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Resource pulses, species interactions, and diversity maintenance in arid and semi-arid environments

Abstract Arid environments are characterized by limited and variable rainfall that supplies resources in pulses. Resource pulsing is a special form of environmental variation, and the general theory of coexistence in variable environments suggests specific mechanisms by which rainfall variability might contribute to the maintenance of high species diversity in arid ecosystems. In this review, we discuss physiological, morphological, and life-history traits that facilitate plant survival and growth in strongly water-limited variable environments, outlining how species differences in these traits may promote diversity. Our analysis emphasizes that the variability of pulsed environments does not reduce the importance of species interactions in structuring communities, but instead provides axes of ecological differentiation between species that facilitate their coexistence. Pulses of rainfall also influence higher trophic levels and entire food webs. Better understanding of how rainfall affects the diversity, species composition, and dynamics of arid environments can contribute to solving environmental problems stemming from land use and global climate change.

Keywords Coexistence · Precipitation · Environmental variability · Storage effect · Relative nonlinearity

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Introduction

The sparse and variable precipitation of arid and semi-arid regions is believed to exert strong control over the life histories, physiological characteristics, and species composition of their biota. While this premise may be intuitive for desert ecologists, we emphasize here that it also has support in species coexistence theory. Although much is known about the resource use and environmental responses of desert plants, there has been little integration of empirical data with theory to examine the consequences of these characteristics for the diversity and long-term persistence of desert communities.

The role of rainfall variability in maintaining the diversity of water-limited ecosystems is particularly relevant to the predictions of global climate models (Loik et al. 2004). The arid southwestern United States, and other regions with a similar climate, are predicted to change profoundly not only in average precipitation, but also, and perhaps more so, in temporal variability of precipitation. Both modeling and long-term climate records indicate that global warming is associated with

an amplification of inter-annual climate cycles, such as the El Niño/Southern Oscillations; thus, both between- and within-year variation in rainfall are expected to increase. Our ability to predict the responses of arid and semiarid ecosystems to these changes depends critically on being able to interpret short-term responses of individuals and populations to precipitation.

Here, we review the theory of competition and coexistence in harsh and variable environments, applying it specifically to the case of pulsed water availability in arid lands. We review the patterns of rainfall and soil water dynamics, their biological consequences for plants, and the adaptations of plants to variable water availability, especially those adaptations that influence plant water use and germination or establishment. We integrate these lines of information to better understand whether pulsed water availability in arid regions is likely to be an important factor in their surprisingly high diversity. Finally, we suggest lines of future research that would be most helpful in understanding the role of pulsed water availability in maintaining species diversity in arid ecosystems.

Pulses of rainfall and competition in arid environments

Arid environments are defined by the dominant role of water in limiting the activities of life. Not only are water supply rates low, they are also highly variable in time and space, reflecting local and regional precipitation patterns. Single rainfall events usually cause brief pulses of soil moisture with limited infiltration depth. However, precipitation events are never evenly spaced in time, and the probability that they will be clustered increases during rainy seasons (Loik et al. 2004). When precipitation is clustered, and especially during winter when evapotranspiration is lower, water infiltrates to greater depths.

The amount of water applied to the soil surface during a pulse of rainfall, the infiltration depth of the water, and the subsequent pattern and duration of the pulse experienced by plants, vary greatly in time and space. This variation stems in part from the stochastic nature of precipitation itself, but additional variation is caused by such factors as soil surface and soil type heterogeneity, which can cause localized variation in the depth and magnitude of infiltration (Loik et al. 2004). The deeper water infiltrates, the longer it usually takes to deplete. Near the soil surface, water depletion is fastest and driven primarily by direct evaporation. With increasing depth, the fraction of water leaving the soil via evaporation decreases and the fraction leaving by transpiration increases, provided water-absorbing roots are present. However, root densities also drop off sharply with depth (Schenk and Jackson 2002a), leading to declining rates of water depletion with depth of soil layer. Thus, soil moisture pulses in shallow soil layers are frequent and brief, whereas in deeper soil layers the average frequency of water recharge is lower but soil water remains at levels that can be extracted by plants for longer times. At moderate depth (e.g., 50–100 cm), soil water typically cycles annually, driven by temperature and plant phenology (Schlesinger et al. 1987), but at 200–500 cm, soil water content is relatively invariant and so low as to minimize plant extraction rates (Andraski 1997).

As the availability of resources, such as water, fluctuates, so too do activity levels in plants, and thus we also expect fluctuating competitive interactions. The two-phase resource hypothesis (Goldberg and Novoplansky 1997) describes such a relationship between rainfall and competition, identifying pulse and interpulse periods that are defined by activities of plants in relation to water availability. Rain falling after a dry period initiates a pulse period. At the beginning of a pulse, low uptake and abundant water imply little competition for water. However, as plants germinate, grow, or become physiologically active, individual plants begin to reduce the availability of water to neighboring plants, i.e., have competitive effects on their neighbors. At some point after a period of rainfall, the combined effects of evaporation and transpiration have reduced soil moisture to levels where active growth of some species ceases, ending the pulse and beginning the interpulse for those species. The interpulse continues until further rain provides adequate water for active growth.

The two-phase hypothesis identifies surviving the interpulse as a critical biological challenge. Species can differ in their survival response to interpulse lengths, even when total water is held constant (Sher et al. 2004). Survival mechanisms include setting seed before dying (e.g., annuals), becoming dormant (e.g., drought-deciduous perennials), minimizing water loss and maintaining turgor in retained leaves (e.g., succulents with water storage and CAM photosynthesis), or tolerating drought while retaining evergreen leaves (e.g., with osmotic or elastic adjustment). Competitive effects of plants occur primarily in their pulse periods, but have consequences for the onset of interpulses, which may be triggered at different times for species with different water-use physiologies or life histories.

Species that differ in physiology or phenology may have different patterns of resource consumption in response to the same rainfall event or pattern. For example, an annual must receive the right germination cues to respond to rainfall by germinating, and a dormant perennial similarly must receive the right cues to trigger bud-break or the development of actively-growing tissue. Thus, the competitive effects of each species are likely to be highly variable over time with important consequences for species coexistence, as discussed below.

