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Plant responses to precipitation in desert ecosystems: integrating functional types, pulses, thresholds, and delays

Received: 1 August 2003 / Accepted: 14 January 2004 / Published online: 6 March 2004
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Abstract The ‘two-layer’ and ‘pulse-reserve’ hypotheses were developed 30 years ago and continue to serve as the standard for many experiments and modeling studies that examine relationships between primary productivity and rainfall variability in aridlands. The two-layer hypothesis considers two important plant functional types (FTs) and predicts that woody and herbaceous plants are able to co-exist in savannas because they utilize water from different soil layers (or depths). The pulse-reserve model addresses the response of individual plants to precipitation and predicts that there are ‘biologically important’ rain events that stimulate plant growth and reproduction. These pulses of precipitation may play a key role in long-term plant function and survival (as compared to seasonal or annual rainfall totals as per the two-layer model). In this paper, we re-evaluate these paradigms in terms of their generality, strengths, and limitations. We suggest that while seasonality and resource partitioning (key to the two-layer model) and biologically important precipitation events (key to the pulse-reserve model) are critical to understanding plant responses to precipitation in aridlands, both paradigms have significant limitations. Neither account for plasticity in rooting habits of woody plants, potential delayed responses of plants to rainfall, explicit precipitation thresholds, or vagaries in plant phenology. To address these limitations, we integrate the ideas of precipitation

thresholds and plant delays, resource partitioning, and plant FT strategies into a simple ‘threshold-delay’ model. The model contains six basic parameters that capture the nonlinear nature of plant responses to pulse precipitation. We review the literature within the context of our threshold-delay model to: (i) develop testable hypotheses about how different plant FTs respond to pulses; (ii) identify weaknesses in the current state-of-knowledge; and (iii) suggest future research directions that will provide insight into how the timing, frequency, and magnitude of rainfall in deserts affect plants, plant communities, and ecosystems.

Keywords Pulse-reserve · Walter’s two-layer model · Resource partitioning · Soil water · Root distributions

Introduction

Stimulated in part by projected climate change in arid regions of the globe, numerous studies in the last several decades have aimed at developing an improved mechanistic understanding of how dryland plants and communities respond to rainfall variability (see reviews by Ehleringer et al. 1999; Puigdefábregas and Pugnaire 1999). Yet, a comprehensive understanding remains equivocal. Two influential paradigms developed nearly thirty years ago—Walter’s (1971) two-layer hypothesis and the Westoby-Bridges’ pulse-reserve hypothesis (M. Westoby and K. Bridges, unpublished data, in Noy-Meir 1973)—continue to serve as the standard for many experiments and modeling schemes that examine rainfall variability relationships in arid ecosystems. The longevity of these two paradigms is undoubtedly related to their simplicity and strong conceptual appeal.

Walter’s (1971) two-layer hypothesis predicts that woody and herbaceous plants successfully co-exist in savannas because they utilize water from different depths in the soil: herbaceous plants (e.g., grasses) root mainly in the upper layers, whereas the roots of woody plants extend to the lower layers. This two-layer model has been the

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underpin of an extensive number of modeling schemes (see Breshears and Barnes 1999; Eagleson 2002), has been used to contrast ecosystem dynamics across a large number of field sites (e.g., Lauenroth et al. 1993), and has been a key element in theoretical developments of niche separation in plants (e.g., Jeltsch et al. 1996). In spite of its attractiveness as a simple paradigm, the two-layer model is not consistently supported by field data (see Belsky 1994; Breshears and Barnes 1999; Reynolds et al. 2000, 2004). We suggest that this is primarily due to two factors: (i) several key plant processes, including the plasticity of rooting habits of woody plants, phenology, and plant age, and (ii) the timing and magnitude of individual rain events, both of which may negate the importance of rooting depths alone.

The Westoby-Bridges' pulse-reserve model (Noy-Meir 1973) addresses the response of various plant functional types (FTs) to pulses of precipitation. It predicts that there are 'biologically important' rainfall events that stimulate plant growth and reproduction and, hence, these events may play a key role in long-term plant function and survival (as compared to seasonal or annual totals of rainfall as per the two-layer model). The importance of discrete rainfall events per se in arid regions has made this paradigm attractive, as exemplified by the diversity of ways it has been adopted, for example, as the conceptual framework underlying landscape processes (Ludwig et al. 1997); to describe complex dynamics of microbial communities and the subsequent availability of soil organic matter (Kieft et al. 1998); and as a tool for synthesizing the effects of El Niño on terrestrial communities of arid islands in the Gulf of California (Polis et al. 1997). The idea of biologically important precipitation events, especially in the context of thresholds that govern plant responses (e.g., Beatley 1974; Schwinning et al. 2003), remains a useful and robust factor in arid systems. However, the pulse-reserve model has limitations because it also neglects vagaries in plant rooting patterns; it applies primarily to annual plants; and it ignores important aspects of soil water availability including antecedent conditions (see Reynolds et al. 2004).

In this paper, we re-evaluate the Walter and Westoby-Bridges' paradigms in terms of their strengths, limitations, and generality. We do this in the context of examining the responses of plant FTs—which have the potential to partition resources (water) either temporally (e.g., due to different phenologies) or spatially (e.g., due to different lateral or vertical rooting patterns)—to pulses of precipitation and the implications for community structure and function in desert systems. We combine the ideas of precipitation thresholds, potential lag (or delayed) responses to rainfall (e.g., Schwinning and Sala 2004), resource partitioning and plant FT strategies into a relatively simple threshold-delay model. We apply the model to develop hypotheses about how different plant FTs respond to pulse precipitation and to identify weaknesses in our current state-of-knowledge. Finally, by merging historical perspectives and recent advances, we suggest future research directions that may provide

greater insight into how the timing, frequency and magnitude of rainfall in arid and semi-arid regions affect plants, plant communities, and ecosystems.

The two-layer model

Walter (1971) proposed that seasonal precipitation characteristics determine large-scale patterns in community composition. He suggested that the co-occurrence of grasses and woody plants in semi-arid savannas depends on the amount of summer rainfall and identified the vertical stratification of soil water and root systems as the primary factor that minimizes competition for water and thus enables coexistence. This explanation is commonly referred to as "Walter's two-layer hypothesis" (Burgess 1995). Here, grasses (or other herbaceous plants) are expected to be shallow-rooted and woody plants are expected to have roots that extend into deep soil layers. Walter proposed that when summer rainfall is approximately 200 mm/year, rains wet the surface layers, which is available mainly to grasses, but some rainwater also penetrates deeper layers, which is accessible by woody plants. This balance allows for grasses and woody plants to grow side-by-side with minimal interference. However, if summer rainfall greatly exceeds 200 mm/year, then woody plants should dominate the system because a larger proportion of water infiltrates in deeper soil layers; conversely, if there is less than 200 mm/year, grasses should dominate because little rainwater penetrates deep layers and grasses are expected to be superior competitors for surface soil water.

