. 4). The overall relationship between NEE and precipitation is slightly nonlinear, with rainfall increments in a low rainfall regime having less impact on NEE than an increment of the same size in a high rainfall regime. However, it is difficult to assess whether this nonlinearity occurs because of inherent differences in ecosystem flux rates or because of differences in rainfall size distributions. To separate the issue of flux rates from the issue of rainfall size distribution we recalculated seasonal fluxes for each desert using the precipitation regimes for all three deserts and compared all combinations of flux and rainfall patterns in Fig. 5. This analysis illustrates this slightly nonlinear relationship, primarily as

Fig. 3a, b The relationship between total seasonal precipitation (July–Sept) and the number of small (<5 mm) versus large (>5 mm) rainfall event sizes for the Sonoran, Mojave and Chihuahuan Deserts. Data were provided by Reynolds et al. (2004, this issue), and based on analyses of data obtained from http://www.wrh.noaa.gov/lasvegas/lasvegas_records.htm (Mojave); http://www.wrh.noaa.gov/Tucson/climate/climate.html (Sonoran); http://jornada-www.nmsu.edu/ (Chihuahuan)

Table 1 Initial model flux rates associated with either the reference state (interpulse values) or the active pulse state (maximal values)[a]. All values are given in μmol CO_2 m^{-2} ground s^{-1}. *Negative values* represent fluxes into the ecosystem, while *positive values* values are fluxes to the atmosphere. When combined with the precipitation distributions to produce seasonal totals, these values were scaled to 24-h estimates [gross ecosystem exchange of CO_2 (*GEE*) was adjusted by a 12-h photoperiod]. R_a Autotrophic respiration, R_h heterotrophic respiration, *ref* reference state, *max* maximal values

Desert	GEE_{ref}	$R_{a,ref}$	$R_{h,ref}$	GEE_{max}	$R_{a,\ max}$	$R_{h,\ max}$
Mojave	−0.9	0.225	0.25	−6.0	1.5	1.0
Sonoran	−2.0	0.5	0.25	−12.0	3.0	3.0
Chihuahuan	−2.0	0.5	0.25	−14.0	3.5	3.5

[a]Data are taken from an experimental Sonoran Desert grassland (Huxman et al. 2004b; T. E. Huxman et al., unpublished data) and a Chihuahuan Desert grassland (Mielnick et al., in press) both of which were assessed by whole-system flux measurements. The data from the Mojave Desert represents small-scale assessments of flux (soil collar and leaf level) that are scaled based on leaf area index and plant cover (Hamerlynck et al. 2000; T. E. Huxman unpublished data)

Table 2 Average event number for rain pulses >3 mm, average size of these rainfall events, and average season (July–September) total precipitation for the wettest (*Wet*) , mid 25% (*Mid*) and driest 25% (*Dry*) 25% of years from long-term (85 years) daily records of rainfall from the three warm deserts of North America[a]

Desert	Effective event no.	Effective event size	Season total precipitation
Mojave			
Wet	4.8	13.1	69.0
Mid	2.2	10.1	36.2
Dry	0.5	5.1	7.0
Chihuahuan			
Wet	14.1	13.8	205.3
Mid	11.1	10.1	125.7
Dry	7.1	8.5	71.8
Sonoran			
Wet	13.2	13.7	197.6
Mid	8.8	10.9	113.6
Dry	5.1	8.1	56.5

[a]Data were provided by Reynolds et al. (2004, this issue), and based on analyses of data obtained from http://www.wrh.noaa.gov/ lasvegas/lasvegas_records.htm (Mojave); http://www.wrh.noaa. gov/Tucson/climate/climate.html (Sonoran); http://jornada-www. nmsu.edu/ (Chihuahuan)

a result of the fluxes from the Sonoran and Chihuahuan Deserts under the driest rainfall regime combinations. As such, the nonlinear response is likely due to the shift in rainfall size distributions from one dominated by small rainfall events in dry years to one dominated by frequent, larger events in wet years. The predicted ecosystem response in the Mojave Desert is the least nonlinear of the three because respiration estimates are proportionally smaller than for the other two deserts, thus the shift to small rainfall events in low precipitation years has a smaller impact on NEE.