## Theory: resource pulses, competition and diversity maintenance

As reviewed by Chesson and Huntly (1997), it is often argued that the harshness and variability of arid environments should render competition ineffectual as a force structuring communities. Theory, however, is strongly at odds with this conclusion. First, no amount of variability or spatial complexity removes the inevitability of intraspecific density dependence (Chesson 1996). Density-

dependent predation might replace competition, but there will always be density dependence, even if highly variable in space and time. Moreover, the key issue at the community level is not the overall strength or variability of competition, but rather the distinction between intra- and interspecific competition (or more generally, density dependence) (Chesson and Huntly 1997; Chesson 2000a). Stable coexistence, even in harsh and variable environments, requires mechanisms that distinguish species ecologically: this is a prerequisite for intraspecific density dependence to be stronger than interspecific density dependence. The kinds of density dependence most considered in discussions of diversity maintenance are competition and apparent competition (density-dependent mortality caused by natural enemies; Holt and Lawton 1994), although there is every reason to believe that other forms of density dependence have important roles. In this article, we primarily consider competition between plants for resources in arid ecosystems. We do not consider neutral coexistence (Hubbell 2001), which we argue elsewhere is unlikely to contribute much to diversity in nature (Chesson and Huntly 1997).

A general theory of resource competition in variable environments identifies two ways in which temporal fluctuations can contribute to diversity maintenance: (1) the storage effect, and (2) relative nonlinearity of competition (Chesson 1994). Both mechanisms require that coexisting species have unique patterns of population growth and resource consumption over time, but these mechanisms differ in the ways these patterns come about. We consider each mechanism in turn, discussing the role of resource pulses in their operation. These mechanisms are illustrated by results of a simulation model presented in the Appendix. We briefly discuss other mechanisms that may function in pulsed environments, but are not necessarily driven by pulses.

Resource pulses and the storage effect

The storage effect relies on differences in phenology (Chesson et al. 2001). For example, annual plant species are noted for temperature-dependent germination (Juhren et al. 1956; Baskin et al. 1993), the patterns of which differ between species and lead to changing probabilities of germination with the time of year that rain occurs (Fig. 1A). The outcome of such differences in germination is illustrated in Fig. 2 for two hypothetical annual plant species whose germination depends differently on temperature in the presence of adequate soil moisture. In the first year, rain comes early, favoring germination of species 1 over species 2, but in the second year later rain favors germination of species 2. As a consequence, these species have different relative abundances in the two years and different patterns of resource consumption over time. The bottom panel of Fig. 2 shows the long-term coexistence of these two species in the presence of year to year fluctuations in rainfall.
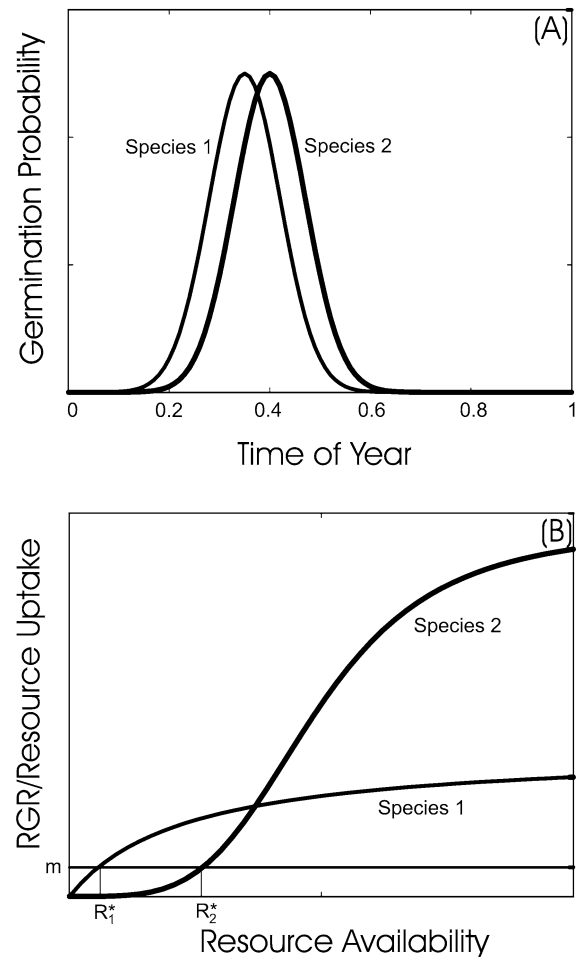
Fig. 1 A Idealized phenological differences between two annual plant species expressed as the probability of germination (when adequate soil moisture is present), as a function of the time of year, for example due to temperature-dependent germination. **B** Resource uptake rates of two species, which would also be proportional to the relative growth rate at constant water use efficiency. Species 1 has no threshold for resource uptake, but experiences a low saturation level achieved at relatively low availability. Species 2 has a threshold resource availability before significant benefit occurs, but has a much higher saturation level. The line at m illustrates the difference in R^* values that these species would have if they had common resource maintenance requirements