The pulse-reserve model

Walter's two-layer hypothesis focuses on seasonal or long-term effects of precipitation on desert plants and communities. But, the question arises: how do plants respond to pulses of precipitation, within a season, and how do these short-term responses integrate to affect the longer term dynamics? The Westoby-Bridges pulse-reserve hypothesis (Noy-Meir 1973) begins to address this question by focusing on how isolated precipitation events stimulate plant growth and reproduction. The original model describes the effect of 'biologically important' or 'effective' rainfall events on pulses of production. Here we employ the 'pulse' terminology when referring to precipitation. Furthermore, while the pulse-reserve model was originally formulated for annual plants, it is applicable to most plant FTs found in arid and semi-arid lands. In general, the model predicts that a rain event triggers a production response (i.e., germination, growth or reproduction), some of which is diverted to reserve (seed for annuals and perennials, or storage such as roots, stems or nonstructural carbohydrates for perennials).

Supporting evidence

We now re-evaluate the Walter and Westoby-Bridges paradigms in terms of the strengths, limitations, and generalities of their predictions at two divergent scales: regional and at the level of individual plants or plant FTs.

Regional predictions

First, in examining large-scale patterns we note that our analysis only applies to Walter's hypothesis because the pulse-reserve model was not developed for this purpose. According to the two-layer model, we ask: are community composition and productivity associated with mean total summer rainfall in arid and semi-arid lands? Surprisingly, few studies explicitly address this question. Along a strong mean annual precipitation (MAP) gradient ($50 < \text{MAP} < 1,100$ mm) in Israel, Kutiel et al. (2000) found that annual herbs were more common in low rainfall regions, while perennials and woody species were dominant in the wetter portion of the gradient, consistent with Walter's hypothesis. Many studies, across a diversity of sites, have shown that aboveground net primary productivity increases with increasing MAP (Sala et al. 1988; Paruelo and Lauenroth 1995; Epstein et al. 1996; Paruelo et al. 1999, 2000; Oesterheld et al. 2001), but Paruelo and Lauenroth (1996) are one of the few to examine relationships with seasonal rainfall totals. Contrary to Walter's expectations, they showed that shrub abundance in North America increased as the proportion of winter rain increased and as MAP decreased.

Paruelo and Lauenroth (1995) did an exhaustive analysis of published vegetation and precipitation data for 49 grass and shrub communities in the western United States. We reanalyzed these data with regard to total and seasonal precipitation to determine if a correlative relationship exists with life-form dominance. As shown in Fig. 1, we found that a shift from grass- to shrub-dominated communities is correlated with summer rainfall ($P < 0.001$). No relation was found with total winter precipitation ($P = 0.38$). Although Walter (1971) argued that grasses should dominate at lower rainfall sites, these data suggest that grasslands in western USA are more common when summer rainfall exceeds 250 mm (Fig. 1).

While many factors (grazing, fire, soil type, topography, etc.) affect species composition and productivity in arid and semi-arid ecosystems (see Knoop and Walker 1985; Bowman and Minchin 1987; Sala et al. 1988; Wondzell et al. 1996; Scholes and Archer 1997; Lane et al. 1998; Jeltsch et al. 2000), rainfall is most influential (Noy-Meir 1973, 1985; MacMahon and Wagner 1985; McClaran and Van Devender 1995). Nevertheless, simple statistics such as MAP are inadequate when addressing the effects of precipitation on the structure and function of dryland ecosystems. For example, what specific precipitation characteristics (seasonal distribution, size of rain events, length of time between rains, etc.) impact the association of woody plants and grasses in savannas? Within a habitat

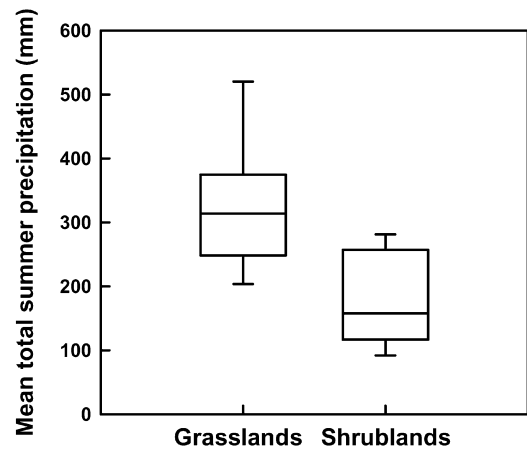


Fig. 1 Box-and-whisker plots illustrating the relationship between total summer precipitation and dominance by shrubs and grasses in the western United States. Data on vegetation type (grassland or shrubland) were obtained from Paruelo and Lauenroth (1995). The boxes show the 25th, 50th (median), and 75th percentiles, and the whiskers show the 10th and 90th percentiles

type (e.g., woodland, shrubland, savanna, grassland), which precipitation characteristics have the greatest influence on plant and ecosystem productivity, and how do they compare to those that determine community composition across habitat types? Reynolds et al. (2004) provide initial insights into the complexity of such relations.

Plant responses

In this section we discuss the effects of rainfall at a smaller-scale: for individual plants or plant FTs. A key element of the two-layer hypothesis is the idea of resource partitioning by different plant FTs, and an important facet of the pulse-reserve model is the view that plants respond to 'biologically important' rainfall events. However, a review of the recent literature suggests that these hypotheses lack several important elements, including: the plasticity in rooting habits and water sources of woody plants and the importance of timing as related to seasonality, plant phenology, plant age, and antecedent conditions (see also Reynolds et al. 2004).

Rooting distributions

Quantifying overlap in root profiles has been employed to infer the potential for resource (water) partitioning by different plant FTs. As compared to grasses and forbs, roots of woody plants generally extend deeper (Cable 1969; Brown and Archer 1990; Lee and Lauenroth 1994; Schenk and Jackson 2002) or the bulk of their root mass is displaced to greater depths (Knoop and Walker 1985; Lee and Lauenroth 1994; Briones et al. 1996; Jackson et al. 1996). In some cases the root systems may have very similar vertical distributions but may be horizontally separated (to some extent, Belsky 1994; Le Roux et al. 1995). Brisson and Reynolds (1994) presented data for a

desert shrub (*Larrea tridentata*) showing that the horizontal growth of root systems is more developed away from the maximum competitive pressure of neighbors. Thus, resource partitioning has the potential to occur along the vertical and/or horizontal dimensions (see also Breshears et al. 1997; Breshears and Barnes 1999). Conversely, others (e.g., Montaña et al. 1995; Mordelet et al. 1997) have shown that the root profiles are indistinguishable between the two life forms, and thus conclude that resource partitioning does not occur.