At their native precipitation regimes, the Sonoran and Chihuahuan Deserts were capable of accumulating a substantial amount of C in summer. For the Mojave Desert, this occurred only during the moderate and high rainfall years. However, this estimate considers only mid-season conditions, so incorporation of the dynamics of canopy construction and non-growing season respiratory effluxes may result in actual NEE for the annual period to be considerably lower.

In summary, our model indicates that NEE can be sensitive to changes in the event size distribution of rainfall. In natural environments, this sensitivity may explain both local changes in NEE between wet and dry years, typically characterized by different numbers of large storms, and inter-site differences in NEE across the three North American warm deserts. Using 5 mm as the threshold for a large storm, total summer precipitation is strongly related to the number of large storms (Fig. 3a) and this relationship is similar among the three deserts. Thus, according to this analysis, differences among deserts in their NEE response to precipitation are almost entirely due to differences in the characteristic ecosystem flux rates
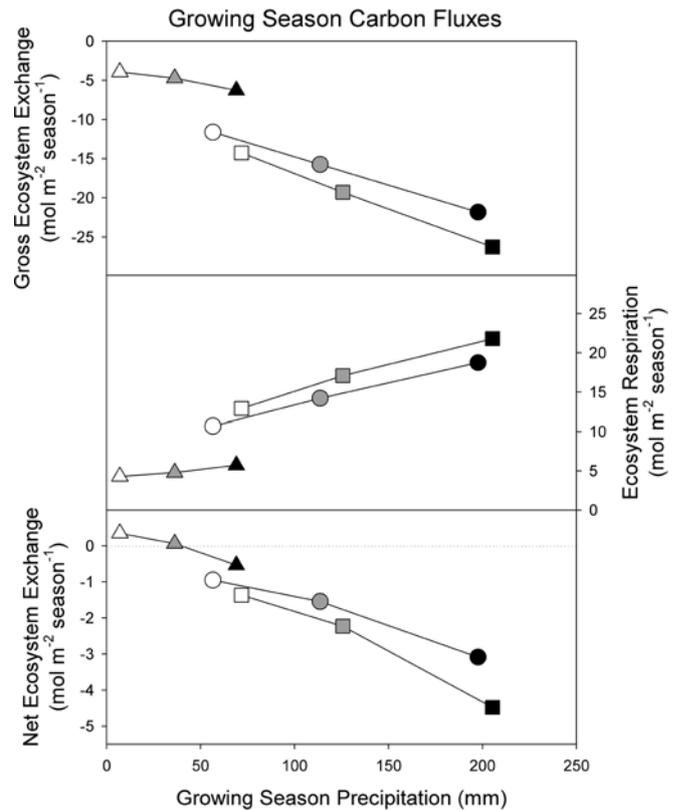
Fig. 4 Plotted are the seasonal cumulative C fluxes of respiration (summed R_a and R_h) and photosynthesis for the three warm deserts of North America. Each data point is constructed from either the driest 25% (*open symbols*), mid 25% (*gray symbols*) or wettest 25% (*black symbols*) of the precipitation record (from Fig. 2). The size distributions in Fig. 2 are translated into time by the relationships given in Fig. 1c, and used to determine the time period of maximum flux rates for a season. The season length (in this case 100 days) minus the duration of high activity gives the time period of reference state activity. The sum of these high and low flux totals gives seasonal GEE and R_e ($R_e = R_a + R_h$). NEE=GEE+R_e. Flux rates used here, associated with each desert are given in Table 1. *Negative values* represent C flux into the ecosystem, while *positive values* represent C loss from the ecosystem. In the *bottom panel*, the compensation point is illustrated with a *dashed line*. *Circles* represent the Sonoran Desert, *squares* represent the Chihuahuan Desert, and *triangles* represent the Mojave Desert. For other abbreviations, see Fig. 1

(see Table 1). Dissimilarities between the deserts (primarily the Sonoran and Chihuahuan contrasted with the Mojave) in their ecosystem-level reference and maximum flux rates may be due to several factors including differences in both canopy cover and the timing and magnitude of previous rain events, which may have the potential to modify the current physiological state of leaves, roots, and microbes.