The phenological difference in germination discussed above involves timing that is independent of water availability, in the sense that rain at the wrong time of the year or wrong temperature would not bring on germination or physiological activity. Species coexistence is also possible by the storage effect when species emerge from a dormant state at different rates following the initiation of a rain pulse (Fig. 3). Species emerging later are likely to be disadvantaged and, if this disadvantage is too great, we would only expect coexistence in the presence of some sort of tradeoff compensating late emergers. The two situations illustrated in Figs. 2 and 3 thus specify two broad categories of species differentiation in resource consumption: by which pulses species use most resources (Fig. 2), and by when during a pulse they are most heavily consuming them (Fig. 3).
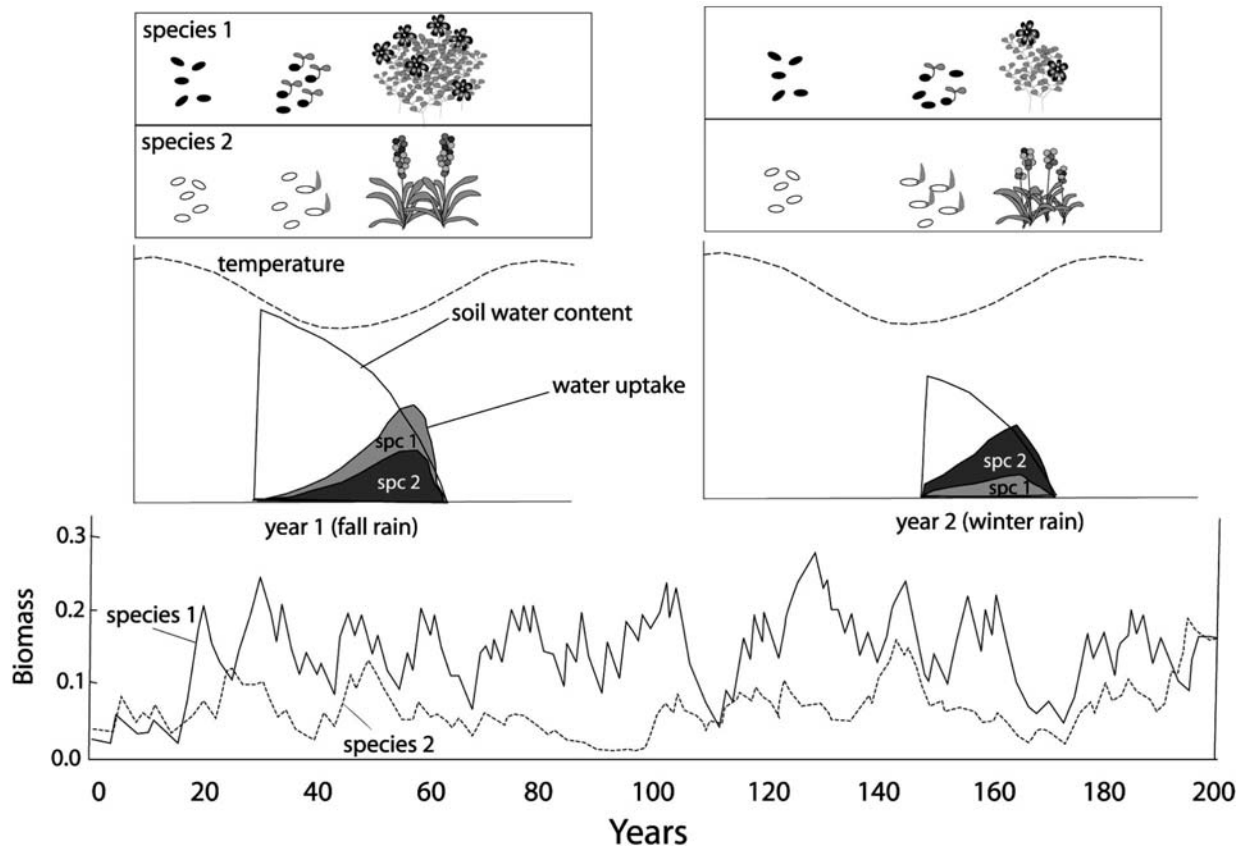
Fig. 2 Coexistence of annual plant species due to phenological differences in germination interacting with year to year differences in timing of rainfall. In the first year, rain comes early in the season, favoring germination of species 1 while, in the second year, later rain favors species 2. Each species dominates resource uptake in the year type that favors its germination. Fluctuations from year to year in the timing of rain favor different species in different years, and they coexist by the storage effect

Differences in timing of resource consumption alone are not sufficient for coexistence, however: two other factors are involved in the storage effect. First, species must have high levels of persistence through times when they are not favored. Such times include not only interpulses, where no growth activity occurs, but also pulses, and times during pulses, that a species finds relatively unfavorable for resource uptake due to its phenology or the competition that it experiences. Such persistence, or "buffered population growth", comes about in a great variety of ways, ranging from seed dormancy to low rates of loss of accumulated biomass on individual plants under stress (Chesson and Huntly 1989; Chesson et al. 2001). In an arid environment dominated by two-phase resource dynamics, life histories fostering persistence through unfavorable times are to be expected: such life histories are integral to coexistence by the storage effect (Chesson and Huntly 1988).

The second additional requirement for the storage effect concerns patterns of covariance between environment and competition, i.e., the covariance over time between the degree to which a species is environmentally primed for resource consumption by its phenology (its "environmental response") and the limitation on resource consumption that it experiences due to competition, both intra- and interspecific. Of most importance, whenever a species is near or above its average abundance, intraspecific resource limitation must occur during those periods when it has its strongest resource consumption rates, i.e., a species must be self-limiting when it is favored environmentally (Fig. 4). In essence, when a species is having its strongest environmental response, it is also drawing resources down most heavily, and therefore having its greatest competitive effect. When species are relatively specialized in their timing of activity, these competitive effects generate mostly intraspecific competition, which will be most pronounced when they are abundant.