The above studies generally support the idea that grasses and herbaceous plants are relatively shallow-rooted (see also Forseth et al. 1984) and primarily rely on near-surface soil water. This is not surprising since these functional types lack secondary thickening, which places morphological and energetic constraints on their capacity to grow deep roots (e.g., Casper and Jackson 1997). Hence, the inconsistencies regarding the potential for resource partitioning based on rooting habits appears to be primarily due to the diversity of rooting habits of woody plants. For example, maximum rooting depths vary greatly across life-forms (Schenk and Jackson 2002). There is also significant variation across woody species (Hellmers et al. 1955; Montaña et al. 1995; Midwood et al. 1998; BassiriRad et al. 1999; Yoder and Nowak 1999; Table 3 in Reynolds et al. 2004), and within a species, rooting behavior can vary greatly within and across sites as illustrated in Fig. 2 for *Larrea tridentata*.

Hence, the rooting habits of woody species appear to be more complex than Walter (1971) originally proposed.

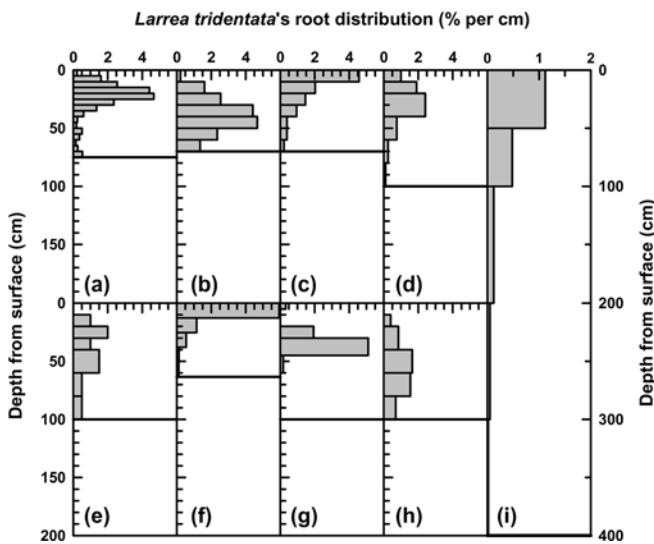


Fig. 2 Root distributions for the desert shrub *Larrea tridentata* from **a** Briones et al. (1996), based on number of roots for *Larrea* in the Mapimí Biosphere Reserve, Mexico; **b** Moorhead et al. (1989), root biomass, Jornada Basin; **c** Montaña et al. (1995), number of roots, Mapimí Biosphere Reserve; **d** Thames (1979), number of roots, Sonoran Desert; **e** Kemp et al. (1997), root biomass, Jornada Basin; **f** Castellanos-Perez (2000), root biomass, Jornada Basin; **g** Ogle et al. (2004), active root area for water uptake, Jornada Basin; **h** McAuliffe and McDonald (1995) as given in Reynolds et al. (2004), Mojave Desert; and **i** Freckman and Virginia (1989), root biomass, Jornada Basin. The *thick horizontal lines* depict maximum rooting and/or sampling depth

Additionally, the spatial distribution and density of roots affect a plant's ability to respond to precipitation pulses of different sizes (e.g., Cohen 1970), suggesting that the threshold for a 'biologically important' rain event will be a function of rooting patterns, which will vary for different plant FTs. This lack of root dynamics and its connection to water uptake is an important shortcoming of the Westoby-Bridges' model (Reynolds et al. 2004).

Methodological issues

Importantly, root biomass or numbers alone are not sufficient for testing the two models because they do not directly correspond to functional properties such as root activity for water uptake (e.g., Midwood et al. 1998; Plamboeck et al. 1999; Yoder and Nowak 1999). The simple water flux model described by Campbell (1991) and modified by Ogle et al. (2004) illustrates key components of root activity for water uptake:

$$\text{flux} \propto \frac{RA}{r_r \times (1 - n)} \left[\ln \left(\frac{r_r \times RA}{2 \cdot v} \right) \right]^{-1} \times (k_{\text{soil}} \cdot \Psi_{\text{soil}} - k_{\text{root}} \cdot \Psi_{\text{root}}) \quad (1)$$

That is, water flux from the soil to the root depends on several critical factors, including active root area for water uptake (RA), soil volume containing roots (v), soil and root water potentials (Ψ_{soil} , Ψ_{root}), and soil and root hydraulic conductivities (k_{soil} , k_{root}). Furthermore, water uptake capacity can differ between roots at different depths in the soil because shallow roots tend to have narrower conduits for transporting water (Pockman et al. 2000) and thus have lower k_{root} values than deep roots (Kramer and Bullock 1966; Wan et al. 1994). More detailed water transport models also illustrate the importance of gradients in Ψ and k within the soil, between the soil and root, and within the plant to hydraulic redistribution of water by roots (Ryel et al. 2002) and to plant cavitation susceptibility and carbon allocation strategies (Sperry et al. 1998). Mechanistic methods that take into account key aspects of Eq. 1 in evaluating water acquisition and resource partitioning by different plant FTs include comparing plant and soil water potentials and/or measuring stable isotopes of hydrogen and/or oxygen in plant and soil water (Ehleringer et al. 1999). For example, Montaña et al. (1995) and Peláez et al. (1994) measured water potentials of co-occurring grasses and shrubs in the Chihuahuan Desert in Mexico and in semi-arid Argentina, respectively. They suggest that some shrubs and grasses may utilize the same water source, but their data also suggest that the shrubs *Prosopis glandulosa* and *P. caldenia* access deeper water than co-occurring grasses and shallow-rooted shrubs. While such data on water potentials are informative in a relative sense—i.e., changes in plant water potentials following a storm or irrigation event are useful for inferring different plant FT responses to rainfall—they

are not appropriate for inferring from where in the soil the plants are obtaining water because plant water potentials do not necessarily reflect soil water potentials at these depths (Donovan et al. 1999, 2001). On the other hand, the stable isotopic composition of water in a plant stem directly integrates over the soil isotope values in the layers from which the plant is obtaining water. Hence, by comparing the isotopic composition of plant and soil water one can estimate the fraction of water acquired from different depths (e.g., Ehleringer and Dawson 1992). The most powerful approach for elucidating plant water uptake patterns is to combine data on water potentials, isotopes, and soil characteristics within the framework of a biophysical water uptake model such as Eq. 1 (Walker and Richardson 1991; Brunel et al. 1995; Ogle et al. 2004).