Our findings suggest that future research should focus on measuring components of ecosystem C exchange to better understand their relationship to rainfall amount and distribution both within and across seasons. For example, base rates for vascular plant activity during interpulse periods probably depend on the amount of water stored in deeper soil layers from fall to spring recharge. However, regional differences in rainfall event size distributions,
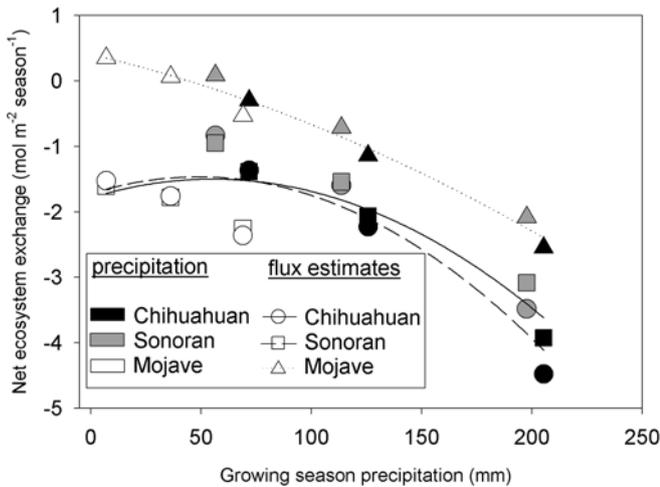
Fig. 5 NEE as a function of the seasonal precipitation event size distributions for the Sonoran, Chihuahuan and Mojave deserts (given in Fig. 2). In this analysis, the precipitation characteristics of each region (dry, mean and wet) are applied to the ecosystem component flux characteristics of each region in a factorial manner so that, for example, the Mojave Desert flux values are applied to the precipitation record of both the Sonoran and Chihuahuan Deserts. *Circles* represent the Chihuahuan Desert specific flux characteristics, *squares* represent the flux characteristics of the Sonoran Desert, and *triangles* illustrate the Mojave Desert all given in Table 1. The different precipitation regimes are: *black filled symbols* Chihuahuan Desert, *gray filled symbols* Sonoran Desert, and *open symbols* Mojave Desert

within the range observed across the three North American warm deserts in summer, may not have a significant effect on the relationship between NEE (or its component fluxes) and total precipitation.

These relationships highlight the importance of designing rainfall manipulation experiments to incorporate realistic relationships between precipitation amount and event size distribution when considering questions about ecosystem C balance. Experiments that explore the effects of contrasting event size distributions while maintaining precipitation amount constant across treatments may be artificial because amount and event size tend to change concomitantly. In fact, such experiments could result in overestimating the importance of rainfall patterns in natural environments, unless care is taken to stay within realistic bounds of rainfall variation. Likewise, experiments that modify total seasonal precipitation, but do not account for wet versus dry year changes in event size distribution may not reflect realistic scenarios.

These statements derive partially from an assumption of the model that individual precipitation pulses act independently, but it is likely that the sensitivity of ecosystem C dynamics to a given storm will depend on antecedent soil water (e.g., Reynolds et al. 2004; Ogle and Reynolds 2004, this issue), which will be partly determined by the timing and size of previous storm events. Only now are researchers beginning to characterize the temporal correlations of rainfall patterns (Davidowitz 2002), and the prediction of these correlations would be a very useful output of climate models. Ultimately, more complex dynamic models will be necessary to understand the

relationships between climate change, precipitation patterns and ecosystem C exchanges. Given the difficulty of manipulations of rainfall on such a large scale, research programs that incorporate reasonable field experiments, with high-resolution measurements of ecosystem component activity, historical data, and modeling are perhaps the most feasible and powerful approach to understanding the linkage between precipitation and ecosystem C exchange in semiarid and arid ecosystems.

