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PULSE EVENTS AND ARID ECOSYSTEMS

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Modifying the 'pulse–reserve' paradigm for deserts of North America: precipitation pulses, soil water, and plant responses

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Abstract The 'pulse–reserve' conceptual model—arguably one of the most-cited paradigms in aridland ecology—depicts a simple, direct relationship between rainfall, which triggers pulses of plant growth, and reserves of carbon and energy. While the heuristics of 'pulses', 'triggers' and 'reserves' are intuitive and thus appealing, the value of the paradigm is limited, both as a conceptual model of how pulsed water inputs are translated into primary production and as a framework for developing quantitative models. To overcome these limitations, we propose a revision of the pulse–reserve model that emphasizes the following: (1) what explicitly constitutes a biologically significant 'rainfall pulse', (2) how do rainfall pulses translate into usable 'soil moisture pulses', and (3) how are soil moisture pulses differentially utilized by various plant functional types (FTs) in terms of growth? We explore these questions using the patch arid lands simulation (PALS) model for sites in the Mojave, Sonoran, and Chihuahuan deserts of North America. Our analyses indicate that rainfall variability is best understood in terms of *sequences* of rainfall events that produce biologically-significant 'pulses' of soil moisture recharge, as opposed to *individual* rain events. In the desert regions investigated, biologically significant pulses of soil moisture occur in either winter (October–March) or summer (July–September), as determined by the period of activity of the plant FTs. Nevertheless, it is difficult to make generalizations regarding specific growth responses to moisture pulses, because of the strong effects of and interactions between precipitation, antecedent soil moisture, and plant FT responses, all of which vary among deserts and seasons. Our results further suggest that, in most soil types and in most seasons, there is little separation of soil water with depth. Thus, coexistence of plant FTs in a single patch as examined in this PALS study is likely to be fostered by factors that promote: (1) separation of water use over time (seasonal differences in growth), (2) relative differences in the utilization of water in the upper soil layers, or (3) separation in the responses of plant FTs as a function of preceding conditions, i.e., the physiological and morphological readiness of the plant for water-uptake and growth. Finally, the high seasonal and annual variability in soil water recharge and plant growth, which result from the complex interactions that occur as a result of rainfall variability, antecedent soil moisture conditions, nutrient availability, and plant FT composition and cover, call into question the use of simplified vegetation models in forecasting potential impacts of climate change in the arid zones in North America.

Keywords Antecedent soil moisture · Storms · Simulation model · Primary production

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Introduction

Noy-Meir (1973) defines deserts as "water-controlled ecosystems with infrequent, discrete, and largely unpredictable water inputs". In this context, Noy-Meir presents a series of generalizations regarding how sparse and sporadic moisture inputs lead to storage of carbon and energy. These generalizations are largely based on the 'pulse–reserve' model developed by Mark Westoby and Ken Bridges (unpublished data), which depicts a simple, direct relationship between rainfall, which triggers 'pulses' of primary production and results in 'reserves' of carbon and energy that accumulate in seeds, storage organs, etc. (Fig. 1a). In the intermittently favorable environment of aridlands, these reserves are inactive until triggered by the next rainfall event. In the absence of 'biologically important' storms, reserves slowly decrease over time (respiration, herbivory, decay), so there are likely to be thresholds on the length of time between storm events that can stimulate a pulse of growth.

The 'pulse–reserve' conceptual model is arguably one of the most-cited paradigms in aridland ecology. It evolves from three "obvious attributes" of arid ecosystems (Noy-Meir 1973): (1) precipitation is *low* and hence the dominant limiting factor, (2) precipitation is highly *variable*, both seasonally and annually, and (3) precipitation is highly *unpredictable*. While there is, of course, a relationship between total annual productivity and total annual or seasonal rainfall over broad spatial gradients or over a period of years (Lauenroth and Sala 1992; Webb et al. 1978), we argue that the relationship between rainfall and productivity in arid ecosystems is not simple nor as direct as suggested by the pulse–reserve model. The three attributes of precipitation (low, variable, unpredictable) in semiarid and arid ecosystems of the world manifest in an extraordinary diversity of observed dynamics, especially with regards to plant community composition and primary productivity (Evenari et al. 1985; MacMahon 1979; Whitford 2002).

Given the suite of complex factors governing the interactions between the timing and amount of rainfall, its subsequent effects on soil water content, and the growth and reproduction of plants, it is extremely difficult to make generalizations regarding rainfall pulses and aridland production. For example, in some instances, substantial precipitation may not translate into any net production, whereas in others, a small amount of rainfall that is suitably timed with the phenology of certain species, can result in relatively large responses (e.g., Reynolds et al. 2000b). A series of small precipitation events are not necessarily equivalent to the same amount of rainfall occurring as a single event, which may incur greater infiltration (Schwinning and Sala 2004), greater runoff (Wainwright et al. 1999), or less evaporation (Sala and Lauenroth 1982). Similarly, dry periods between rainfall events will affect soil water availability and plant growth. For example, light showers, each separated by dry periods, will result in short growth episodes associated with ephemeral soil moisture. In contrast, if the same amount of rain comes in more closely spaced events, soil water recharge will be greater and the growth episode will be longer (Burgess 1995; Noy-Meir 1973). Precipitation event size and distribution further interact with local topography and soils, which affect the extent and depth of soil water recharge (Ludwig et al. 1997; Noy-Meir 1973). Variability of precipitation over longer periods determines differential water availability for specific plant types (Chesson and Huntly 1993; Golluscio et al. 1998; Jobbágy and Sala 2000; Schwinning et al. 2003; Weltzin and McPherson 1997). For example, *within year* variability

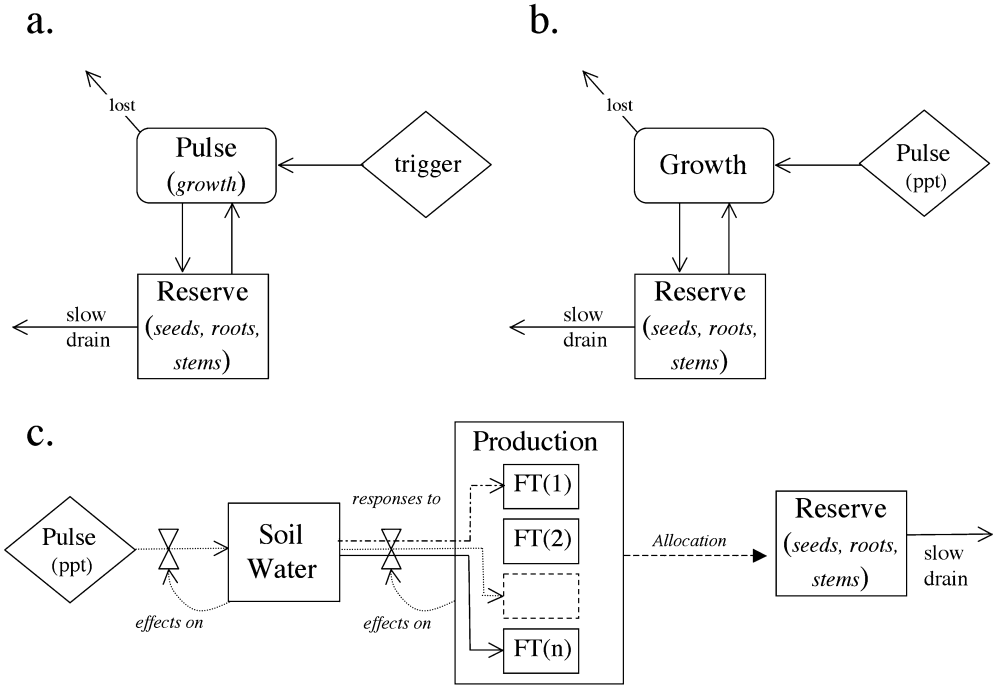

Fig. 1a–c Pulse–reserve models. **a** Pulse–reserve paradigm of Ken Bridges and Mark Westoby (unpublished data, presented in Noy-Meir 1973). **b** Depiction of pulse–reserve model as commonly interpreted in literature in which 'pulse' events are equated with the triggering events of precipitation, *not* with a pulse of growth as envisioned in previous panel. **c** Our modified pulse–reserve model, which explicitly identifies three components of the relationship between precipitation and plant production: pulses of precipitation, the role of soil water (e.g., antecedent conditions, soil type), and plant functional types (*FT*)

affects the recruitment and survival of annual species and the productivity of 'warm' vs 'cool' season species, *year-to-year* variability affects annuals and short-lived perennials to a greater degree than long-lived perennials, and *decadal* variation can affect long-lived perennials.

In light of these complexities, why is the pulse–reserve paradigm so often cited? We suggest that the heuristics of 'pulses', 'triggers', and 'reserves' in the context of arid ecosystems are highly intuitive and thus appealing. Nevertheless, we believe that the value of pulse–reserve is limited, both as a paradigm of how pulsed water inputs are translated into primary production and also as a framework for developing quantitative models. In Fig. 1c, we present a revised pulse–reserve conceptual model. Ironically, in our review of the literature—and as can be seen in papers of this special issue of *Oecologia*—the overwhelming number of references to the classic pulse–reserve paradigm in fact equate pulse events with the triggering events of precipitation (or a "pulse event of water availability"; Schwinning and Sala 2004) and *not* a pulse of growth, as originally proposed by Westoby and Bridges. Thus, our first change in the pulse–reserve model is to acknowledge this common usage of 'pulse' (compare Fig. 1b, a). Furthermore, to account for the diversity of plant responses to precipitation, the model is modified to include two new components, soil water and plant functional types (FTs). Many of the complex observed patterns of growth and rainfall alluded to above may be directly attributed to soil water availability. Hence, the role of *soil water* pools (storage) is crucial to understanding and predicting the fate of pulses of rainfall in arid ecosystems. The level of antecedent moisture may dampen or amplify the effect of an individual precipitation pulse. Once water enters the soil, we explicitly account for the role of *plant FTs* or life forms in translating soil water into production and transpiration losses. The use of plant FTs (e.g., winter/summer annuals, evergreen/deciduous shrubs, perennial forbs, C4 grasses, etc.) is a helpful simplification to group those species with similar responses (Reynolds et al. 1997), especially where the responses to water availability are due to the same mechanisms (Gitay and Nobel 1997). Furthermore, integration of plant water use with soil water availability helps distinguish plant *responses to* soil water availability from plant *effects on* soil water availability (Goldberg 1990). While these nonlinear feedbacks are difficult to separate, they play a crucial role in plant–soil water dynamics in arid ecosystems.