On the other hand, when a species is at low density (i.e., well below its average abundance) it has little competitive effect, either intra- or interspecific, and its rate of resource consumption has little influence on the intensity of competition, which comes from other species. As a consequence, a species at low density can experience negative covariance between environment and competition, consisting of times during which especially strong population growth occurs, and times that are especially harsh for population growth. Such negative covariance results when species have opposite patterns of resource consumption, for then a species at low density can experience low competition (because high density species are not then consuming resources) when the low-density species finds the environment favorable for resource
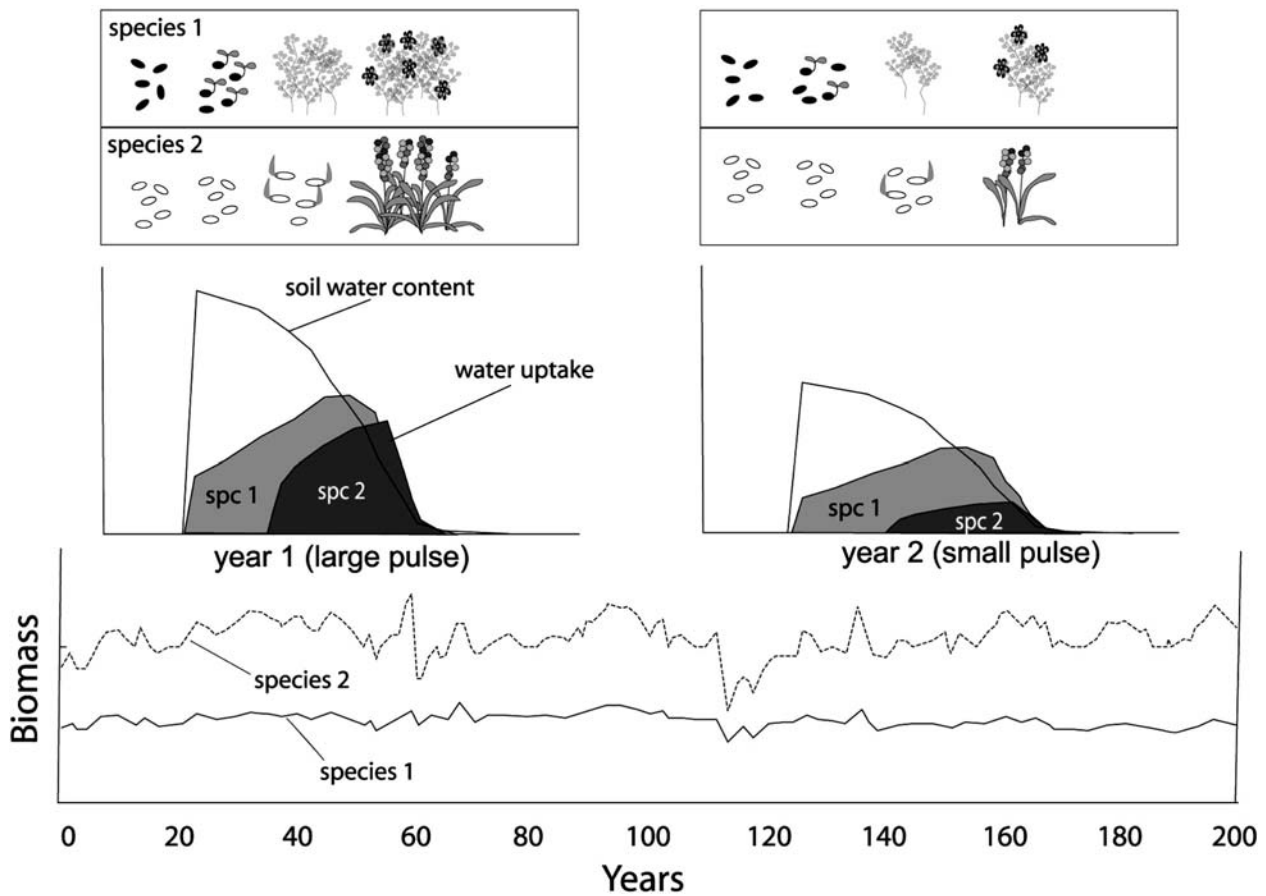
Fig. 3 Coexistence of annual plant species due to differences in the rate of breaking dormancy in response to a pulse. Species 1 germinates sooner after rain than species 2, but species 2 compensates by having higher water use efficiency and accumulates biomass faster than species 1. Although the amount of rain affects the relative performances of the species, with species 2 benefiting more from larger rainfalls, the mechanism of coexistence is the species difference in the rate of response to the pulse

consumption. Conversely, this low-density species will also experience high competition during times that are also environmentally unfavorable for resource consumption. More generally, species do not have opposite responses to environmental conditions but do have some differences that translate into lower covariance between environment and competition for species at lower density. This lower covariance means that a low-density species has both more times when conditions are strongly favorable for population growth and more times when conditions are strongly unfavorable for population growth than does a species at high density (Chesson and Huntly 1989).

Buffered population growth has a critical role translating lower covariance between environment and competition into net benefits for a species at low density. Buffered population growth means that less is lost during unfavorable conditions (high competition and an unfavorable environment) than is gained during favorable conditions (low competition and a favorable environment), leading to a net gain when averaged over time. This effect is illustrated in Fig. 4. Comparing the top and bottom rows, or the middle two rows, we see a low-density species experiencing negative covariance between environment and competition making major gains in its representation

in the seed bank during favorable times, but experiencing only small losses during unfavorable times due to high persistence in the seed bank. Comparison of rows 1 and 2, or 3 and 4, in Fig. 4 illustrates positive covariance for a high-density species, which prevents it from gaining much advantage from favorable times for resource consumption. Thus, we see that positive covariance between environment and competition prevents a high-density species from increasing its dominance, and the lower covariance for a low-density species, coupled with buffered population growth, allows a low-density species to gain more during favored times than it loses in disfavored times. As a consequence, there is an average tendency for species to have positive growth rates when they become low-density species, and they then return to a higher density (Fig. 4). This is the storage effect.

So far, we have focused on competition during the entire growing phase of a plant. However, competition may vary in importance over the lifecycle, and some species may be differentiated from one another primarily during establishment. These regeneration niche differences (Grubb 1977) are another variation on the storage effect. Species compete for resources to establish, which may be provided during pulses; and different species may be

Fig. 4 Illustration of the storage effect. Each row shows the development of an annual plant community from the seed bank at the beginning of one year to the seed bank at the beginning of the next year. First and third rows: germination is high for the rare species but not the common species. Competition is low because the common species has low germination. Individual plants grow large and the rare species benefits greatly, substantially increasing its representation in the seed bank. Second and fourth rows: germination is low for the rare species but high for the common species. Competition is high, and individual plants remain small. The common species changes little in the seed bank. The rare species avoids catastrophic decline due to high survival of dormant seed

A: Fall rain favors species 1:

B: Winter rain favors species 2:

favored by different sorts of resource pulses, as discussed by the examples below.

Relative nonlinearity

Relative nonlinearity shares with the storage effect the idea that species differ in their patterns of population growth and resource consumption over time, but considers not phenology of resource consumption, but rather how growth and resource consumption change directly as functions of the availability of the resource. Species are said to be relatively nonlinear when they have differently-shaped curves defining growth as a function of resource availability (Chesson 1994), as depicted in Fig. 1B. For the case of water as the resource and constant water-use efficiency, growth and resource uptake are proportional, and we assume that case (for simplicity) in the present discussion, even though proportionality of growth and uptake is not necessary for the mechanism.