Since the assumptions taking us to these conclusions were quite simple, possible sources of error should be carefully considered. First, the degree of nonlinearity in the relationship between NEE and precipitation is clearly affected by the choice of ecosystem flux parameters (Table 1) and by the assumptions regarding pulse duration. Small pulse–interpulse differences in the flux rates, or a bias towards a small heterotrophic/autotrophic activity ratio ($R_{h, max}$/GEE_{max}), would tend to minimize nonlinearities by weakening the effect of shifts in rain event size distribution. Similarly, either very short periods of microbial activation or patterns of microbial respiration that are more similar to those of vascular plants would make the relationship between NEE and seasonal precipitation more linear. These relationships can be easily tested in the field, as assessments of maximum and minimum flux rates are fairly straightforward to make.

Second, above the threshold for vascular plant activity, the relationships between GEE and pulse size were assumed to be linear over a wide range, so that the combined effects of all event sizes above 5 mm depended only on total precipitation. There may be several mechanisms, some of which are discussed below, that would introduce nonlinearities also in this range of rainfall sizes.

Future challenges

Hydraulic redistribution

One of the major challenges today is to quantify the effect of hydraulic redistribution, not just on the water use patterns of vascular plants, but also on the microbial community and hence the balance of microbial respiration and plant photosynthesis. Plant roots can redistribute water upward or downward. Upward redistribution of water (i.e., hydraulic lift) occurs during interpulse periods when the soil close to the surface has dried out but soil moisture at depth is still high (Richards and Caldwell 1997; Caldwell and Richards 1989). Hydraulic lift increases water availability to understorey plants that grow underneath the hydraulic lifters during interpulse periods (e.g., Caldwell and Richards 1989; Dawson 1993), thereby sustaining less drought-tolerant species and increase their capacity to respond to subsequent rainfall pulses. By the same token, hydraulic lift may also prolong the activity of microbial communities near the soil surface. Downward redistribution occurs during pulse periods when surface soil is nearly saturated and deeper soil layers are partially

depleted (Burgess et al. 1998, 2000; Schulze et al. 1998; Smith et al. 1999; Ryel et al. 2002). It has been argued that this downward redistribution of water may slow the depletion of deeper water stores that sustain the activity of growth forms with deeper rooting depths (Ryel et al. 2002). What has not been considered so far is whether this redistribution also has the capacity to accelerate the onset of dry conditions near the soil surface, thereby suppressing microbial activities.

Eco-hydrologic effects of vegetation structure

In most aridland systems, vegetation cover rarely exceeds 75% and bare soil is always a significant feature (e.g., Schlesinger et al. 1990; Vinton and Burke 1995). Infiltration capacity is typically greater in sub-canopy soil compared to bare soil because of differences in soil texture (Dunkerley 2002), soil organic matter content (Kelly and Burke 1997) and root system development (e.g., Devitt and Smith 2002). A comparison of rainfall effects in a grassland (~50% plant cover and small, discrete interspaces) and a shrubland (~30% plant cover and large, connected interspaces) showed less infiltration under bare soil in both systems, and greater sub-canopy infiltration under shrubs than under grasses (Bhark and Small 2003). Surface microtopography may also favor infiltration in sub-canopy versus bare soil areas (e.g., Dunne et al. 1991; Bergkamp 1998), and may be modified by cryptobiotic crusts (Eldridge and Greene 1994). Local physical structure can thus strongly influence the final horizontal and vertical patterns of water availability to the microbes and plants that so influence ecosystem pulse responses.

Ecosystem structure may also affect the functional response of ecosystem C fluxes to rainfall size, via modification of the infiltration patterns (Fig. 6). Plant canopies intercept a fraction of incoming precipitation (e.g., Kropfl et al. 2002). If the rainfall events are small,

intercepted water may evaporate rapidly and never reach the soil (Tromble 1988). Although bare soil infiltration is typically less than in sub-canopy soil, small rainfall events may only recharge bare soil (e.g., Bhark and Small 2003). As pulse size increases, throughfall occurs and stem flow may focus some intercepted water at the base of the plant (e.g., Whitford et al. 1997). Thus, small rainfall events would primarily trigger microbial respiration in the canopy interspaces, while larger rainfall events would be required to funnel water to support vascular plant photosynthesis.