Our revised pulse–reserve conceptual model (Fig. 1c) explicitly identifies key issues that need to be addressed in order to develop a more complete and mechanistic understanding of the relationship between precipitation and plant production in arid and semiarid regions. Here, we use a simulation model (patch arid lands simulator, PALS; Gao and Reynolds 2003; Kemp and Reynolds 2004; Kemp et al. 1997; Kemp et al. 2003; Reynolds et al. 2000a, 2000b) to address these issues. We focus primarily on ecosystem water dynamics, with implications for productivity, by examining simulated soil moisture storage and water utilization by various plant FTs in response to rainfall pulses that occur in the three principal warm desert regions of North America. These desert regions, while contiguous and sharing similar plant FTs, provide a high diversity of rainfall pulses, including distribution by seasons, total amounts, and storm sizes, making their comparison of general interest. We investigate three related questions for three sites, one each in the Mojave, Sonoran, and Chihuahuan deserts:

1. What constitutes a 'biologically significant' pulse of rainfall? We focus on quantifying the size of individual precipitation events, their frequency of occurrence (seasonal/annual), and a grouping of these events into 'storms' in which we identify the *total*

Table 1 Temperature and rainfall characteristics for representative sites in the Mojave (http://www.wrh.noaa.gov/lasvegas/lasvegas_records.htm), Sonoran (http://www.wrh.noaa.gov/Tucson/climate/climate.html), and Chihuahuan (http://jornada-www.nmsu.edu/) deserts used in this study

	Las Vegas, Nev. (Mojave)	Tucson, Ariz. (Sonoran)	Jornada, N.M. (Chihuahuan)
Temperatures (1980–2000)			
Mean annual (°C)	20.0	20.8	14.9
January mean max (°C)	14.2	18.8	13.6
January mean min (°C)	2.1	4.2	−6.0
July mean max (°C)	39.6	37.9	34.9
July mean min (°C)	25.2	23.2	17.1
Rainfall means (1915–2000)			
Annual (Oct.–Sept.; mm)	116	270	247
Seasonal			
Winter (Oct.–March; mm)	68 (59%)	124 (46%)	84 (34%)
Spring (April–June; mm)	14 (12%)	21 (8%)	30 (12%)
Summer (July–Sept.; mm)	34 (29%)	125 (46%)	133 (54%)
Number of rain days (1915–2000)	3,485	5,950	4,250
Mean number of rain days year^{-1}	41	70	50
Mean number of rain days year^{-1} <1 mm (trace events)	26 (63%)	37 (53%)	17 (34%)

amount of precipitation in a storm, its *duration*, and the number of days (or *gaps*) between the occurrence of storms.
2. How do rainfall pulses translate into usable soil moisture pulses? We examine the probability of recharge (or wetting) with depth in a soil profile, given a particular storm size and antecedent soil water content. Two questions of particular interest are: (1) whether there is a separation of soil water into different pools with depth, and (2) how these relationships vary with soil texture.
3. How do plant FTs partition/utilize soil moisture pulses for growth? We argue that the wide range of potential outcomes resulting from any particular pulse of rainfall—and its entry into the soil—is largely the result of the interactions between plant FT diversity and water availability. We ask: what are the seasonal and annual patterns of water uptake by plant FTs with respect to different pulses and soil water pools located at different depths, how are individual pulses of rainfall (storms) translated into short-term community productivity and the growth of individual FTs, and, finally, how do FTs and rainfall pulses interact? Are productivity and growth responses mediated by antecedent soil water?

Materials and methods

Climate regimes and rainfall analyses

Since we are interested in the question of how 'pulses' of precipitation result in soil moisture recharge that can be utilized by a group of co-occurring plant FTs, we analyzed rainfall at specific locations as opposed to the rainfall averaged over a region, which would be more relevant to regional hydrology, for example. We obtained 85 years of climate data, from 1915 to 2000, for three sites: Las Vegas, Nev. (Mojave Desert), Tucson, Ariz. (Sonoran Desert), and Jornada Experimental Range, N.M. (Chihuahuan Desert; Table 1). For the purposes of this study, we define three seasons: *summer* (July–September), *winter* (October–March), and *spring* (April–June).

Each location is characterized by hot summers and cool winters, the latter of which differ somewhat among the sites. While daytime temperatures in winter are usually well above freezing, nighttime frost is highly likely at the Chihuahuan desert site, less likely at the Mojave desert site, and least likely at the Sonoran desert site (Table 1). The proportion of seasonal precipitation reflects geographic location and precipitation source regions (Conley et al. 1992; MacMahon 1979; Sheppard et al. 2002): each site receives winter precipitation from Pacific frontal systems, while summer precipitation is a result of monsoonal systems from the Gulf of Mexico or Gulf of California that deliver moisture as convectional storms. Spring is dry in all three deserts. These patterns result in the Mojave Desert being dominated by winter rains, the Chihuahuan Desert by summer rains, and the Sonoran Desert having a bimodal distribution.

We explored patterns of rainfall distribution to identify what constitutes a moisture pulse of 'biotic significance' (e.g., Burgess 1995). We conducted a frequency analysis of the sizes of precipitation pulses at three scales: *individual* events, *storm* events, and *seasonal* events. A storm is defined as any sequence of precipitation that occurs on successive days; and storms are separated by gaps of intervening rain-free days. Seasonal rainfall was summarized using the seasons as defined above. Annual rainfall is summed from October of the preceding year to September of the current year, which is more relevant to biological activity in these deserts than is the calendar year rainfall (e.g., Gibbens and Beck 1988; Neilson 1986).

Description of model

Overview

PALS is a physiology-based ecosystem model that simulates one-dimensional fluxes of carbon (C), water, and nitrogen (N) in a representative patch of desert vegetation of approximately 1–10 m^2 (Chen and Reynolds 1997; Gao and Reynolds 2003; Kemp et al. 1997, 2003; Reynolds et al. 1997, 2000b). The version used for the simulations reported here consists of four principal modules: (1) soil water distribution and its extraction via evaporation and transpiration, (2) energy-budget/atmospheric environment, (3) C/N cycling in soil organic matter pools and the resulting availability of inorganic N, and (4) the phenology, physiology, and growth of six principal plant FTs found in the three warm deserts of the Southwestern United States. The FTs are: (1) evergreen shrubs (represented by *Larrea tridentata*), (2) small deciduous shrubs and subshrubs (e.g., *Gutierrezia* spp, *Ambrosia* spp), (3) perennial forbs (short-lived C3 species active from winter through autumn), (4) perennial grasses (long-lived C4 species active from spring though autumn), (5) winter annuals (C3 species that germinate in autumn or early winter and flower and die in late winter or spring), and (6) summer annuals (C4 species that germinate in summer and flower and die in summer or early autumn). Aspects of the model structure of PALS relative to Fig. 1c are briefly described below.

Soil water

Soil water in PALS is modeled using a simple soil water budget (SWB) scheme, as presented by Kemp et al. (1997), Reynolds et al. (2000b), and Gao and Reynolds (2003). The SWB module was extensively evaluated using field data obtained from 90 locations along a 2-km desert slope (*bajada*) transect in the Chihuahuan desert in southern New Mexico. Based on its capacity to simulate soil water as a function of rainfall, soil texture, and evapotranspiration processes, we are confident that this module provides a robust representation of soil water distribution, availability, and its use by various plant FTs. In the version presented here, soil water is partitioned among six layers (the upper two layers are 10 cm thick, the rest 20 cm). Infiltration adds water to soil layers in a cascading fashion, according to the water-holding capacities of each layer, with no further redistribution between layers. Run-off is not considered in the version of PALS used here (see Gao and Reynolds 2003 for a version with run-off/run-on). The water-holding capacity of each layer is based on soil moisture retention between water potential values of −0.025 MPa and −10 MPa. The water potential at saturation (−0.025 MPa) follows Kemp et al. (1997) and the choice of the lower limit of water retention (−10 MPa) is assumed to be the lowest level of water that can be removed by desert shrubs or evaporation (the specific value has only a minimal effect upon water holding capacity and resulting soil water predictions). Soil water potential is determined as a function of soil texture using the relationship of Campbell et al. (1993) for clay contents above 20%. For clay contents below 20%, we use the relationship given by Kemp et al. (1997). Water is removed from the top layer by evaporation, following Linacre (1973), which is based on the evaporative energy input to the soil surface. Energy absorbed by the surface is partitioned between soil (evaporation) and vegetation (transpiration) by assuming a uniform interception of solar radiation by the vegetation canopy (see Kemp et al. 1997; Nichols 1992).

Removal of soil water via transpiration is modified from the energy-budget method employed in SWB by Kemp et al. (1997) and Reynolds et al. (2000b). The transpiration rate of each plant FT is calculated separately as a function of stomatal conductance and the

individual values are summed to yield the total daily transpiration. The water transpired by each FT is extracted from the soil layers in direct proportion to their root fractions (Kemp et al. 1997, Eq. 4). The stomatal conductance for each FT is a function of its water potential and the atmospheric vapor pressure deficit (Kemp et al. 1997, Eq. 7), whereas the water potential of each plant FT is calculated as the average water potential of the soil weighted by the fraction of roots in each layer (Reynolds et al. 2000b, Eq. 3). Based on the New Mexico study site, Kemp et al. (1997) and Reynolds et al. (2000b) established rooting distributions for each plant FT to minimize the deviations of predicted soil water contents from observed soil water contents (see Reynolds et al. 2000b, Table 2). This rooting distribution proved somewhat inadequate for the broader application used in the present study, which includes a much greater range of soil textures and smaller rainfall amounts (e.g., Mojave Desert). To minimize potential variations in predictions that could be associated with using different rooting patterns across these deserts, we used a single rooting distribution for each plant FT (Table 2). These distributions are only slightly different from that of Kemp et al. (1997) and correspond closely with observed root distributions for the specific plant FTs found in the three desert regions (Table 3).