Fig. 1B shows growth/uptake curves for two hypothetical species, one characterized by a threshold resource level before significant uptake occurs, and the other by a maximum uptake rate that is achieved at a relatively low level of resource availability. In such circumstances, species differences in resource consumption are driven

primarily by resource availability and cause different temporal patterns of growth and resource uptake (Fig. 5). Species 1 would be the winner in equilibrial competition with constant resource supply, because it is able to persist at lower resource abundances and would drive resources to its resource equilibrium R_1^*, where respiratory losses, tissue death, and mortality balance photosynthetic gains. Species 2 would have a negative population growth rate at this constant level of resource availability and go extinct according to Tilman's R^* rule (Tilman 1982). Species 2 would benefit from resource fluctuations, however, because it needs, and can take advantage of, relatively high resource levels due to its threshold before significant resource uptake occurs, and higher resource saturation level. Pulsed resource supply would ensure that resource levels would not stay at R_1^*, giving species 2 a chance to persist. Indeed, species coexistence may occur in these circumstances by a mechanism first investigated by Armstrong and McGehee (1980) for a situation in which oscillatory consumer-resource interactions drive resource fluctuations.

It is important to recognize, however, that species coexist by this mechanism only if each species, when abundant, modifies the resource pulse dynamics in a way that favors its competitor (Chesson 1994, 2000a). While
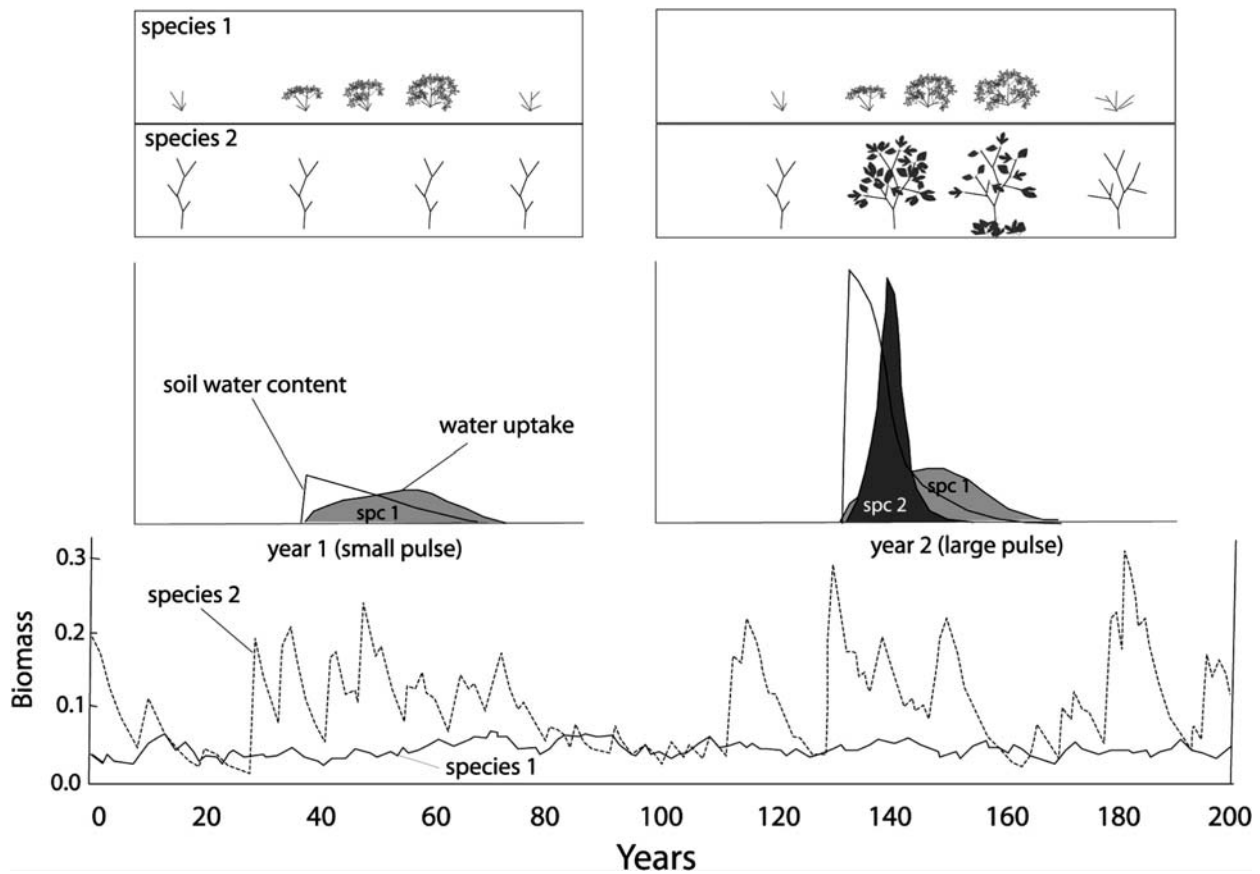
Fig. 5 Coexistence of species due to different nonlinear uptake rates (from Fig. 1B), with year to year variation in amount and timing of rainfall. In the first year, the small pulse does not lead to uptake by species 2, and only species 1 benefits. The large pulse in the second year leads to greater uptake by species 2, although species 1 can continue to take up water after uptake by species 2 has ceased

resource fluctuations can have external causes (e.g., pulsing rain), each species must nevertheless modify resource fluctuations to its relative disadvantage. Fig. 6 illustrates one way in which resource dynamics might be modified promoting species coexistence. A build-up in the abundance of species 2, relative to species 1, should accelerate the onset of resource levels that favor species 1, and shorten the amount of time that species 2 is able to acquire resources for growth (Fig. 6B). Likewise, a relative build-up of species 1 would extend the time spent at the high resource levels that favor species 2 (Fig. 6A). The high resource uptake that species 2 has at high resource levels would diminish time spent at these levels, but its threshold uptake rate would mean that is it ineffective in reducing lower resource levels. In contrast, species 1 reduces high resource levels less effectively, because its maximum resource uptake is lower and is achieved at low resource levels. Thus, species 1 would extend the time spent at high resource levels, favoring species 2. This reciprocity, where each species promotes conditions that give the other species a relative advantage, is behind the stable coexistence that occurs through relatively nonlinear competition (Armstrong and McGehee 1980; Chesson 2000a).