Water uptake

The diversity of rooting habits of woody plants is the likely explanation for the highly variable water acquisition patterns characteristic of this life-form (e.g., Ehleringer et al. 1991; Dodd et al. 1998; Schwinning et al. 2002). Gebauer et al. (2000) irrigated five dominant shrub species in southern Utah during different seasons and based on stable isotope data, found that the use of simulated rain varied between species and time of year. In early spring (May) all species used less than 10% of the irrigation water; in summer (July) only two species used a significant amount of the applied water; and, in late summer (September) the majority of the water was taken-up by all five species. Others have also employed stable isotopes to show differential use of water sources by co-occurring woody plants (e.g., Flanagan et al. 1992; Donovan and Ehleringer 1994; Lin et al. 1996; Williams and Ehleringer 2000). Conversely, although Midwood et al. (1998) showed that trees and shrubs growing in a Texas savanna have dissimilar root distributions, all had comparable isotope signatures and were most likely accessing soil water at similar depths.

Some shrub species apparently possess the ability to “switch” between water sources (e.g., Evans and Ehleringer 1994; Dodd et al. 1998). For example, Schwinning et al. (2002) used stable isotopes to show that two shrubs native to the Colorado Plateau, *Artemisia filifolia* and *Coleogyne ramosissima*, used deep soil water in the spring but gradually switched to surface soil water derived from recent rains during the summer as the deep reserves were gradually depleted. Similarly, Ogle et al. (2004) reconstructed a bimodal active root area profile for *Larrea tridentata* growing in the southern Chihuahuan Desert (Fig. 2g). The small fraction of active roots near the soil surface may allow *L. tridentata* to rapidly acquire summer-derived, ephemeral surface water and the large fraction of roots at intermediate depths may serve to provide a relatively stable, winter-derived water source (this is consistent with the behavior of *Larrea* as reported by Reynolds et al. 1999). However, having a bimodal root

activity profile does not necessarily make these shrubs superior competitors relative to shallow-rooted grasses because many grasses have greater total root density (Knoop and Walker 1985; Belsky 1994; Montaña et al. 1995; Briones et al. 1996) and thus may still have the advantage over neighboring shrubs. Regardless, having the ability to use both shallow and deep soil water clearly allows some shrub species to use precipitation pulses of different sizes, duration, and timing, and may also improve their capacity to acquire nutrients.

Seasonality

Another critical element not accounted for by the two-layer and pulse-reserve models is the importance of timing such as the seasonality of rainfall. For example, Schenk and Jackson (2002) evaluated the applicability of the two-layer model across a wide range of vegetation types and found that the paradigm is most useful in systems with a wet cold season. Similarly, the pulse-reserve scheme overlooks the importance of seasonality whereby a rain event in winter may stimulate an entirely different plant response than a summer rain (e.g., Reynolds et al. 1999; Gebauer and Ehleringer 2000).

There is some evidence that winter rainfall may be more important than summer rainfall to plant FT responses and community structure (Reynolds et al. 1999; Schwinning et al. 2002). This is especially the case in deserts with biseasonal rainfall where, for example, winter rains recharge deep soil, making water available to relatively deep-rooted species during the spring-summer growing season. Ehleringer et al. (1991) illustrate the importance of winter rains; they estimated the sources of water for 26 species common to the high elevation deserts of Utah and found that nearly all relied on winter-spring recharge for spring growth, but only annuals and succulents completely depended on summer precipitation for summer growth. Additionally, preferential use of summer versus winter precipitation appears to depend on which season dominates total annual rainfall. Williams and Ehleringer (2000) found that the relative uptake of summer rains by three dominant tree species in Utah and Arizona increased, in a threshold-type manner, as total summer rainfall increased. Despite the potential consequences of winter precipitation, historically most rainfall manipulation studies have focused on the growing season. Some recent studies altered water availability during all seasons (e.g., Reynolds et al. 1999; Gebauer and Ehleringer 2000; Weltzin and McPherson 2000; Schwinning et al. 2002) and studies designed to examine the interactive effects of winter and summer rainfall are needed.

Plant phenology

Timing is also key because of variability in plant phenology. For example, two species growing side-by-side and accessing the same water source, with respect to

spatial position, can avoid competition for water by being active during different times of the year (e.g., Cable 1969; Golluscio et al. 1998; Nobel and Zhang 1997; Peláez et al. 1994; Reynolds et al. 2000; Roupsard et al. 1999). Within a community, different phenologies affect the temporal dynamics of species-specific leaf area indices, which in turn determines which species use, and how much, seasonal precipitation (Schwinning et al. 2002). Reynolds et al. (2000) suggest that the relatively shallow distribution of soil water in the Jornada Basin (Chihuahuan Desert) leads to little opportunity for vertical partitioning (see also Reynolds et al. 2004), but different plant FTs can avoid competition by exploiting particular intervals of soil water availability that coincide with their phenologies. Different phenologies of grasses and shrubs in the Jornada Basin contribute to the observed dynamics of seasonal and annual aboveground NPP (Huenneke et al. 2002). Here, grasslands exhibit greatest NPP during the summer and shrub (i.e., *Larrea* and *Prosopis*)-dominated sites have highest NPP during the spring.

Plant age

An additional aspect of timing is plant age. Donovan and Ehleringer (1994) examined seasonal water use patterns of major shrub species in the Great Basin. For species that are deep-rooted at maturity, adult and establishing individuals used rainfall during different seasons and of different sizes. Likewise, deep-rooted woody species such as *Quercus emoryi* (emory oak) and *Prosopis glandulosa* (honey mesquite) use deep soil water as juveniles and adults, and thus do not compete with neighboring grasses for water (Brown and Archer 1990; Weltzin and McPherson 1997). Brown and Archer (1990; 1999) suggest that *P. glandulosa* seedlings have the ability to rapidly elongate roots such that nearby grasses and herbaceous plants have little/no effect on seedling establishment, gas exchange, or growth. On the other hand, Weltzin and McPherson (1997) showed that recently germinated seedlings (<1 year old) of *Q. emoryi* are coupled to water immediately below the soil surface, so shallow that they also avoid interference by grasses. However, there is a brief period, on the order of one year, where seedlings and grasses use the same water source, and competition at this stage may be crucial to the regeneration phase of woody plants (Weltzin and McPherson 2000).