FT production, biomass, and reserves

The growth of each of the FTs is determined from net carbon uptake, which is a function of plant water potential (see above), plant nitrogen content, and average daily air temperature. The specific parameter values for each of the plant FTs were obtained from our field and laboratory studies, the literature, and in some cases, best guesses (see Gao and Reynolds 2003; Kemp and Reynolds 2000). The synthesis of structural matter follows Johnson and Thornley (1983), i.e., the amount 'lost' in Fig. 1c. Carbon is allocated to roots, stems, and leaves in a fixed proportion, specific for each functional type (Reynolds and Kemp, unpublished data). All biomass compartments incur a 'slow drain' associated with maintenance respiration and tissue death, which are functions of daily temperature and long-term water deficits.

The model includes phenology mechanisms specific to each plant FT (Kemp and Reynolds 2000). Growth of shrubs and subshrubs occurs whenever air temperature is above freezing and the growth of all other FTs is cued by phenological controls that track running air temperature means to signal the onset or breaking of dormancy. In addition, modeled growth of annual plant FTs are subject to greater phenological controls associated with seed germination and establishment, shifts from vegetative growth to flowering, and death associated with dry days or seed-set, as generalized by Bachelet et al. (1988) from Beatley (1974) and Kemp (1983). An important aspect of annual plant FTs is the 'all or none' response to pulses of rain. In PALS, the threshold for germination is 10 mm of rainfall, which is considerably less conservative than the 25 mm used by Beatley (1974), but is consistent with others (Freas and Kemp 1983; Tevis 1958).

Table 2 Rooting distributions for the various plant functional types (FTs) as used in model simulation

Depth layer (cm)	Plant FT				
	Larrea (%)	Subshrubs (%)	Grasses (%)	Forbs (%)	Annuals (%)
0–10	10	10	20	20	30
10–20	20	30	30	20	30
20–40	30	25	25	30	30
40–60	30	25	15	20	10
60–80	10	10	10	10	–
80–100	–	–	–	–	–

Details of the specific formulations used to simulate growth and phenology of plant FTs are described by Kemp and Reynolds (2000) and Gao and Reynolds (2003). Modeled responses of FT growth and phenology were verified using plant growth data over a 6-year period from the New Mexico site (Gao and Reynolds 2003, Reynolds and Kemp, unpublished data). However, the growth responses of FTs simulated by the model appear reasonable for all three desert regions.

In PALS, the carbon uptake of FTs is dependent, in part, upon the N content of plants, which is derived from soil N availability and uptake. The soil N levels in the model are described using a modified version of the CENTURY model that simulates decomposition and mineralization of surface and root litter (Kemp et al. 2003). Plant uptake of N is a function of soil water uptake for each FT (Reynolds and Kemp, unpublished data).

Simulation conditions

Using the environmental data for the three sites (Table 1), we ran PALS for 85 years, from 1915 to 2000. In addition to daily rainfall records, model simulations require inputs of daily air and soil temperatures, humidity, and total shortwave radiation. These values were produced with a simple weather generator fit to 20-year average data from Las Vegas, Tucson, and the Jornada Experimental Range (Kemp and Reynolds 2004). All simulations were initiated with the same total biomass and the same distribution of that biomass among plant functional types for each site. The initial values are meant to be representative of a generic patch found in each of the three deserts, where *Larrea* is considered dominant at the beginning of the simulation (100 g m^{-2}), with subordinate amounts of subshrubs (45 g m^{-2}), grass (10 g m^{-2}), and forbs (5 g m^{-2}). These values are equivalent to an initial cover of 20%. The annual plant FTs germinate and grow in response to rainfall, as described by Bachelet et al. (1988) and Kemp and Reynolds (2000). Thus, over the course of the 85-year simulation, the biomass of all FTs changes in response to patterns of rainfall and the resulting soil water and N.

Analyses of simulated productivity due to rainfall and soil water

For each site, we first addressed the effects of soil texture on variation in soil water recharge and distribution. For this analysis, we explored the model responses for seven different soil textures represented by the following clay contents: 6% (sand), 12% (loamy sand), 18% (sandy loam), 24% and 30% (sandy clay loam), and 36% and 42% (sandy clay). We estimated soil water recharge with depth by tracking the number of times in which the soil water in each layer was increased to *any* extent following rainfall. We summarize these data as simply the percentage of years in which soil water in each layer was recharged. Soil water partitioning by FTs was obtained by summing soil water use by each plant FT for each soil layer during the growth year (October through September).

Assessing the extent to which rainfall pulses are translated into soil water and, in turn, the productivity of various plant FTs is complicated by many factors, including the antecedent rainfall and soil moisture and the previous productivity, which determine the size of the antecedent 'reserve'. There is often a great difference in the size of the 'reserves' of various FTs (e.g., small seeds of annuals vs large perennial shrubs). Thus, we used several different analyses to emphasize various aspects of the pulse responses. The simplest was to examine plant FT productivity in response to rainfall, regardless of antecedent conditions. We assessed the response to rainfall in two ways: (1) response to total *storm* amounts, and (2) response to total *seasonal* amounts. To compare productivity responses to individual storms, we concluded that a simple sum of net carbon uptake for a 5-day period following the storm was the best compromise between capturing the complete response, which could last for more than 5 days with relatively complete soil water recharge, versus overestimating the response to small storms by

Table 3 Rooting distributions (%) for various plant FTs in three warm desert regions from typical upland sites with various soil characteristics, but excluding dunes and areas with significant water tables. *M* Mojave, *S* Sonoran, *C* Chihuahuan

Desert	M	C	C	S	S	M	M	C	C	S	M	S	C
Plant FT	Shrubs/subshrubs						Grasses			Annuals		Others	
Depth layer (cm)	*Larrea*[a]	*Larrea*[b]	*Larrea*[c]	*Larrea*[h]	Shrub[d]	Subshrub[a]	Grass[f]	*Hilaria*[c]	Grasses[b]	Summer[g]	Winter[g]	Open[d]	Mixed[e]
0–10	0	8	46	10	4	5	45	29	18	30	40	2	25
10–20	4	36	23	19	18	16	35	22	36	40	40	13	14
20–40	17	46	23	48	47	58	20	30	31	25	20	58	32
40–60	33	6	7	15	24	21		16	12	5		23	22
60–80	31	4	1	5	6	0.5		3	3			4	7+
80–100	14			3	1	0.1						0	

[a] McAuliffe and McDonald (1995): loamy sand/sandy loam soils (subshrub is *A. dumosa*)
[b] Briones et al. (1996): clay loam (with clay below 25 cm), grass is primarily *H. mutica*
[c] Montaña et al. (1995): sandy clay loam (with clay loam below 15 cm), grass is *H. mutica*
[d] MacMahon and Schimpf (1981): coarse textured soils (shrub is *A. deltoidea*), roots unidentified
[e] Moorhead et al. (1989): coarse-textured soils with a calcic horizon at about 40 cm (principal species are *L. tridentata*, subshrubs, and the succulent *Opuntia phaeacantha*)
[f] Nobel (1997): sandy loam soils (grass is *Pleuraphis rigida*), although the site is in NW Sonoran desert, the climate is more characteristic of the Mojave
[g] Forseth et al.(1984): sand to loam soils in the Sonoran desert and Mojave desert (winter annuals) at low elevations
[h] Thames (1979): soil texture not described, site dominated by *Larrea*

including more productivity than was associated with that storm, given that the average frequency of gaps between storms was just over 5 days. For seasonal response to rainfall, we simply summed the total productivity for a given season.

To evaluate the interactions of antecedent soil water and reserve size with respect to simulated productivity responses to rainfall pulses, we constructed contour plots of relative productivity responses to storm size versus the antecedent soil moisture prior to that storm. Relative responses to storm events were calculated by comparing total aboveground biomass (AGB; g m^{-2}, summed across all FTs) and the productivity rate of individual plant FTs (g m^{-2} day^{-1}) on the day after the storm versus the day before the storm (i.e., percent relative response $=100\times(x_{after}-x_{before})/x_{before}$, where x is either AGB or FT productivity rate). First, we evaluated the response of total AGB to precipitation pulses over the 85-year period by constructing contour plots that exhibit how productivity is coupled to storm events and antecedent soil water. Antecedent soil water is the absolute soil water content (centimeters) in the 0–80 cm profile on the day before the storm. Contour plots were constructed by fitting a smooth surface to the values of relative change in AGB, with storm size and antecedent soil water content as continuous predictor (independent) variables. The smooth surface was obtained by running a local regression analysis (PROC LOESS; SAS Institute, Cary, N.C.), which uses a non-parametric, weighted least-squares method for fitting local regression surfaces (Cohen 1999). Quadratic functions were fit at the center of 'neighborhoods', where each neighborhood contained ca. 10% of the data: *N* (number of storms in 85 years) = 2,042, 3,019, and 2,763 for the Mojave, Sonoran, and Chihuahuan deserts, respectively. A neighborhood was determined for each point and the contribution of other data points in the neighborhood to the local fit was determined by a smooth, decreasing function of their distance from the center. A grid of storm size by antecedent soil water content was set-up to span the range of observed and simulated values and the fitted surface was employed to interpolate the relative response values at each point in the grid. Finally, the interpolated data were used to construct a contour plot that demonstrates the relationship between changes in AGB, storm size, and antecedent soil water content.

Second, we examined the responses of individual plant FTs to storm events and antecedent plant water potential. We used plant water potential (vs soil water content, as in the above analysis), because the different plant FTs are characterized by different rooting patterns and thus are exposed to dissimilar soil water environments. Plant water potential reflects the integrated soil water environment for each plant FT calculated as the root-weighted average of soil water potential of each layer containing roots. We used the LOESS procedure to obtain interpolated values of relative change in productivity rate for a grid of storm size by antecedent plant water potentials. The analysis was conducted for three key plant FTs within their active growth periods: evergreen shrub *Larrea* (active March–November), perennial grasses (March–November), and winter (C3) annuals (October–March). We note that, although contour plots do not provide information on the statistical significance of responses, they are appropriate for visual evaluation, given the multiple nonlinear interactions among the variables analyzed.

Results

What constitutes a biologically significant pulse of rainfall?