Other coexistence mechanisms

Other mechanisms that do not depend on differential use of resource pulses are also expected to operate in arid communities. Vertical partitioning of soil moisture by species with different root distributions (Cody 1986) is a potentially important mechanism that does not require pulses but is greatly affected by pulse size and frequency (see Plant traits and vertical partitioning section). In arid lands, like elsewhere, different species are favored by different physical conditions in horizontal space, such as soil type, slope, and aspect (Cody 1986), potentially greatly contributing to diversity maintenance (Snyder and Chesson 2003). Mechanisms fundamentally involving changes in biological conditions in both space and time are competition-colonization tradeoffs (Tilman 1994), in which species with higher competitive ability have poorer dispersal ability, and the related successional mosaics mechanism, which is the version of the disturbance hypothesis most strongly supported by models (Chesson and Huntly 1997). For the successional mosaics mechanism, competition-colonization tradeoffs drive succession, and a mosaic of habitat patches in different successional stages collectively supports high diversity (Hastings 1980; Chesson and Huntly 1997). There has been limited

Fig. 6 Effects of nonlinear resource uptake on the pattern of resource decline following a pulse. Uptake rates are from Fig. 1B. When species 1 is at high density, water availability is reduced slowly, benefiting species 2, which requires high availability. When species 2 is at high density, water availability is reduced rapidly initially, but as this species has threshold uptake, uptake by this species ceases at a level still beneficial to species 1. Since species 1 is at low density, species 1 can continue to take up the resource for longer. Thus each species creates conditions that are relatively more advantageous to the other species
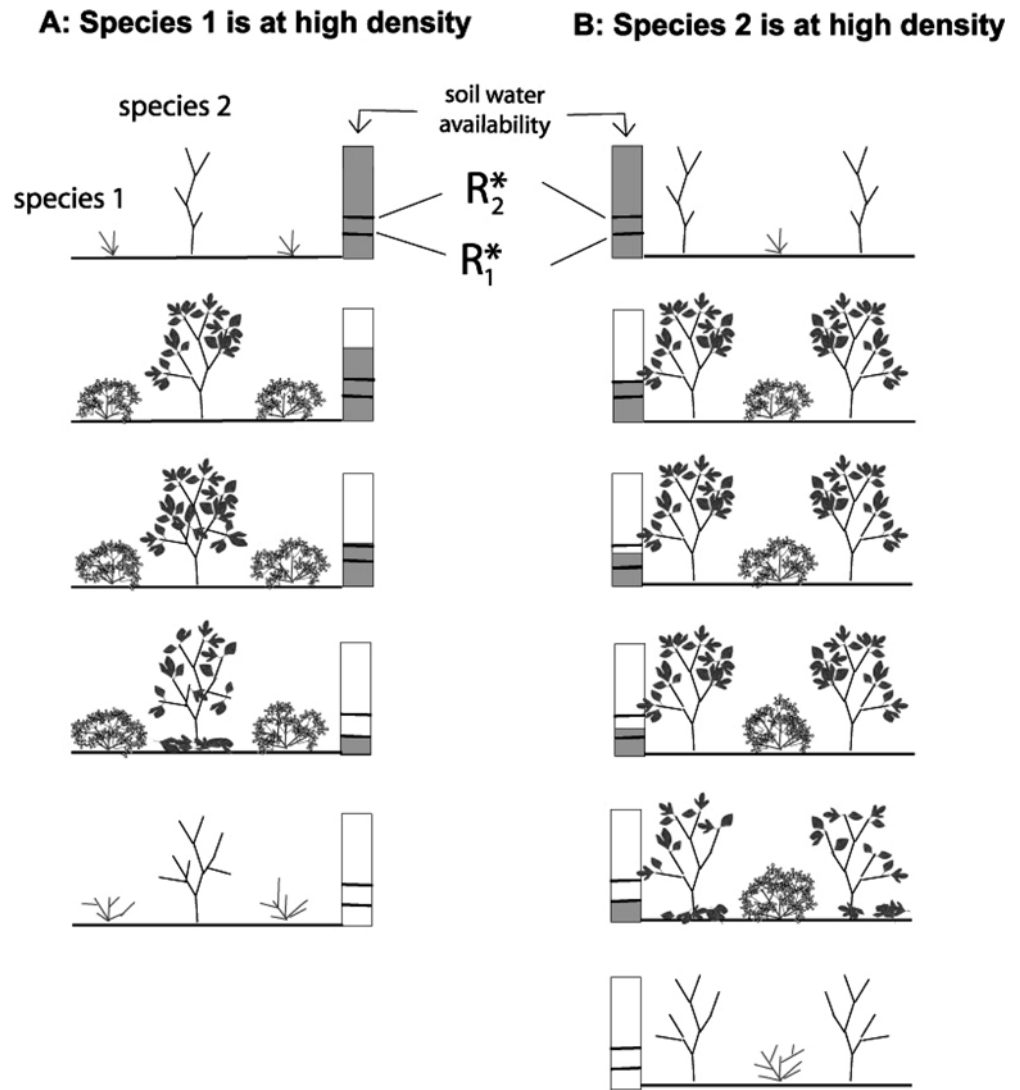
exploration of the potential for pulsed resources to play a role in the development of successional mosaics in arid ecosystems. For example, Fernandez-Illescas and Rodriguez-Iturbe (2003, 2004) propose that rainfall variation causes variation in competitive ranking along with negatively correlated variation in functions determining colonizing ability, issues deserving further examination.

In all of the mechanisms discussed so far, we have focused on the indirect interactions between plant species through shared resources. However, increased plant growth in response to precipitation pulses provides resource pulses to consumers of plants. In turn, these consumers can have roles in the maintenance of plant diversity (Huntly 1991). The storage effect and relative nonlinearity of competition may occur, but with competition replaced by apparent competition, the indirect interaction that results from sharing of natural enemies (Huntly 1991). Additionally, consumers may promote diversity when different consumers prefer different plant species (Davidson et al. 1985), or when foraging efforts are concentrated on more abundant species (Krivan 2003)

or competitive dominants (Lubchenco 1978; Chesson 2000a).