In addition, pooling of water in bare soil areas may initiate horizontal redistribution of water. Runoff may not occur at larger spatial scales (Bergkamp 1998) suggesting that locally redistributed water eventually infiltrates in the sub-canopy areas, which also receive throughfall and stem flow inputs. As a result, larger pulses should lead to disproportionately greater sub-canopy soil water content than smaller pulses (Loik et al. 2004). Field data confirm that small pulses lead to greater bare soil infiltration and that sub-canopy infiltration surpasses bare soil as pulse size increases, and that these relationships are modified by the community structure (Bhark and Small 2003). Overall, these patterns of horizontal redistribution of precipitation would enhance the nonlinearity in the relationship between NEE and precipitation (Fig. 2), because a disproportional amount of precipitation in a low rainfall regime would stimulate only bare soil microbial respiration, with a tendency to reverse this trend as total precipitation, and thus the proportion of large rainfall events, increases. Furthermore, we would expect the shape of this relationship to change with vegetation structure. For example, the nonlinear trend between NEE and precipitation would be expected to increase with the encroachment of shrubs into grasslands, potentially reinforcing the loss of primary production in low rainfall years. Even if climate remains relatively constant, such changes in ecosystem structure can affect the frequency with which the system is a net sink or source for C.

precipitation pulse size class
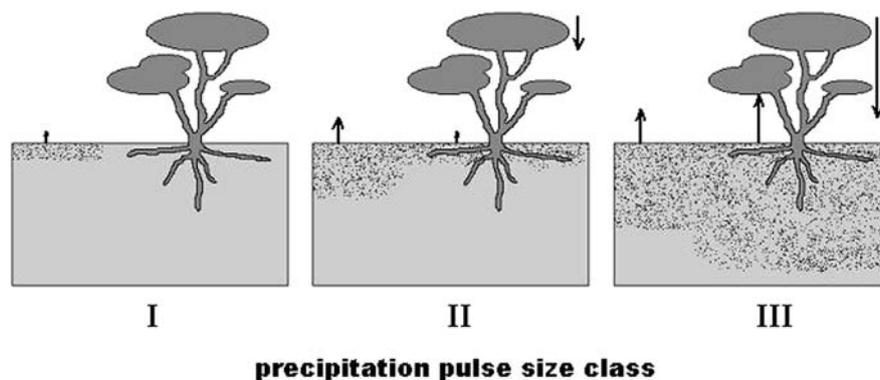
Fig. 6 Hypothesized relative soil water content and subsequent C fluxes under bare soil and sub-canopy areas of an arid or semiarid ecosystem are shown following a pulse of one of the three size classes (*I–III*) defined by the distribution of water on the surface. Under bare soil, water content after the pulse is roughly proportional to pulse size. Sub-canopy water content increases only above the threshold, when canopy interception allows throughfall and stem flow to wet the sub-canopy soil. Above an additional size threshold, water redistribution from bare soil to sub-canopy leads to increased water content in sub-canopy soil, a response that favors large photosynthetic responses by plants. Soil water content and depth is shown by *shading* in the soil box, while fluxes of CO_2 are shown from bare soil areas, sub canopy and plants with *arrows* where length is proportional to the flux response

Geomorphic and edaphic variability

Edaphic characteristics translate precipitation pulses into biologically available water in the soil (McAuliffe 2003). In aridland ecosystems, variation in soil surface and subsurface layer development influences patterns of water infiltration, runoff, deep soil recharge and water content/water potential relationships (Noy-Meir 1973; McAuliffe 2003). For example, the presence of cemented subsurface calcic horizons and surface vesicular components affect soil water balance, and thus, plant water-relations and net primary productivity (Cunningham and Burke 1973; Hamerlynck et al. 2002). The interaction between plants and soil characteristics are important for hydrological processes, such as runoff and sediment transport (Wainwright et al. 2002). Variation in soil characteristics can modify precipitation events into differential biological activity, impacting vegetation composition and performance (McAuliffe 1994, 1999; Parker 1995; Smith et al. 1995; Hamerlynck et al. 2002, 2004). Thus, whole-ecosystem C dynamics can be substantially influenced by the manner in which surface and subsurface soil characteristics modify precipitation pulses, through impacts on the infiltration response of the vertically stratified microbial and autotrophic components of ecosystem C exchange.