In all three deserts, a large proportion (34–63%) of the individual rainfall events over the 85-year period from 1915 to 2000 consisted of trace amounts (Table 1). However, even when trace events (<1 mm) are excluded from the analysis, the precipitation bin containing the most rain events is the 1–5 mm size category (Fig. 2a).

There are some differences among the three sites, primarily the fewer number of total events in all categories in the Mojave (see rain days in Table 1). The Sonoran site has more small events (<5 mm) than the Chihuahuan, but slightly fewer rainfall events between 5 mm and 15 mm. When we grouped all rainfall events occurring on sequential days as 'storms', we found that the storm-size category with the highest frequency is again the smallest size class (<5 mm); and the Mojave Desert again has the lowest frequency of all events (Fig. 2b). In our analysis, we also considered including 1–2 intervening rain-free days when defining a storm event but found only a small effect (data not shown).

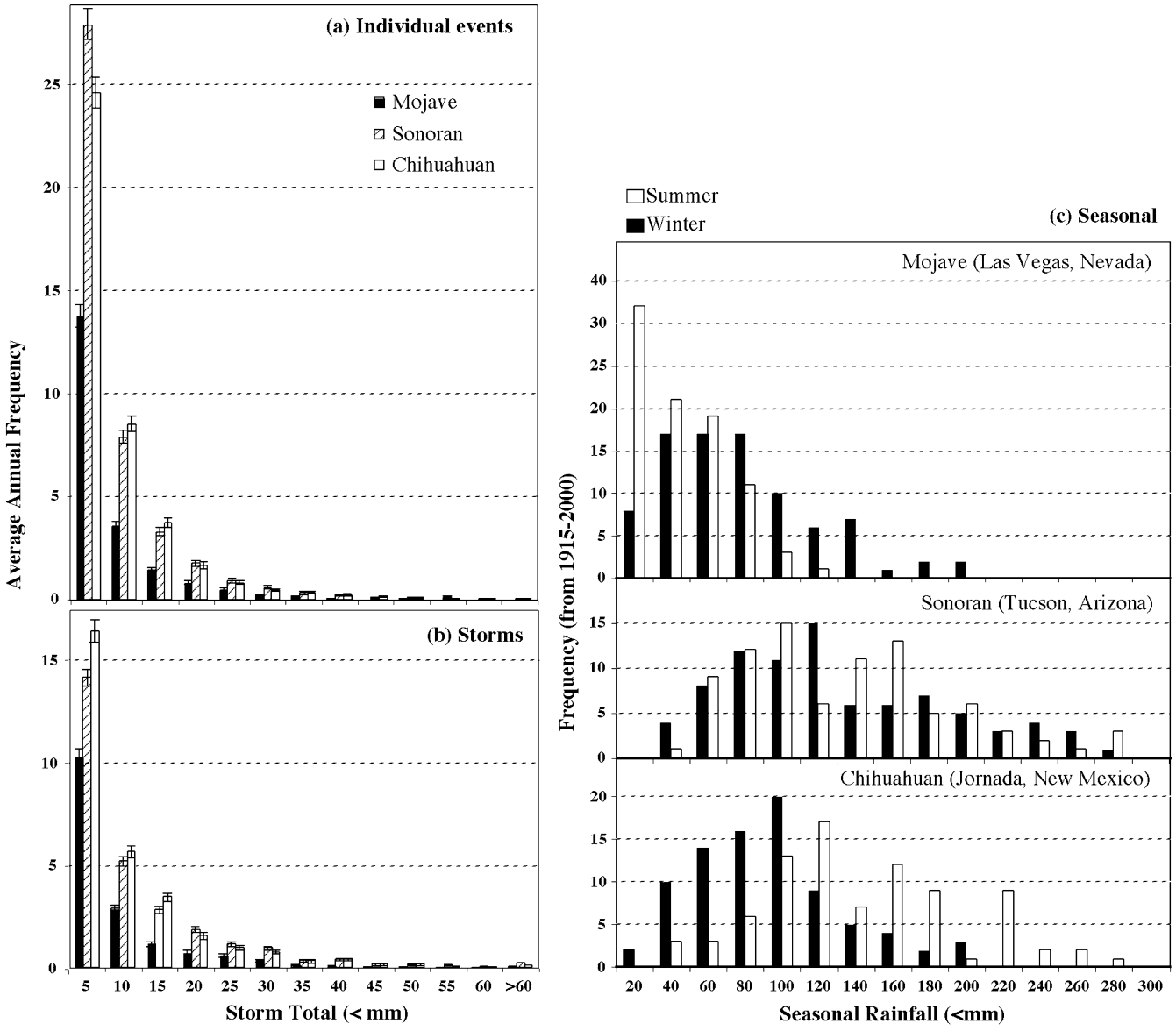

Fig. 2a–c Frequency analysis of size of precipitation events for the Mojave, Sonoran and Chihuahuan sites. **a** Averages for individual events (events <1 mm excluded). **b** Averages for storm events (i.e., sequences of precipitation occurring on successive days, separated by gaps of rain-free days). **c** Frequency (number of years) for total precipitation during winter and summer seasons. Averages are based on data covering the period 1915–2000

Finally, we grouped all rainfall into *seasonal* summer and winter 'pulses'. We found substantial differences among the deserts, which is related to their climatic patterns (Sheppard et al. 2002). Winter rainfall in the Mojave is substantially greater than summer: most years have winters with 20–100 mm and most summers have anywhere from 0 mm to 60 mm, with the 0–20 mm category being most common (Fig. 2c). Both the Sonoran and Chihuahuan sites have high probabilities of moderate seasonal rainfall in both winter and summer (Fig. 2c). The Sonoran site has relatively similar distributions for both seasons, reflecting the tendency for the monsoonal systems from the Gulf of Mexico to deliver about the same amount of rainfall over 3 months in summer as the frontal storms from the Pacific deliver over the 6-month period of fall/winter (Sheppard et al. 2002). The Sonoran and Chihuahuan sites differ primarily in the frequency distribution of fall/winter precipitation over the 85 years examined, such that the Sonoran site is more likely to have winter precipitation exceeding 100 mm, compared with the Chihuahuan site (59% vs 27%; Fig. 2c).

If seasonal rainfall constitutes something akin to a 'pulse', it must be more than a summation of widely dispersed rainfall events. Rather, it must have a relatively high probability of occurring as a collection of events capable of producing soil water recharge useful to some plant FTs for a significant fraction of the season (Burgess 1995). We specifically address soil water recharge and use by plant FTs below. However, we also assessed the *potential* for rainfall to recharge soil water by analyzing

the frequency of gaps between storms within a season. The frequency distribution of gaps between storms (Fig. 3) reveals that the majority of storms—especially within the key winter and summer growth seasons—are strongly clustered in all three sites, with most storms having gaps of less than 10 days and a majority of those gaps being less than 5 days. Summer storms at the Sonoran and Chihuahuan sites are the most consistently connected, with more than nine storms per year connected by less than 5 days. Similarly, winter rainfall in both the Mojave and Sonoran sites is relatively strongly linked, having an average of five and seven storms per year that are separated by 5 days or less (Fig. 3).

How do rainfall pulses translate into usable soil moisture pulses?

Using the 85-year model simulations, driven by daily rainfall recorded from each of the three sites coupled with the prospective water utilization by different FTs and loss by evaporation, we assessed the potential for soil water recharge over a range of soil textures at each site by calculating the percentage of years in which recharge (evaluated as any increase in soil water in that layer) occurred to various depths (Fig. 4). The only soil texture for which there is consistent (>50% of years) recharge below 80 cm in any season is sand (6% clay). For sandy loam (18% clay) and finer, there is no consistent recharge below 60 cm for any of three rainfall regimes of different sites. There are marked differences among the three sites in the predicted soil water patterns of loamy sands (12% clay). The Mojave rainfall regime produces recharge of the 40–60 cm layer in 36% of the years but in only 15% of the years for the 60–80 cm layer. There is recharge of these two layers in 67% and 44% of the years, respectively, at the Chihuahuan site and in 83% and 53% of the years, respectively, at the Sonoran site (Fig. 4). In conclusion, given our defined 'recharge' as *any* increase in soil moisture at a given depth, these results suggest that deep recharge (>80 cm) is an uncommon event. These results suggest, however, that there is a relatively clear distinction between depth of soil water recharge in coarse- versus fine-textured soils and hence further results are shown for representative coarse- (9% clay) and fine-textured (21% clay) soils (see below).

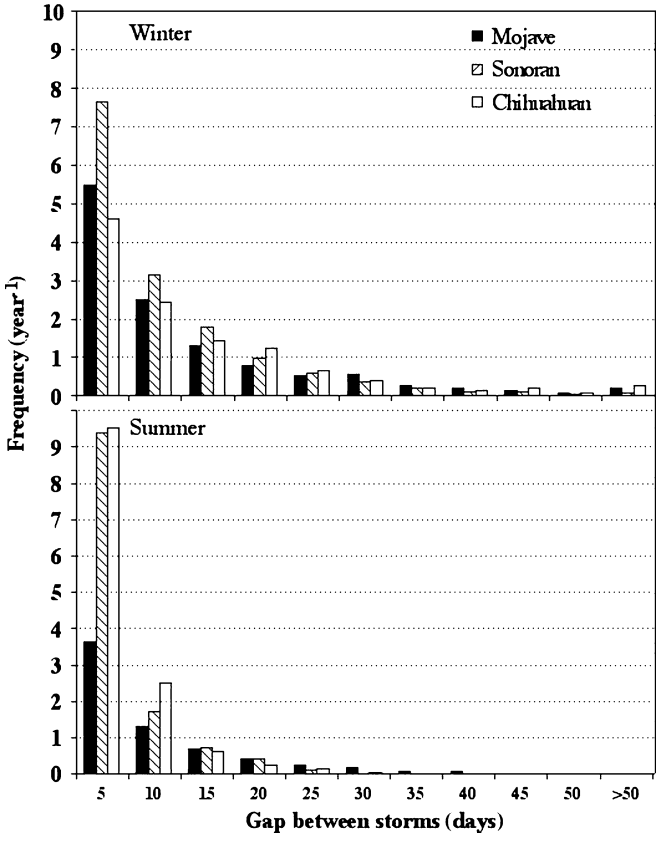

Fig. 3 Frequency analysis (annual average based on data covering the period 1915–2000) of the average gap (or number of days) between individual precipitation events for the Mojave, Sonoran, and Chihuahuan desert sites

How do FTs partition/utilize soil moisture pulses for production?