Mechanisms in combination

In any community, multiple mechanisms undoubtedly contribute simultaneously to maintenance of diversity. For example, species in a desert community are likely to differ in rooting depth, phenology of water use, and shape of resource uptake curve. It is thus important that mechanisms be considered in combination. This is possible in models, and Chesson (1994) gives examples of coexistence involving the simultaneous action of several different mechanisms. Most important are techniques that quantify the total diversity stabilizing effect of all mechanisms in a system in terms of how strongly competitive exclusion of any given species is opposed. This quantity is partitioned into components due to different mechanisms, permitting the relative importances of different mechanisms to be evaluated (Chesson 1994, 2000b, 2003). These techniques also express the stabiliz-

ing effects of each mechanism in terms of the functional components that comprise it. For example, a general formula for the storage effect is given involving quantitative measures of each essential component: buffered population growth; covariance between environment and competition; and species-specific responses to the environment. Similarly, relative nonlinearity of competition is quantified in terms of measures of relatively nonlinear uptake and variance in resource availability. These techniques are only just beginning to be applied to field data (Huntly et al., in review), but measurement of essential components, such as covariance between environment and competition, appears to be an especially promising way of revealing the functioning of coexistence mechanisms in nature (Melbourne et al 2004).

Although these techniques measure the strengths of mechanisms, we have as yet no satisfactory guide as to how strong a mechanism or combination of mechanisms must be to explain any observed level of diversity. Competitive exclusion occurs when the species in a community differ too greatly in average fitness relative to the total strength of all diversity stabilizing mechanisms in that community (Chesson 2000a, 2003). Thus, if species living in a common environment have very similar average fitness, their stable coexistence is possible in the presence of relatively weak mechanisms. General arguments claiming that a particular mechanism cannot be strong enough to maintain diversity have no validity in the absence of knowledge of average fitness differences, which are rarely known. Robust evidence for or against a particular mechanism must come from measurements capable of revealing the mechanism at work in a community. The kinds of field quantification of mechanisms discussed here are a new development, with the critical benefit of allowing the relative importances of mechanisms to be assessed even though average fitness differences may not be known.

Generalists, specialists and plasticity

All the mechanisms of stable coexistence that we discuss involve species differing in their ecology in some particular way. For instance, species that coexist through the storage effect have different times of maximal resource use. One might ask if the presence of a species that uses resources over a broad range of times is evidence against the storage effect. It has been argued that generalist resource use might often be advantageous in environments where species face a great deal of uncertainty, with phenotypic plasticity being one particular means by which broad resource use is possible (Schlichting 1986). However, plasticity, or any generalist resource consumption behaviors, including those involving drought resistance, may come at a cost (Alpert and Simms 2002; Schwinning and Sala 2004). In such circumstances, there is no contradiction that a generalist can coexist with specialists so long as the specialists are in fact superior performers during the times or conditions that favor them, and there

are some times when no specialists are favored so that the generalist is then superior. The stable coexistence of two or more generalists, however, is more problematic. Though any two generalists are likely to differ quantitatively in some respect, their coexistence may not be strongly stabilized if they both take advantage of most of the resource opportunities most of the time. Thus, if subtly different generalists are to coexist stably, they must have very similar average fitnesses.

Plant traits, resource pulses, and diversity maintenance

Empirical studies of competition in arid ecosystems have primarily focused on changes in the intensity of competition along environmental gradients. As emphasized above, however, such observations contribute little to our understanding of diversity maintenance unless the response patterns to such gradients are compared between species of the same community. Unfortunately, few studies have compared species responses to resource pulses which permit tests of the theoretical ideas discussed here. Hence, we will discuss the relevance of existing information and indicate where additional studies are needed to investigate the role of resource pulses in diversity maintenance.

Plant growth and pulse use: the storage effect

The theory section identifies two ways in which species might differ in temporal patterns of water use and hence coexist: (1) differences in which pulses species use most, with use controlled by environmental factors other than water (e.g., temperature, relative humidity, and photoperiod), and (2) differences in when during a pulse a species most heavily uses water. Timing of water use during a pulse could depend intrinsically on the rate at which a plant undergoes physiological changes that are required to initiate water uptake after drought. There also is a third possibility that in essence is an interaction of (1) and (2): previous use of a pulse, because it came at the right time for a species, might leave that species physiologically able to participate earlier in a subsequent pulse.

Differences between species in phenology (i.e., the seasonal schedule for growth and leaf and flower display) often cause differences in the timing of resource use. Such phenological differences are relatively well documented (e.g., Beatley 1974; Kemp 1983; Abd El-Ghani 1997; Pavon and Briones 2001). Moreover, seasonal variation in use of water (Gebauer and Ehleringer 2000; Sperry and Hacke 2002) and nitrogen pulses (Bilbrough and Caldwell 1997) have been observed. Seasonal differences in pulse use and growth potential are often linked to differences in canopy leaf area (Comstock et al. 1988; Smith et al. 1997). Both drought- and winter-deciduous species typically shed all their leaves at once when leaves become carbon sinks (Mooney and Dunn 1970) or when the integrity of the hydraulic transport system is at risk (Tyree et al. 1993; Sperry et al. 2002). Deciduous species therefore give up

opportunities for pulse use and carbon gain during either the driest or coldest part of the year (Comstock et al. 1988; Smith et al. 1997; Reynolds et al. 1999). Evergreens also adjust their leaf area to some degree, even though they rarely lose all their leaves at once. Therefore, evergreens can maintain some level of activity when deciduous species are dormant (Noy-Meir 1973) and can take advantage of smaller rainfall events that are insufficient to break dormancy in deciduous species. Seasonal differences in water pulse use and growth have also been linked to photosynthetic responses to temperature of C_3 and C_4 species. Cooler temperatures during the winter and early spring rainy season tend to favor C_3 species, while C_4 species preferentially use water pulses during the hot summer months (Mulroy and Rundel 1977; Kemp 1983).

Species coexistence by the storage effect can occur on a smaller timescale when species divide up a single large rain storm or a series of smaller rainfall events. Species that emerge quickly from the interpulse are able to use water at the onset of the pulse, while slower species are limited to using water at the tail end of the pulse (e.g., Fig. 2). These species differences in response time can be related to the rates at which new fine roots establish (Nobel 1994), hydraulic conductance is restored, stomatal conductance and photosynthesis increase (Gebauer et al. 2002; Schwinning et al. 2002), and new leaf growth is initiated (Beatley 1974). Coexistence would be promoted only when this temporal pattern entails tradeoffs, e.g., when later pulse users are able to draw down soil moisture to lower levels than are early users.