Antecedent conditions

Both the two-layer and the pulse-reserve models neglect the role of antecedent soil water, and although there are few studies on this topic, existing ones suggest that this is an important oversight (Dougherty et al. 1996; Golluscio et al. 1998; Reynolds et al. 2004). For example, Golluscio et al. (1998) found that shrubs in the cool semi-arid Patagonia steppe did not consistently respond to large rain

events, which they attribute to the effect of antecedent deep (30–60 cm) soil water content; they found that shrubs exploited large precipitation pulses only when deep horizons were relatively dry. Reynolds et al. (2004) provide an alternative critique of the pulse-reserve model and conclude that its omission of soil moisture renders it an ineffective tool for identifying the central causes of variability in aridland productivity. They also note that antecedent soil moisture is a critical player as it may diminish or amplify the effect of a precipitation pulse on plant growth or photosynthesis.

Site heterogeneity

There are many other factors that affect community composition and plant FT responses to rainfall in arid and semi-arid systems. An important one overlooked by Walter (1971) and Westoby-Bridges (Noy-Meir 1973) is the effect of heterogeneity in site characteristics. For example, variation in soil type can affect rooting habits (Knoop and Walker 1985; Lee and Lauenroth 1994; for a counter example, see Singh et al. 1998) and water sources by modifying hydraulic properties such as infiltration rate, water holding capacity, and the topsoil: subsoil water content ratio (Bristow et al. 1984; Knoop and Walker 1985). These effects ultimately lead to differences in community composition (Bowman and Minchin 1987) and productivity (Sala et al. 1988). Site topography is also critical because it affects the redistribution of water and thus alters community structure and productivity at potentially both the landscape and local scales (e.g., Bowman and Minchin 1987; Wondzell et al. 1996).

The threshold-delay (T-D) model

In this section, we focus on the responses of plant FTs to precipitation pulses, and ask: how do pulses of precipitation translate to individual plant responses? And, how do these responses—in terms of timing and duration—differ across plant FTs? To address these questions and to overcome some of the limitations of the two-layer and pulse-reserve hypotheses, we present the threshold-delay (T-D) model. The T-D model is a simple, phenomenological model that contains six key parameters that encapsulate a suite of behaviors exhibited by a variety of plant FTs. It implicitly incorporates aspects of Walter's ideas about rooting patterns and resource acquisition and Westoby-Bridges' theme of 'triggering pulses' of rainfall but is an improvement because it (i) allows for differential plant FT responses and potential delays in these responses; (ii) inherently captures the importance of antecedent conditions; (iii) incorporates precipitation thresholds; and (iv) is formalized with explicit equations.

Below, we develop the essential components of the T-D model and discuss the six key parameters. While the version we present is of the simplest form, because of its flexible structure the T-D model has the potential to

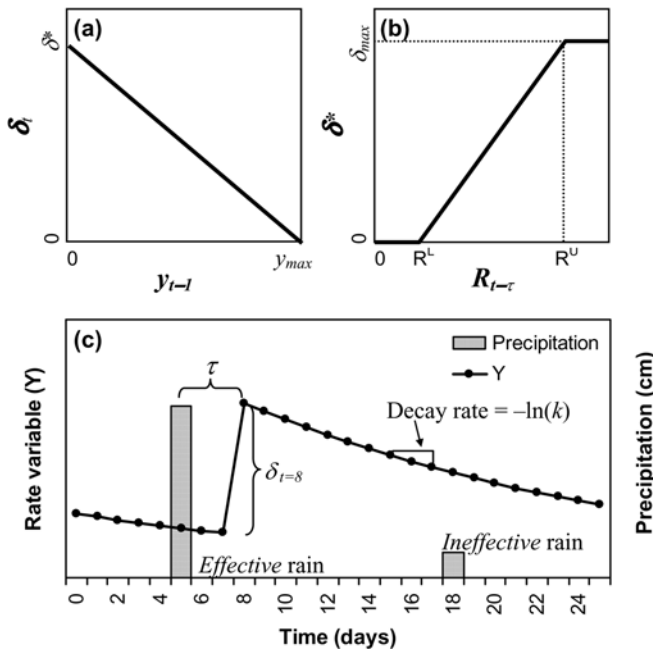


Fig. 3 Conceptual diagram of the threshold-delay model based on Eqs. 2, 3, and 4; **a** is the relationship between δ_t (the magnitude of the increase in the response variable due to a precipitation pulse) and the previous state of the response variable (y_{t-1}), where δ_t^* is the maximum potential increase and y_{\max} is the maximum potential value of the response variable; **b** is the relationship between δ_t^* and rainfall size at lag τ (days). R^L is the lower threshold such that rain events smaller than R^L do not stimulate a response. R^U is the upper threshold such that rain events larger than R^U do not yield additional benefits; and **c** provides a hypothetical response curve

accommodate more mechanistic processes including, for example, the effects of season, phenology, plant age, community composition, and soil water status.

Model description

The T-D model assumes that there are lower and upper thresholds on the size of a precipitation pulse that stimulates a plant response (e.g., increased photosynthetic rate). Also, we assume that there are upper limits on the magnitude of the response such that, for example, photosynthetic rates cannot exceed some maximum value that is constrained by plant functional (e.g., leaf-level biochemical or enzyme properties) or structural (e.g., xylem cross-sectional area, stomatal density, leaf anatomy) properties. We formalize these ideas in a series of equations. First, we allow for a dynamic model where the value at one point in time depends on the previous state:

$$y_t = k \cdot y_{t-1} + \delta_t \quad (2)$$

where y_t is the rate variable of interest (e.g., growth rate, photosynthetic rate, transpiration rate) at time t and k describes the reduction in the rate variable over time, in absence of significant rainfall. An effective precipitation

pulse will stimulate a response of magnitude δ_t :

$$\delta_t = \text{Min} \left[y_{\max} \times (1 - k), \delta_t^* \times \left(1 - \frac{y_{t-1}}{y_{\max}} \right) \right] \quad (3)$$

where y_{\max} is the maximum potential value, and the left-most argument in the *Min* function ensures that y_t does not exceed y_{\max} . The right-most argument assumes that the response depends on the prior state (y_{t-1}) such that if y_{t-1} is close to y_{\max} then the response to rainfall is diminished because the plant is already operating near its maximum rate (Fig. 3a). The maximum potential response is given by δ_t^* and is realized when $y_{t-1} = 0$ (Fig. 3a). The dependency of y_t on y_{t-1} in Eq. 2 and via δ_t in Eq. 3 implicitly accounts for antecedent conditions such that the response at time t is likely to be constrained by, for example, the antecedent amount and activity level of enzymes (or active roots or leaf area or soil water, etc.).