We first analyzed the response of the plant FTs to rainfall directly by examining the amount of accumulated growth during each 5-day period following individual storm events. Overall, there is a relatively poor relationship between net production and storm size (Table 4). The strongest relationships are for annuals and forbs in the Chihuahuan desert; and the weakest relationships are for *Larrea* and grasses in any of the sites. The relation between total productivity (all FTs grouped) and storm size is greatest for the Chihuahuan desert site, which is primarily driven by the coupling of annuals' and forbs' growth to individual summer storms at this location (Bachelet et al. 1988; Kemp and Reynolds 2000; Table 4).

Next, we examined the relationship between the productivity (seasonal, annual) of the various plant FTs and the total seasonal or annual precipitation for both coarse- (9% clay) and fine-textured (21% clay) soil types over the 85-year period (Table 5). The most consistently strong positive relationships are between: (1) the annuals' FTs and seasonal moisture (C3 annuals during the winter, C4 annuals in the summer), (2) the forbs' FT and winter rainfall, and (3) total productivity to total annual precipitation, although this is generally low and highly variable (29–64%). Most of the plant FTs are correlated to seasonal rainfall for particular sites and/or soil textures (Table 5). For example, subshrubs are correlated with summer rainfall in the Chihuahuan desert and with winter rainfall at the Mojave site in the coarse-textured soil. *Larrea* is the only plant FT in which productivity is not even weakly correlated with seasonal or annual rainfall. Total growth is moderately (Mojave site) to strongly (Chihuahuan site) correlated with total rainfall over the year (October–September; Table 5).

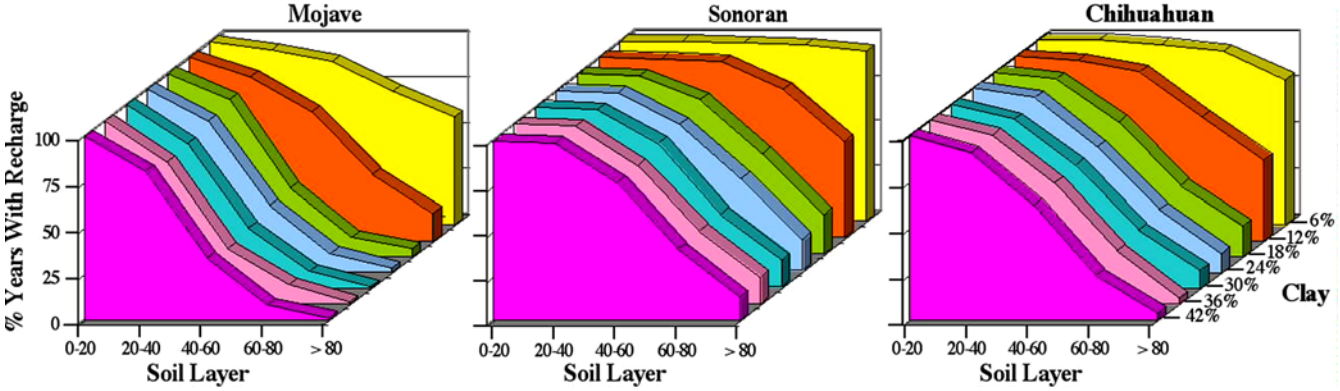

Fig. 4 Summary of model simulations over the period 1915–2000, showing the percent years in which there is soil water recharge. Results illustrated as a function of depth and texture (percent clay content). Recharge is considered to occur if any water enters a soil layer. Hence, this is a conservative approach and it shows that at the deepest soil depths (>80 cm) recharge is a rare event, except for the sandiest soils

We assessed the potential for different plant FTs to partition soil water use by depth by calculating the average amount of water taken up annually by each FT from each 20-cm soil layer (Fig. 5). Although the rainfall regimes at the three deserts are quite different, plant FTs obtain more than 60% of their annual water from the top 40 cm at all three sites; and this is the case for both coarse- and fine-textured soils. In the coarse-textured soil (9% clay), an average of about 36% of the total annual available soil water is obtained from lower soil layers (40–60 cm). In the fine-textured soil (21% clay), uptake from these layers averaged about 25% of the total annual water uptake. There is a difference in the proportional water uptake among the various FTs with depth, but this difference is mostly due to the decreasing proportion of water taken up by the two annual FTs with increasing depth and a concomitant increasing proportion of water taken up by subshrubs (Fig. 5).

Finally, we summarized average productivity of individual plant FTs over the 85-year simulations for the winter and summer season periods for each of the desert sites (see Fig. 6). While these results reveal some interesting shifts in productivity among the various plant FTs with shifts in rainfall regime (site) and/or soil texture, perhaps the most notable result is that total growth is greatest during the winter season under all conditions, except for coarse-textured soils at the Chihuahuan site, which had similar winter and summer productivity. This is only partly consistent with general rainfall patterns, which suggest that we might expect a shift from a winter maximum in productivity at the Mojave site (where 59% of the annual rainfall falls during the winter season) to a summer maximum for Chihuahuan productivity (where 54% of annual rainfall falls during the summer; see Table 1). However, summer rainfall is apparently not as effectively converted into productivity as is winter rainfall by this group of co-occurring plant FTs (Reynolds et al. 1999). This is a reflection of both higher evaporative losses in summer vs winter seasons and patterns of biomass persistence and phenology of specific FTs. Over the course of these simulations, shrubs and subshrubs had the most consistent aboveground biomass from year to year ('reserve') and were thus most able to take advantage of winter rainfall. In contrast, while grasses and summer annuals are the strongest responders to summer rainfall (Table 5), their biomass is highly variable from year to year and they typically contribute a smaller percentage to total patch biomass, which constrains their ability to utilize summer moisture in some years. For example, the simulated cover of perennial grasses was quite low in the decade following the drought of the 1951–1956 at both the Sonoran and Chihuahuan sites; and hence their response to summer rainfall was limited during this time (data not shown).

Table 4 Coefficient of determination (R^2) between storm size and productivity for the 5-day period following a storm for each of the plant FTs over the 85-year simulation period (annuals and forbs are combined, since any or all may respond, depending upon timing of rainfall). The total number of storms (N) = 2,095, 1,926, and 1,652 for the Sonoran, Chihuahuan, and Mojave sites, respectively

Soil type	Site	Plant FT				
		Larrea	Subshrubs	Grasses	Annuals and forbs	Total
9% clay	Mojave	0.05	0.11	0.00	0.11	0.15
	Sonoran	0.02	0.06	0.01	0.09	0.10
	Chihuahuan	0.07	0.17	0.10	0.27	0.34
21% clay	Mojave	0.01	0.03	0.00	0.16	0.17
	Sonoran	0.04	0.12	0.05	0.19	0.23
	Chihuahuan	0.10	0.18	0.08	0.22	0.30

Table 5 Coefficient of determination (R^2) between seasonal and annual rainfall and productivity for each of the plant FTs over the 85-year simulation period (N=85). *Annuals* are C3 winter annuals or C4 summer annuals, which are matched with their particular seasons. The C3 winter annuals have the highest correlation with annual rainfall in all cases, which is the value given. *Italics* indicate relationship is negative

Site	Texture (% clay)	Season	Plant FT					
			Larrea	Subshrubs	Grasses	Annuals	Forbs	Total
Mojave	9%	Winter	0.06	0.28	0.04	0.36	0.24	0.45
		Summer	0.00	0.00	0.37	0.30	*0.01*	0.01
		Annual	0.04	0.19	0.25	0.18	0.13	0.36
	21%	Winter	0.01	0.08	0.07	0.31	0.15	0.23
		Summer	*0.01*	0.06	0.37	0.35	0.00	0.11
		Annual	0.03	0.08	0.31	0.18	0.11	0.37
Sonoran	9%	Winter	*0.04*	0.00	0.00	0.10	0.44	0.29
		Summer	0.00	*0.03*	0.00	0.17	0.00	0.04
		Annual	0.00	*0.02*	0.00	0.10	0.31	0.29
	21%	Winter	*0.06*	0.04	0.11	0.30	0.32	0.31
		Summer	*0.01*	0.00	0.03	0.32	0.00	0.16
		Annual	*0.05*	0.04	0.11	0.17	0.22	0.48
Chihuahuan	9%	Winter	0.00	0.07	0.10	0.25	0.08	0.17
		Summer	0.00	0.24	0.17	0.20	0.00	0.48
		Annual	0.00	0.32	0.26	0.10	0.00	0.64
	21%	Winter	0.00	0.13	0.07	0.16	0.13	0.17
		Summer	0.00	0.20	0.18	0.13	0.00	0.45
		Annual	0.01	0.30	0.25	0.10	0.03	0.60