Summary and future directions

In summary, pulse size plays an important role in regulating C balance of arid ecosystems through its differential effects on ecosystem respiration and photosynthesis (Fig. 1). Small, shallowly infiltrating storms primarily increase microbial respiration while larger storms infiltrate to sufficient depth to increase plant gas exchange. Importantly, the physical structure of the system frequently acts to strengthen this pattern because surface redistribution of water leads to greater infiltration and a disproportionate increase in plant activity following large pulses (Fig. 6). Because of the differential rates of response of respiratory and photosynthetic processes in arid land ecosystems, the frequency of high levels of biological activity becomes important in regulating C balance. All things being equal, a pulse results in a large initial efflux of C from the ecosystem that can be several orders of magnitude larger than rates of CO_2 exchange during the interpulse. This net loss is followed by a period of C accumulation as soil layers dry and water becomes increasingly scarce for shallowly located microbial communities while deeper soil water remains available to plants. As a result, the frequency distribution of ecosystem fluxes in arid systems, versus systems with a gradual decline in soil moisture, can be characterized by frequent, large oscillations between short periods of high activity and protracted periods in a low activity reference state.

We have summarized what we think is critical for understanding how climate influences biological processes in arid ecosystems, but our conclusions are somewhat limited due to a general lack of quantitative information. In order to accurately gauge the potential impacts of changes in precipitation and temperature associated with global climate change scenarios, a more detailed series of studies across a range of arid systems addressing the above issues is required. Of particular interest are those studies which address: (1) the separate contributions of autotrophic or heterotrophic activity to soil CO_2 efflux following a rain event, (2) the influence of microtopography and vegetation structure on the relationship between precipitation pulses and biological activity, and (3) the interaction of precipitation effects on ecosystem C balance over both short (within season) and longer (interannual to decadal) time scales in an eco-hydrological system.

Appendix

We compiled flux duration curves [analogous to the stream flow duration curves (Searcy 1959)], to illustrate the differences in ecosystem CO_2 exchange characteristics for a pulsed ecosystem [a desert grassland (Jornada Experimental Range; Mielnick et al., in press)] and an ecosystem that experiences a relatively steady-state decline in soil water availability in time [a coniferous forest (Niwot Ridge AMERIFLUX site; Monson et al. 2002)]. We used 30- and 20-min averaged (Niwot Ridge and Jornada, respectively) peak growing season (June–August) NEE values observed over 4 years (1999–2002 and 1997–2000, Niwot Ridge and Jornada, respectively). Briefly, NEE data for the period of interest at each site were assigned a rank (r) in order of descending magnitude, positive to negative. A probability of exceedance (F) was calculated for each ranked NEE value (r) according to the formula:

$$F = [r/(n + 1)] \times 100$$

where n is the number of ranked NEE values for the period of interest. Like flow duration analysis in hydrology (Searcy 1959; Vogel and Fennessy 1995; Potts and Williams 2004), flux duration analysis provides a

convenient and repeatable standard for comparing patterns of ecosystem exchange between sites and between years at the same site. By ranking and assigning a frequency to ecosystem exchange values, flux duration analysis incorporates episodic high activity periods, such as those associated with precipitation pulses, and sustained low level fluxes during interpulse periods into a single calculation. As additional ecosystem scale flux data sets become available, it may be possible to broadly classify ecosystem flux duration curves as "pulsed-dominated" and "steady-state" similarly to the way hydrograph-derived flow duration curves can be described and classified by the physical, biotic and anthropogenic factors controlling stream flow (e.g., Vogel and Fennessey 1995; Smakhtin 2001).

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