The increase in y_t following precipitation is expected to depend on the size of the rain pulse. However, if the pulse is less than some critical, lower threshold (R^L) then it does not affect the plant's behavior (e.g., Schwinning et al. 2003). Similarly, if the pulse exceeds some upper threshold (R^U) then any additional rain beyond R^U does not affect the response. In this regard, δ_t^* in Eq. 3 is assumed to vary with rainfall amount (Fig. 3b):

$$\delta_t^* = \begin{cases} \frac{\delta_{\max}}{R^U - R^L} \cdot (R_{t-\tau} - R^L) & R^L < R_{t-\tau} < R^U \\ 0 & R_{t-\tau} \leq R^L \\ \delta_{\max} & R_{t-\tau} \geq R^U \end{cases} \quad (4)$$

The “delay” in the T-D model is depicted in Eq. 4 by τ , which is the number of days it takes for a rain event to stimulate a response. Such delays or time lags may occur for various reasons, such as slow infiltration of rainfall to soil layers where active roots reside (T. Huxman et al., unpublished data); once wetted, roots may require a period of time to become physiologically ‘reactivated’ (Passioura 1988); and often a period of acclimation of leaf-level physiology must occur (T. Huxman et al., unpublished data). An example kinetic response curve is shown in Fig. 3c that is based on Eqs. 2, 3, and 4.

Model application

The T-D model is not meant to serve as a predictive tool per se because it does not explicitly depict the underlying structural and physiological mechanisms responsible for plant use of rainfall. Rather, it serves as a powerful heuristic tool for elucidating how co-occurring plant FTs are coupled to pulse precipitation. For example, if two plant FTs differ in their photosynthetic response, can the difference be attributed to dissimilar precipitation thresholds (R^U or R^L), lags (τ), potential responses (δ_{\max}), maximum photosynthetic rates (y_{\max}), or a combination thereof? Although the relatively fine-resolution data

necessary to fit the T-D model are lacking, especially for long time periods, several studies provide qualitative predictions about how parameters in the model may vary for different plant FTs. Next, we review these studies and develop a set of testable hypotheses about how co-occurring FTs differ in their response to pulse precipitation.

First, we identify seven key plant FTs representative of arid and semi-arid zones of North America: (i) cacti or succulents, (ii) summer active annual grasses and herbaceous plants, (iii) winter active annual grasses and herbaceous plants, (iv) perennial grasses and herbaceous plants, (v) shallow-rooted woody plants, (vi) deep-rooted woody plants, and (vii) woody plants with bimodal root distributions. These are consistent with plant FTs identified by Beatley (1974), Burgess (1995), Breshears and Barnes (1999), and Reynolds et al. (2000). We propose that Table 1 represents a set of testable hypotheses about how the six parameters in Eqs. 2, 3, and 4 vary across these plant FTs. The relative values (as compared to each plant FT) in Table 1 are based on our review of the literature and our underlying knowledge of the plant FTs.

We expect that shallow-rooted cacti, grasses, and forbs will respond relatively quickly to rain events (short τ). Because total root density is greatest in the topsoil (e.g., Jackson et al. 1996), these plant FTs should be exposed to heightened competitive pressures and their strategy should be to rapidly take-up available water (e.g., Cohen 1970). Conversely, deep-rooted shrubs and trees may respond more slowly (long τ) because they also have access to deep soil water, which is not available to most FTs, and deep soil water may be sufficient for maintaining their physiological activity (e.g., Hacke et al. 2000). Also, based on the physics of soil water transport, grasses should respond faster to rains because the surface soil zones are wet first, immediately exposing all/most of their root mass to available water. If the pulse is large enough then the rainwater will eventually percolate to deep layers dominated by roots of woody plants. Woody plants with bimodal root distributions may be intermediate in their time to respond (medium τ) because they have some fraction of roots in the topsoil.

Table 1 Hypothesized relative values (*med* medium or intermediate; *v short* very short) for the parameters in the T-D model (Eqs. 2, 3, and 4) for six key plant FTs found in the arid and semi-arid zones of North America. Based on a review of the literature, these values are chosen to reflect growth, photosynthetic, or transpiration rates during the vegetative stage, following establishment. [k is the reduction in the response variable (y_t) over time, in

At depth there are few roots (Jackson et al. 1996) and little to no water losses via evaporation (Barnes and Allison 1988); hence deep soil water is more stable and drops slower than shallow soil water during a dry-down (e.g., Schlesinger et al. 1987). Consequently, woody plants that are more coupled to deep soil water should maintain physiological activity and growth for longer intervals following a moderate-large rain event than grasses with roots in more dynamic topsoil (e.g., Cohen 1970). This means that the duration of the plant response to a precipitation pulse should be greater for woody plants, implying a high k -value (or low decay rate).

Based on work in the Colorado Plateau, Schwinning et al. (2002) suggest that the summer active C_4 grass *Hilaria jamesii* principally utilized surface water derived from simulated rains within one day of watering (short τ) and afterwards its use quickly dropped (low k). Conversely, the shrubs *Artemesia filifolia* and *Coleogyne ramosissima* maximum use was realized 2 days after irrigation (medium τ) and gradually diminished thereafter (medium-high k). Likewise, Montaña et al. (1995) observed that midday xylem water potentials of the grass *Hilaria mutica* peaked within four days of watering, but water potentials of the shrubs *Flourensia cernau* and *Larrea tridentata* reached their maximums after eight days. In general, grasses and forbs respond quicker (lower τ) and their response drops off more rapidly (lower k) than co-occurring woody plants (see also, Lauenroth et al. 1987; Briones et al. 1998)

Additionally, the precipitation threshold for shallow-rooted FTs is expected to be relatively low (low R^L and R^U) because less rainfall is required to wet the soil layers in which their roots reside (relative to deep-rooted woody plants). Montaña et al. (1995) found that the phreatophyte *Prosopis glandulosa* did not respond to irrigation (long τ and/or high R^L), presumably because most of its roots occur well below depths that the water infiltrated. Schwinning et al. (2003) suggest that the shrubs *Ceratoides lanata* and *Gutierrezia sarothrae* required a relatively high R^L to stimulate a photosynthetic or water potential response, but the C_4 grass *H. jamesii* had a lower threshold.

the absence of rainfall (as k increases, the decay rate decreases; see Fig. 3c); y_{\max} is the maximum potential value of y_t ; δ_{\max} is the maximum potential response to a precipitation pulse (i.e., the magnitude of the response δ_t when y_{t-1} is close to zero; see Fig. 3a, b); τ is the delay effect (number of days after a rain event before a response is observed; Fig. 3c); and R^L and R^U are lower and upper precipitation thresholds for the plant response (Fig. 3b)]