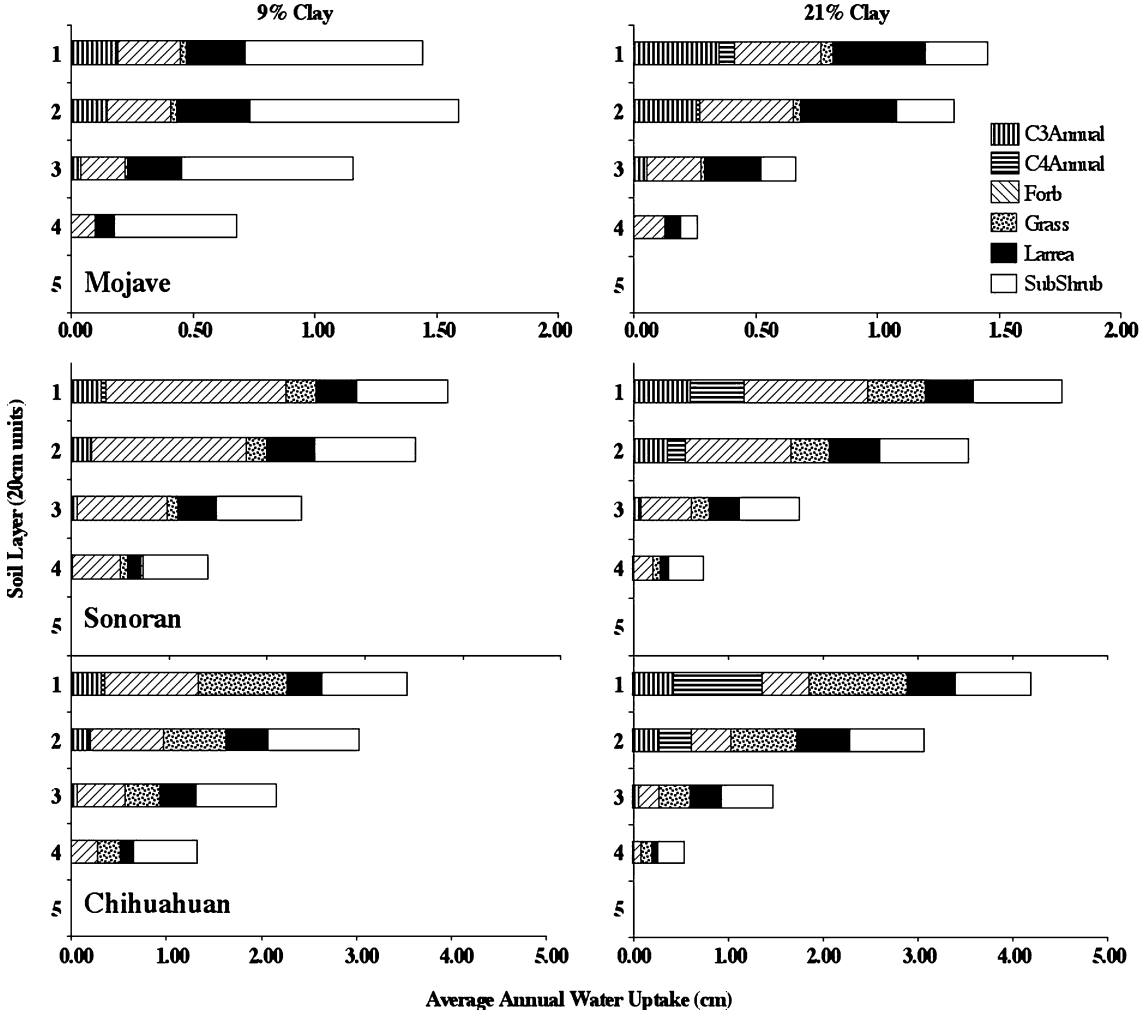

Fig. 5 Average annual water uptake by various plant FTs shown for 20-cm increments in soil depth. Average is based on simulation covering the period 1915–2000

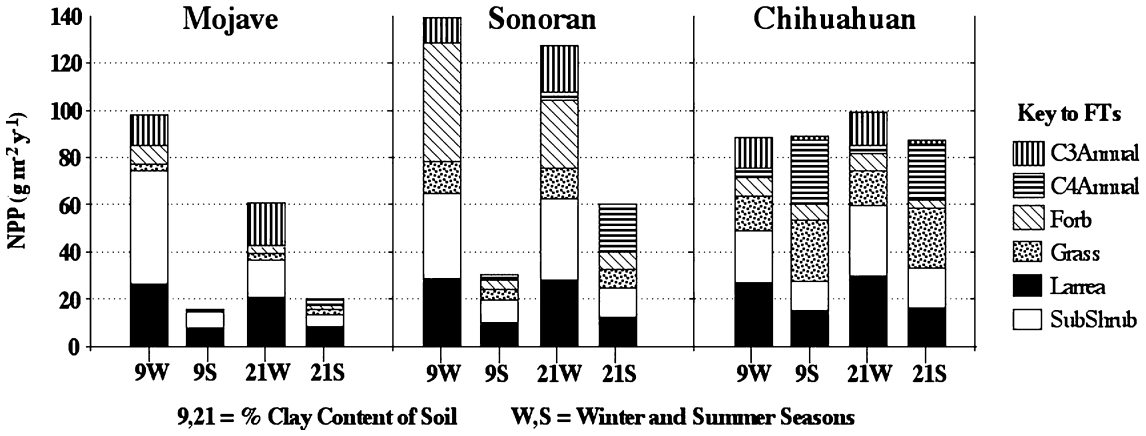

Fig. 6 Average simulated plant FT productivity during the summer (July–September) and winter (October–March) seasons for the 85-year period 1915–2000

Interactions: storm size, soil water, and plant FT response

Our revised pulse–reserve model assumes that plant FT growth responses to pulse precipitation are mediated by antecedent soil water. To test this, we examined the relationship between growth, storm size, and antecedent soil water content. First, we evaluated total AGB production, which sums overall plant FTs for the three desert sites. Production responses are similar across soil types, the main difference being that the effect of antecedent soil water content on the growth response to rainfall is dampened slightly for coarser soils (9% clay content; data not shown) and thus we focused on soils with 21% clay. The contour plots in Fig. 7 show that antecedent soil water content and precipitation pulses interact in complex ways to affect growth. The contours are the percent relative change in AGB over the range of representative storm sizes and water contents. A scatter plot of daily observed storm size versus simulated antecedent soil water content is overlaid to show their distribution over the 85-year period. The three deserts primarily differ in three aspects: (1) the magnitude of the growth response, (2) the range of storm sizes and water content that yield high responses, and (3) the degree of interaction between storm size and soil water.

First, over the range of storm sizes and water contents captured in Fig. 7, a maximum of a 35–40% increase in total AGB following a storm is predicted for the Mojave and Sonoran sites (Fig. 7a, b), but only up to a 20–25% increase in the Chihuahuan site (Fig. 7c). Additionally, a reduction in biomass is expected to occur in both the Mojave and Sonoran sites following large storms under extremely wet conditions, i.e., for initially wet soils (however, this may be an artifact of the response surface fitting to limited data for these conditions). No reduction in biomass following a storm is expected in the Chihuahuan site. Second, in the Mojave, the greatest increase in biomass is expected for moderate rainfall when antecedent soil water is low; and, in the Sonoran, the largest growth response also occurs for initially dry soils, but there is no optimal storm size (i.e., AGB increment increases with increasing storm size for dry soils). In the Chihuahuan site, the greatest response occurs at the largest storm site, regardless of soil water content. Third, in both the Mojave and Sonoran sites, storm size and antecedent soil water strongly interact in complex, yet dissimilar, ways to affect growth, as indicated by the diverging and curved contours. Conversely, antecedent soil water is less important in controlling the growth response to rainfall in the Chihuahuan desert; and the response to small (<2 cm) and large (>5 cm) storms is essentially independent of soil water, whereas intermediate sized storms (2–5 cm) produce growth responses dependent upon antecedent soil water. In all deserts for storms <ca. 1 cm, initial soil water content has little effect on the growth response to precipitation.

We selected three key plant FTs (*Larrea*, perennial grasses, C3 winter annuals) to examine the coupling between individual FT growth responses, storm size, and antecedent plant water potential. The contour plots in Fig. 8 illustrate substantial variation in the growth patterns for these three FTs. Growth rates of the C3 annuals and grasses are much more sensitive to storms and soil/plant water status than *Larrea*, as indicated by their more closely spaced contour lines and greater range in values of percent change in growth rate. The maximum-response regions of the environmental plane (>500%) differ greatly across FTs, but only slightly across sites. With respect to antecedent water potential, the range is relatively narrow for grasses compared with C3 annuals, but C4 grasses [perhaps due to their large potential growth rates (Fernández and Reynolds 2000), which are accounted for in the model] exhibit higher growth responses for lower water potentials, at least for the Mojave and Chihuahuan desert sites (Fig. 8). For all FTs, the least pronounced changes in the growth rates occurred for prior wet conditions (less negative water potentials) and, in the case of the grasses, for very dry antecedent conditions (low water potentials). In general, for C3 annuals and grasses, the contour lines are nearly vertical for storm sizes exceeding 1–2 cm, indicating that storm size has little

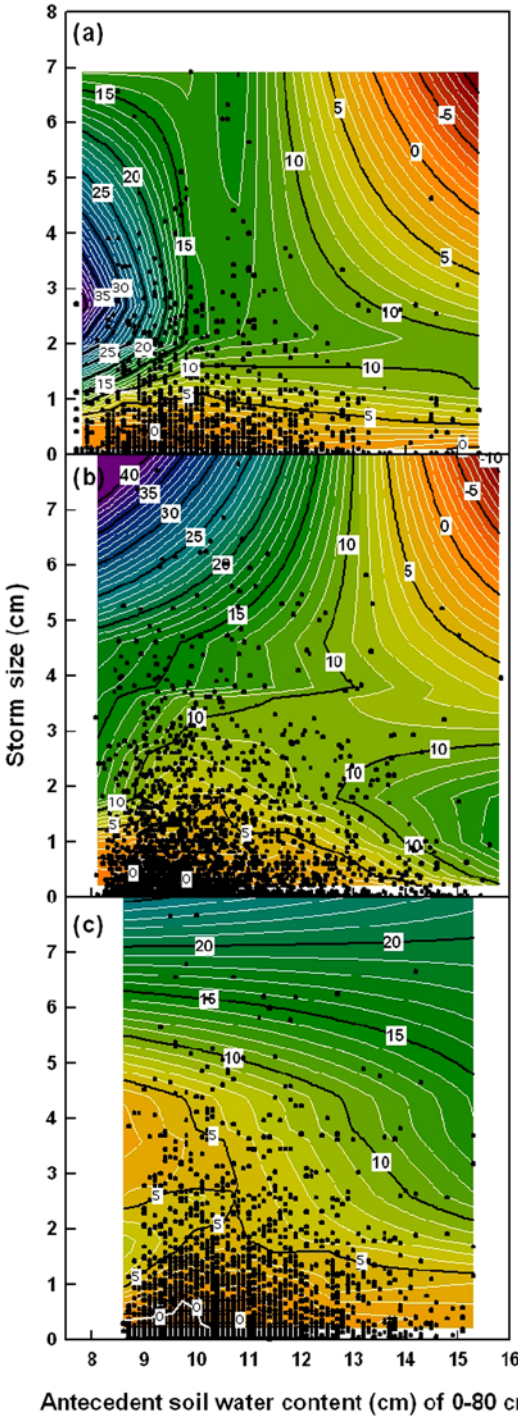

Fig. 7a–c Contour plots of the relative change in total aboveground biomass (%) following a storm relative to its size and antecedent soil water content. Scatter plots of simulation model output for an 85-year period are overlaid. Results for soils with 21% clay content and are shown for each site: **a** Mojave, **b** Sonoran, **c** Chihuahuan

effect on the growth response to storms >2 cm (Fig. 8) and growth is exclusively a function of soil water content (as indicated by plant water potential). However, since most of the storms are <2 cm, both storm size and antecedent soil water are important determinants of growth following most storms. The *Larrea* FT group is unique in that it has a more conservative growth response and is predicted to be more efficient at translating rainfall into production when it is initially water-stressed (has very negative water potentials). Interactions between storm size and water potential are also stronger for *Larrea* than the other two FTs, as indicated by the generally curved contour lines (Fig. 8). We note that the plant FT responses are relatively similar across the three desert regions, a result that is not unexpected given that the model functions are similar.

Discussion

The majority of rainfall events in arid and semi-arid regions are small (see Fig. 2a, b; Green 1960; Sala and Lauenroth 1982; Smith and Schreiber 1974). There is considerable debate regarding the importance of these small events to plant growth and survival (Beatley 1974; Dougherty et al. 1996; Paulsen and Ares 1962; Sala and Lauenroth 1982; Schwinning et al. 2003; Weaver 1982), much of which focuses on individual rainfall events taken in isolation. While Sala and Lauenroth (1982; 1985) showed that small rains (<5 mm) stimulate the growth of grasses in semi-arid regions and concluded that these small events may provide a shallow source of moisture for some plant FTs, others suggest that small rainfall events do not reach the roots of plants (Dougherty et al. 1996; Nobel 1976; Weaver 1982). Indeed, the usefulness of small rainfall events (<5 mm) as determinants of plant growth would seem quite limited in warm deserts of the southwestern United States, given the very low numbers of roots in the top few centimeters of soil (Franco and Nobel 1991; MacMahon and Schimpf 1981; Rundel and Nobel 1991) and the high evaporation losses from the soil surface (Reynolds et al. 2000b; Samis and Gay 1979). The resolution of this dilemma lies with a consideration of additional factors that influence the 'biological significance' of individual rainfall events: namely, antecedent soil moisture conditions and the chance of that rainfall event becoming part of a sequence of consecutive events. In fact, whereas the simple 'pulse–reserve' paradigm of desert ecosystems (Fig. 1b) suggests a strong linear relationship between pulses of rainfall and plant productivity, we find that only when rainfall is summed as seasonal amounts do we begin to find a relationship between rainfall and productivity (Tables 4, 5).

Our findings suggest that the biological significance of individual rainfall events accrues primarily from their summation into 'storm events' and the collection of such storms within a season. Storm events are most likely to produce soil moisture recharge of sufficient depth to induce and maintain a significant productivity response (i.e., to be biologically significant). Further, our analysis of frequency distribution of gaps between storms over an 85-year period for the Southwestern United States demonstrates that there is, indeed, a propensity for storms to occur in temporal proximity. Such a conclusion is contrary to traditional probability analyses of rainfall data from

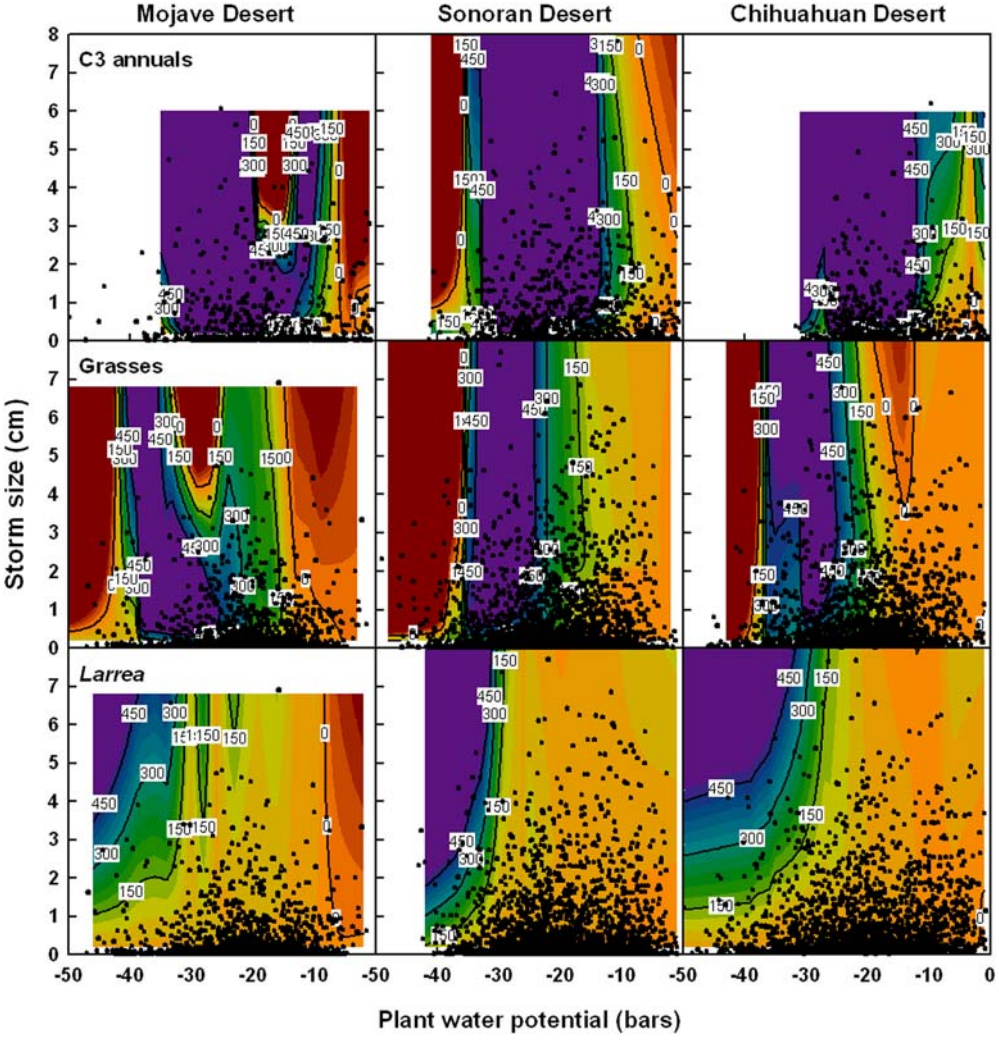

Fig. 8 Contour plots of the relative change in individual plant FT growth rates (%) following a storm. Contours show regions of maximum (*purple*) and depressed (*red*) growth, which vary with FT (*Larrea*, perennial grasses, C3 winter annuals), site, storm size, and antecedent plant water potential. Scatter plots of observed storm sizes and simulated antecedent plant water potential for the 85-year period are overlaid. 1 bar = 100 kPa

desert regions. For example, Green (1960) writing about rainfall in Arizona observed: "The probability that any day during (July and August) will be the beginning of even a 3-day rainy period is quite small, ... suggest(ing) that precipitation at any given point rarely falls on more than two successive days during the July and August 'rainy season'." While such a conclusion may well characterize long-term probabilities for particular dates, it does not accurately reflect the chance that at some point during the season there will be a sequence or sequences of rain events that recharge soil moisture to some degree. It also does not seem to reflect the conditional probability that, once the first storm occurs, the probability of subsequent rains/storms is relatively high, which is a result of persistent storm tracks characteristic of both summer and winter in these regions (Sellers and Hill 1974; Sheppard et al. 2002). Storm events are relatively more likely in some years or sequences of years than in others (Higgins et al. 1998; Sellers and Hill 1974) and our analysis of frequency distributions of seasonal rainfall totals for the years 1915–2000 indicates that the probability of persistent rainfall varies with the desert region and season. The probability of persistent rainfall is relatively high for the Sonoran Desert in both winter and summer and for the Chihuahuan Desert in summer; and it is somewhat less likely for the Chihuahuan and Mojave Deserts in winter and not likely at all for the Mojave Desert in summer.

Our proposed conceptual model for the pulse–reserve paradigm (Fig. 1c) demonstrates that productivity in deserts is *not a direct response to rainfall*, but rather to soil water availability. Thus, the best way to predict productivity responses to rainfall pulses is not through an analysis of the rainfall events alone, but rather via an analysis of soil water recharge and availability, which is affected not only by the timing of rainfall sequences but also by antecedent soil moisture and its vertical distribution in the soil profile. All of these are affected by soil texture, topography, atmospheric conditions, and plant cover and biomass, which interact with one another in multiple, nonlinear ways.

Our use of the PALS ecosystem model to examine patterns of soil water recharge and growth over a relatively long-term period (85 years) for representative sites in the Chihuahuan, Sonoran, and Mojave deserts reveals a high variability in both soil water recharge and growth with respect to the high variability in water input. Nevertheless,

several general patterns emerge from this exercise. Simulations suggest a relatively consistent pattern of vertical soil water availability among the three desert sites, in spite of very different rainfall regimes. There appears to be a threshold with respect to soil texture, which determines the extent of deep soil water recharge. This threshold varies to some extent with the particular rainfall regime, but is around 12% clay (loamy sand). In sand (6% clay), a significant amount of soil water recharge occurs below 60 cm (i.e., recharge in >50% of years, with about 20% of the total soil moisture found there) for all three rainfall regimes. In loamy sand (12% clay), only the Sonoran and Chihuahuan rainfall regimes produced recharge below 60 cm in >50% of years, but this amounted to only about 10% of the total soil moisture. In sandy loams (18% clay) and finer-textured soils, there was no reliable soil water below 60 cm in any of the regimes. Irrespective of this textural separation, we found that the majority of soil water is retained within the top 20 cm of soil for all textural classes and is generally quickly removed by soil evaporation or transpiration by phenologically-active plant FTs. With respect to transpiration, about 65–75% of the water was obtained from the top 40 cm of soil for both coarse- (9% clay) and fine-textured (21% clay) soils, respectively, when averaged over the 85-year simulation (Fig. 5).