Plant functional type	k	y_{\max}	δ_{\max}/y_{\max}	τ	R^L	R^U
Cacti and succulents	high	low	high	short	low	low
Summer annual grasses and forbs	low	high	high	short	low	low
Winter annual grasses and forbs	low	med/high	high	short	low	low
Perennial grasses and forbs	med	med	med	short/med	low/med	med
Shallow-rooted woody plants	med	low	med	med	med	med
Deep-rooted woody plants	high	low	low	long	high	high
Woody plants with bimodal roots	med/high	low	med/low	med	med	high

Sala and Lauenroth (1985) assert that the physical properties of the root system will determine the capacity of plants to use pulse precipitation. For instance, shrubs and trees primarily have coarse roots and thus cannot efficiently or rapidly use increments in soil water resulting from small rains. Conversely, grasses have a dense root system consisting of many fine roots, and thus have a greater capacity to use water from small rain showers. These root characteristics should result in different τ and k values (as described above), but should also produce dissimilar δ_{\max} values because the magnitude of the response may be constrained by the ability of the roots to quickly and efficiently acquire available water. For example, in the Sonoran desert, photosynthesis of the bunchgrass *Pleuraphis rigida* increased faster (potentially indicates high δ_{\max}) with increasing soil water potential than it did for the sub-shrub *Encelia farinosa* (Nobel and Zhang 1997).

Essentially, the parameters k , τ , R^U , and R^L portray complex interactions between root profiles, density, structure and morphology and soil water dynamics (e.g., depth distribution and changes in water content); the parameters y_{\max} and δ_{\max} reflect inherent differences in physiology and growth strategies (Table 1). To increase the predictive power of the T-D model requires modifications that incorporate these feedbacks. For example, the model could be revised to include expressions that link k to the rate of soil water depletion such that $k = f(\Delta\theta, \beta)$, where $\Delta\theta$ is change in soil water content and β is a set of parameters describing the relationship between k and $\Delta\theta$. Thus, different plant FTs are expected to vary with respect to β . Similarly, antecedent water availability affects a plant's ability to use precipitation (Dougherty et al. 1996; Golluscio et al. 1998; Reynolds et al. 2004), and this effect could be incorporated into the lag or threshold response such that τ and/or R^L are reduced by high initial water content. Likewise, the ability to capitalize on moisture pulses varies with season (Schwinning et al. 2002), and this dependency could be captured by functions that relate y_{\max} and/or δ_{\max} to environmental conditions (e.g., temperature, humidity, nutrient availability, etc.) or

plant characteristics (e.g., leaf age; leaf, root, or sapwood area allometries; plant nitrogen concentrations; stomatal behavior, etc.) that vary across seasons.

Example application

In this section we illustrate the behavior of the T-D model by estimating numerical values for the six parameters in the model. This represents a preliminary exercise to demonstrate the potential of the approach and, as shown in Table 1, we are less concerned with the absolute values of the parameters but, instead, their relative values across plant FTs. We focus on the Jornada Basin LTER site in the northern Chihuahuan Desert (see Reynolds et al. 1999) where we have extensive field and modeling experience.

Because of limited field data, we fit the T-D model to growth data generated by the Patch Arid Lands Simulator (PALS) for an 85-year period (1915–2000) (i.e., see the Chihuahuan Desert, 21% clay scenario in Reynolds et al. 2004). PALS is a mechanistic ecosystem model that incorporates modules on plant physiology and phenology of the major plant FTs of the Jornada Basin and describes soil water dynamics as affected by plant transpiration, evaporation, and precipitation inputs (Kemp et al. 1997, 2003; Reynolds et al. 2000). Based on the PALS output, we obtained estimates for three of the parameters and for three different plant FTs. These values are given in italics in Table 2 and agree with the relative ordering in Table 1. Parameter values that could not be derived from the PALS output data were approximated from the hypothesized relationships in Table 1.

We now examine the consequences of this particular parameter set (Table 2) on the temporal growth dynamics of each plant FT in response to precipitation pulses. Figure 4 illustrates time-courses for simulated growth rates of the five plant FTs, for two different 100-day blocks. Both 100-day blocks have the same total precipitation (7.22 cm), but dissimilar distributions of rainfall within the block, leading to markedly different growth trends across blocks and plant FTs. For example, based on the parameter

Table 2 Hypothesized numerical values for the parameters in the T-D model (Eqs. 2, 3, and 4). Estimated values (*italics*) were obtained by comparing the T-D model to simulated growth data for the Jornada Basin based on the Patch Arid Lands Simulator (PALS, Reynolds 2004); other values were chosen based on the estimated ones and the relative values in Table 1. [Based on simulated growth rate (grams of biomass produced per gram of aboveground biomass per day, $\text{g}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$), we obtained estimates of k , y_{\max} , and δ_{\max} for summer active annuals (PALS FT C4 annuals), perennial grasses and herbaceous plants (PALS FTs perennial grasses and perennial

forbs), and shallow-rooted shrubs (PALS FTs sub-shrubs and evergreen shrubs) by qualitatively fitting the model to the PALS output. Because of how PALS is formulated, there are no lag effects (i.e., $\tau = 1$ day for all FTs), thus hypothetical values for τ (and R^L and R^U) were chosen according to Table 1. We did not conduct a rigorous statistical analysis of the PALS data and T-D model, but rather use the PALS output in demonstrating potential parameter values. We do not include the cacti or winter annuals FTs in this analysis]

Plant functional type	k	y_{\max} ($\text{g}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$)	δ_{\max} ($\text{g}\cdot\text{g}^{-1}\cdot\text{day}^{-1}$)	τ (day)	R^L (cm)	R^U (cm)
Summer active annual grasses and forbs	<i>0.550</i>	<i>1.000</i>	<i>0.109</i>	1	0.1	1
Perennial grasses and forbs	<i>0.928</i>	<i>0.217</i>	<i>0.015</i>	2	0.35	5
Shallow-rooted woody plants	<i>0.970</i>	<i>0.041</i>	<i>0.002</i>	3	0.5	5
Deeply rooted woody plants	0.990	0.041	0.0005	5	1	10
Woody plants with bimodal roots	0.980	0.041	0.001	3	0.5	10

values in Table 2, the annual plant FT has the largest growth response when rainfall is distributed in several small storm events (second 100-day block, right column); all woody plant FTs have their largest growth response when a few large storm events occur (first 100-day block, left column). Additionally, the combination of low k (high decay rate), high y_{\max} , high δ_{\max} , and low τ values for the annual plant FT (Table 2) results in a large and rapid response to each pulse event that rapidly diminishes thereafter (Fig. 4). Based on the low y_{\max} and intermediate k , δ_{\max} and τ values for the shallow-rooted woody plant FT (Table 2), the behavior of the T-D model suggests a small-moderate growth response that lags somewhat behind each ‘effective’ precipitation pulse and then slowly declines (Fig. 4).