Analysis of the total AGB and individual plant FT productivity over the 85-year simulation period indicates that growth is driven by complex and nonlinear interactions between soil water and precipitation pulses (Figs. 7, 8). These results emphasize the importance of explicitly considering soil water effects in conceptual models of plant growth responses to rainfall pulses. The majority of storms are small and occur on relatively dry soils (i.e., the points in Fig. 7), for which we can expect relatively low productivity responses in all desert regions. Community-level productivity generally increases with increasing storm size, but with quite different interactions with soil water status across the different desert regions (Fig. 7). Storms of intermediate size (2–4 cm) have the greatest impact on growth in the Mojave desert, with relatively dry soils, but have only moderate impact in the Sonoran desert, at any soil water level; and they have no impact in the Chihuahuan desert, with dry soil conditions. Large storms (>5 cm) have the greatest impact on growth in the Sonoran desert, with relatively dry soils, whereas they induce moderate increases in productivity in the Chihuahuan desert, at all soil water levels; and they have no impact in the Mojave and Sonoran deserts, with wet soils (Fig. 7). These differences partly reflect the seasonal differences in moisture between the deserts. For example, intermediate-sized storms (2–4 cm) are most likely to occur in winter in the Mojave, about equally likely in winter and summer in the Sonoran, and most likely to occur in summer in the Chihuahuan desert. Rains of this size will penetrate about 20–40 cm in dry soil of moderate texture; and this moisture will be subject to low evaporation in winter but high evaporation in summer. Thus, soil moisture recharge in the Mojave (mostly in winter) will incur less evaporation and have more available water for plant use, whereas soil moisture recharge in the Chihuahuan (mostly in summer) will incur more evaporation and have less available for plant growth. Also, wintertime moisture in the Chihuahuan is less available to plants than in the Mojave and Sonoran because of low temperature limitations. The Mojave site exhibits greatest growth responses to intermediate sized storms (ca. 3 cm) with relatively low antecedent soil water. This situation is what would be expected following the first significant storms of winter that recharge relatively dry soil and induce growth of perennials and germination of annuals (Beatley 1974). At the Sonoran site, the greatest growth responses occur following large storms with relatively dry soil. This situation would likely occur at the start of the winter season, as in the Mojave, or may occur at the start of the summer monsoon season following a dry spring. These conditions in the Mojave and Sonoran sites perhaps most nearly represent the simple pulse–reserve model envisioned by Noy-Meir (1973). However, note that there are very few data points in either of these geographical regions (Fig. 7a, b), i.e., these events are rare. In the Chihuahuan site, there is only a moderate productivity response to storms of any size, regardless of antecedent soil moisture, suggesting that there is a more gradual onset of the seasonal cycles with a series of storms inducing only moderate growth responses to each storm.

Storm duration is another factor that may potentially play a role in the observed differences between the three deserts in terms of soil water recharge and storm size. However, we found no significant differences in the duration of storms among the deserts and only a small correlation between storm size and duration in all deserts (R^2=0.28, 0.32, and 0.28 for the Mojave, Sonoran, and Chihuahuan deserts, respectively).

We found that growth rates of individual plant FTs are dissimilarly affected by antecedent soil water (or water potential) and pulse precipitation (Fig. 8). Furthermore, variation in FT productivity responses is generally more pronounced across FTs than across the three deserts or rainfall regimes. Both of these observations support the division of the ‘production’ compartment in our revised pulse–reserve model into plant FTs (Fig. 1c). At all three desert sites, there are similar and pronounced differences in the responses of the plant FTs to individual storms. The annuals are most responsive to storms that occur with moderate to high levels of soil moisture, reflecting their strongest physiological responses when well hydrated. Grasses have greatest responses in moderately dry soils, reflecting their responses to soil re-hydration following moderate drought, whereas *Larrea* is most responsive following large storms that occur with relatively dry soils, reflecting a strong response to a recharge of the soil profile (Fig. 8).

Analysis of seasonal growth demonstrates the importance of winter moisture in all three deserts, irrespective of their actual differences in proportional seasonal rainfall. Precipitation that falls in winter appears to provide a more biologically useful seasonal pulse than does summer rain.

This is best demonstrated by the results of seasonal productivity for the Chihuahuan site, which on average, has about twice as much rain in summer as winter, yet has similar (in coarse soil texture) or greater (fine soil texture) growth in winter (Reynolds et al. 1999). A number of factors probably contribute to this effect, including: (1) frontal storms of winter deliver more persistent storms (Sheppard et al. 2002), (2) temperatures are lower in winter and thus evaporation of surface water is lower in winter (as is plant water use in some cases), thus fostering soil water accumulation and carryover between storms, and (3) the plant FTs that are best adapted to use soil moisture in winter, such as the evergreen shrub *Larrea*, have relatively high water-use efficiencies, which leads to relatively high rain-use efficiency.

It is pertinent to question the extent to which our findings are predicated on the assumptions of the model and especially the functional relationships employed for soil water distribution, rooting distribution, and soil water extraction. The simple SWB model we use in PALS does not account for detailed movements of soil water that could occur as a result of redistribution associated with soil water potential gradients, plant hydraulic lift, or movement of water through pores, such as root channels. Nor does our model account for heterogeneity associated with soil features, such as vesicular and caliche layers (Gile and Grossman 1967; Gile et al. 1966; McAuliffe and McDonald 1995), or for complex and intricate root distribution patterns that may result from soil physical characteristics or root distributions associated with resource patches (Gile et al. 1998; Reynolds et al. 1999; Robinson and van Vuuren 1998). These phenomena could conceivably lead to considerably different soil water profiles than those predicted by the current version of PALS employed in this study. However, we are confident in PALS in part because simulated soil water distributions are consistent with the conclusions of numerous studies in all three desert regions that have found limited or no percolation of soil water into deep soil layers (>60 cm depth), based on field measurements of soil water (Herbel and Gibbens 1987, 1989; Reynolds et al. 1999; Scanlon 1994; Smith et al. 1995), measurements of accumulations of water-soluble ions (Schlesinger et al. 1989), and distributions of radioactive tracers in soils (resulting from nuclear bomb testing in the early 1950s; Phillips 1994; Scanlon 1992).

Another important consideration affecting the distribution of soil water and its availability to different plant FTs is the choice of rooting distributions (Kemp et al. 1997; Reynolds et al. 2000b). The distributions we use are based on numerous field studies in these deserts (Briones et al. 1996; MacMahon and Schimpf 1981; McAuliffe and McDonald 1995; Moorhead et al. 1989; Reynolds et al. 1999; Wallace et al. 1974; see Table 3). Of course, these root distributions may not reflect *fine* root distributions, which are important in soil water uptake, nor do they necessarily reflect variation in rooting distributions associated with different rainfall patterns, soil textures and heterogeneity, landscape positions, and vegetation. Furthermore, information about rooting distribution alone is probably insufficient to precisely determine root water uptake among the different plant FTs and soil layers, since roots of different FTs may vary in their specific activities and hydraulic conductivities with depth, which does not reflect root mass distribution (Wan et al. 1993; Yoder et al. 1998). In view of this uncertainty, we consider the generalized root distributions and relatively simple mechanisms of water extraction used in PALS to be reasonable approximations that account for general patterns of water extraction by desert plants and a good starting point for addressing differences among desert rainfall regimes and plant FTs.

Our analysis of the pulse–reserve paradigm for the warm deserts of North America leads us to the following general conclusions. First, because of the importance of soil moisture storage to plant growth (especially perennial plant FTs), the Westoby-Bridges pulse–reserve model as described by Noy-Meir (1973) is an inadequate paradigm for these deserts. Without a consideration of soil moisture, it is impossible to identify the underlying causes of variability in aridland productivity with respect to rainfall (e.g., Le Houérou et al. 1988). Second, even with a consideration of soil moisture, it is difficult to make generalizations regarding plant responses to rainfall pulses. There is a strong relationship to antecedent soil moisture, which varies among the deserts (Fig. 7); and the response to rainfall pulses is quite different among different plant FTs (Fig. 8). Third, most of what constitutes moisture pulses in these deserts are not simply single rainfall events, which Noy-Meir (1973) refers to as "triggers." Rather, pulses of "biotic significance" are more likely to occur as collections of rains (storms) and collections of storms that produce reliable soil moisture recharge in either the winter (October–March) or summer (July–September) growing season. Fourth, the vertical distribution of soil water across all three deserts is such that the vast majority of water is likely to be in the top 50–60 cm of the soil, implying that virtually all plant FTs, including annual and perennial forbs, grasses, shrubs, and subshrub, are "drinking from the same cup" as colorfully put by Hunter (1989) and supported by Reynolds et al. (2000b). There appears to be little opportunity (in a general sense) for plant FTs to be able to key on stratified soil moisture sources of either small amounts near the surface or reservoirs of moisture stored deep in the soil. Thus, coexistence of plant FTs in a single patch as examined in this study is likely to be fostered by factors that promote: (1) separation of water use in time (seasonal differences in growth), (2) relative differences in utilization of water in the upper soil layers, or (3) separation in responses of plant FTs as a function of preceding conditions, especially soil water and physiological and morphological 'readiness' of the plant (i.e., the plant has accumulated leaves that are actively ready for water uptake and growth).

Finally, it is important to note that we sought and presented generalizations at the expense of not portraying the extensive seasonal, annual, and decadal variability in

productivity that characterizes the model simulations and which is characteristic of arid regions (Le Houérou et al. 1988). This variation results from the complex interactions that occur as a result of specific rainfall sequences, antecedent soil moisture, nutrient availability, and plant FT composition and cover (Reynolds et al. 2000b). Furthermore, the simulations for a single patch do not adequately reflect the variability in productivity that occurs over the landscape as a result of the reduction or amplification of moisture due to runoff, soil heterogeneity, and numerous other factors that may interact with rainfall to effect productivity, as shown by Gao and Reynolds (2003). Nevertheless, our results call into question the use of simplified vegetation models that rely heavily on correlative relationships between daily rainfall and primary production and which are used to forecast the potential impacts of climate change in the arid zones in North America.

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