Although relatively simple, the T-D model produces qualitative patterns (e.g., Fig. 4) that are consistent with field observations of how the plant FTs of the Jornada Basin respond to rainfall. While it is encouraging that only six parameters are necessary to capture such complex dynamics, before utilizing the T-D model for more robust quantitative assessments it will be necessary to consider the following: (i) explicit linkages to soil water dynamics, which are vital to dryland ecosystems (e.g., Reynolds et al. 2004); (ii) parameterization of the model with extensive field data; and (iii) employment of rigorous statistical

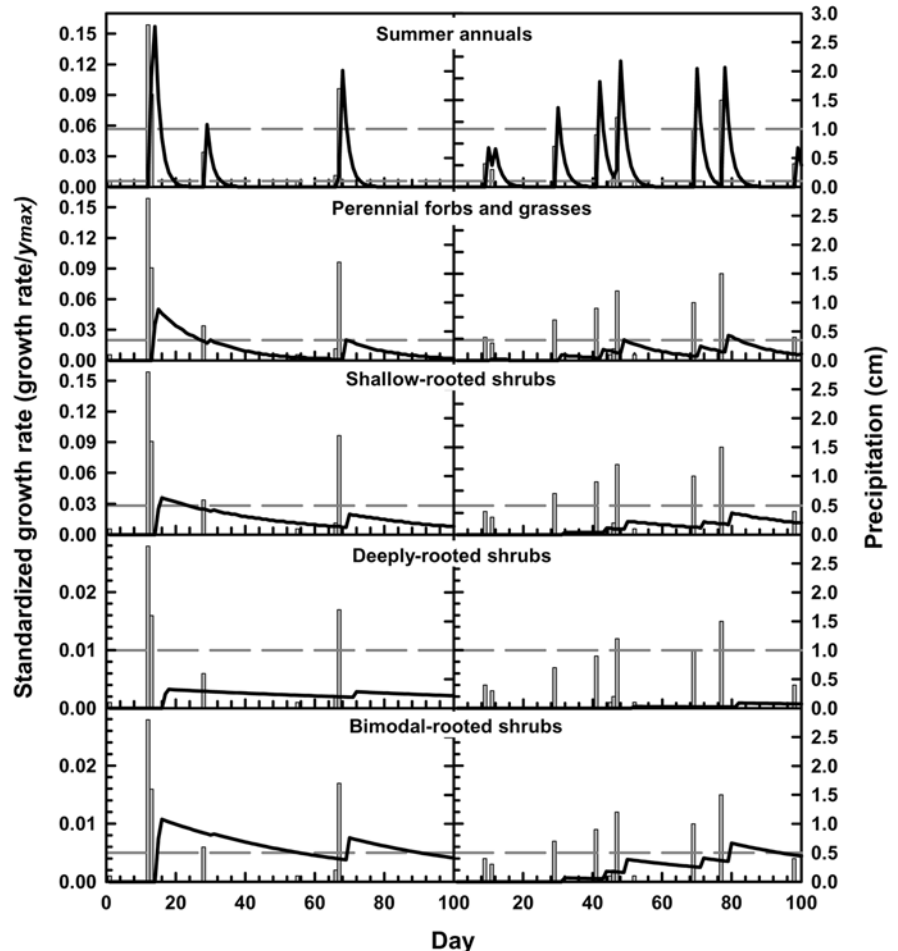
fitting procedures that can accommodate the highly nonlinear nature of the T-D model.

Discussion

In attempting to summarize our current state-of-knowledge regarding the differential responses of desert plant functional types to pulse precipitation, many questions remain unanswered. For example, how common is water source ‘switching’ or bimodal root distributions among tree species? How accurately do physical root distributions reflect root activity profiles? How does antecedent soil water modify plant responses to pulse precipitation? Are there critical pulse sizes that stimulate a plant response or that do not provide additional gain to the plant (e.g., in terms of biomass increment)? How does antecedent soil water status affect precipitation thresholds and plant delayed responses to rain events? Importantly, what are the implications of short-term plant FTs responses to pulse precipitation for long-term productivity and plant community structure?

The threshold-delay (T-D) model we present (Eqs. 2, 3, and 4, Fig. 3) is an integrative framework to begin addressing these questions and to help identify weaknesses in our current state-of-knowledge. Unlike the Westoby-

Fig. 4 Example time-courses of growth rates for five different plant FTs based on the threshold-delay model and parameter values in Table 2. Plots are shown for two different 100-day intervals in which total precipitation is the same (7.22 cm), but the distribution of rain events within the interval differ (compare right vs left columns). Overlaid are bars of the rainfall amounts and dashed vertical lines representing the lower and upper precipitation thresholds for each FT (the upper threshold, R^U , is only visible for the annuals, all other plant FTs’ R^U values exceed the precipitation scale). Note that the growth y -axis is scaled differently for the deep- and bimodal-rooted shrubs compared to the other plant FTs



Bridges' pulse-reserve and Walter's two-layer paradigms, the T-D model formalizes how different plant FTs will potentially respond to pulse precipitation by explicitly coupling precipitation pulses and thresholds with plant functional type strategies, delayed responses, and resource partitioning. We apply the model to observations obtained from the literature and suggest that the relative values of the parameters in the T-D model (Table 1) represent testable hypotheses about the differential pulse-use behavior of major desert plant FTs. Although relatively simple, the T-D model captures important complex and non-linear behaviors. Nevertheless, while valuable as a heuristic tool, substantive work is needed to evaluate and refine the T-D model by testing it with field data and modifying it to accommodate, for example, the effects of community composition, competition, soil water depletion, nutrient limitations, seasonality, phenology, or plant age. By so doing, we suggest that we will gain greater insight into how the timing, frequency, and magnitude of rainfall in arid and semi-arid regions affect plants, plant communities, and ecosystems.

Acknowledgements Susanne Schwinning, Michael Loik, Travis Huxman, David Tissue and two anonymous reviewers provided helpful comments and suggestions on earlier drafts. This work was stimulated by the "Workshop on Resource Pulse Use in Arid Ecosystems" held at the University of Arizona, Tucson (2002). This research was supported by a NASA Earth System Science Fellowship (#NGT5-30355) to K.O. and by USDA Specific Cooperative Agreement #58-1270-3-070 and NSF-DEB-02-12123. This paper is a contribution to the Jornada Basin LTER.

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