As an example, we contrast the pulse use of succulents and shallow-rooted annuals or perennial graminoids. Succulents, which typically have shallow and widely spreading roots, can take up shallow soil water quickly after a pulse event. New roots grow within 6–24 h and approximately 40% to 80% of existing roots rehydrate within 1–3 days (Nobel 1994). However, because of their water storage strategy, succulents must maintain relatively high water potentials and avoid leaking water into the surrounding soil as it dries out. To prevent water loss, the hydraulic connections of their roots to the soil are cut relatively early during the draw-down of a pulse of soil water (Nobel 1994).

Shallow-rooted annuals and grasses respond somewhat less rapidly to rainfall. Unlike the succulents, their rate of uptake depends not only on roots, but on the establishment of high transpiration rates, which is typically delayed by 24 h even when leaves are already present (Sala and Lauenroth 1982). Once the physiological adjustments have taken place, these annuals and grasses are able to absorb water rapidly from a pulse because of typically high specific root conductance, low root:shoot ratios, and high photosynthetic capacities with large maximal leaf conductances (Cohen 1970; Smith et al. 1997). Compared to succulents, annuals and shallow rooted perennial grasses are more effective in using the entire water pulse, since they can assume the lower plant water potentials necessary to extract soil moisture to lower levels (Franco and Nobel 1988).

The interaction between the rate of response to increases in soil moisture and time of year allows species that are active within the same season to partition the available soil moisture over time. Differences in pulse response times and in sensitivity to pulse and interpulse periods may place species in different physiological states, affecting their pulse use. For example, evergreen species that maintain some foliage are likely to respond relatively rapidly to a water pulse, needing only to open stomata to increase carbon assimilation. Because of the cost of maintaining photosynthetic tissue, this strategy might only be advantageous when pulses are frequent, but has the benefit that small frequent pulses can be used by such species (Reynolds et al. 1999). For large, infrequent water pulses, the addition of new leaf area is necessary for optimal water use in both deciduous and evergreen species. The unfolding of leaves can start within 1–7 days after a rainfall, and the dynamics of leaf area expansion vary greatly between species (Beatley 1974). In a temperature-controlled experiment, after application of a single large summer pulse that followed a 4-month interpulse without rain, the leaf numbers of drought-deciduous shrubs and perennial grasses peaked much earlier than those of evergreen shrubs (Schwinning, personal observation). This observation suggests a possible tradeoff between the speed and extent of the foliation response to a pulse and the ability to retain leaves as the soil dries out.

As emphasized above, critical to coexistence by temporal differences is covariance between environment and competition, i.e., the intensity of competition increases as environmental conditions become more favorable for resource consumption. Although not difficult in principle, this part of the theory has rarely been addressed in empirical studies. There is some indirect evidence that the intensity and direction of competitive interactions in annuals can vary considerably in space and time (Pantastico-Caldas and Venable 1993; Pake and Venable 1995, 1996; Kadmon 1997; Brooks 2000; Melbourne et al. 2004). In other cases, we infer such relationships because of the strong mechanistic linkage between carbon gain and water loss at the leaf level (therefore, water uptake) or, more generally, between the rate of growth of a plant and whole plant resource uptake. Thus, a plant that is physiologically more active at the time of a resource pulse must exhibit stronger competitive effects relative to its size than a less active plant with a currently lower resource demand.

Covariance between environment and competition is expected to be strongest when plant resource uptake is a major cause of resource depletion after a resource pulse. In the upper soil layers, however, large evaporational water losses decrease the contribution of shallow-rooted plants to soil moisture depletion (Cable 1969; Noy-Meir 1973; Dyer and Rice 1999), therefore decreasing the link between uptake and resource shortage (Kadmon and Shmida 1990; Gebauer et al. 2002, Sher et al. 2004). As a result, the effectiveness of temporal resource partitioning by the storage effect would be lower in shallow-rooted species, because covariance between environment and

competition would be less pronounced. Conversely, the storage effect should be stronger for plants rooted in soil layers where plant use of water is the dominant mode of depletion (Cable 1969; Dyer and Rice 1999).

A final requirement for coexistence by the storage effect is buffered population growth, which refers to mechanisms that allow carbon, nutrients, or water to be carried over through unfavorable periods (Chesson and Huntly 1988), limiting the harm to a population during those times. For ephemerals and annuals, large quantities of dormant seed (Cohen 1966; Went 1979) provide this carry-over mechanism. The storage of water in conjunction with water-conserving CAM metabolism allows succulents to maintain a positive carbon balance during long interpulse periods, without experiencing lethally low water potentials (e.g., Pimienta-Barrios et al. 2002). Perennial grasses and shrubs persist through unfavorable periods by a variety of drought-avoidance and tolerance mechanisms and by storage of carbon and nutrients in stems or belowground organs (Warner and Chesson 1985; Chapin et al. 1990). Drought-avoidance and tolerance mechanisms are relatively well studied and include, for example, osmotic and elastic adjustment (Forseth and Ehleringer 1984; Meinzner et al. 1988), reduction of leaf conductances (Smith and Nobel 1986), and shedding of leaves and branches to maintain the integrity of the hydraulic transport system (Tyree et al. 1993; Sperry et al. 2002), but little is known about the amount and control of seasonal storage of carbon and nutrients and its effect on buffering populations against decline.

Among the conditions required for the storage effect, covariance between environment and competition has been least investigated empirically. The design of experiments and statistical methods to evaluate the covariance between environment and competition are new (Chesson and Sears, in preparation) and so far have been applied only to spatially varying environments (Melbourne et al. 2004). In principle, such studies are not difficult. Standard procedures used to determine changes in interaction intensities along environmental gradients can be applied to quantify covariance between environment and competition (Melbourne et al. 2004). Use of these methods could provide strong tests of the contributions of the storage-effect to coexistence.

Plant growth and pulse use: relatively nonlinear uptake

The coexistence mechanism called relative nonlinearity involves species using soil moisture pulses differently because the pattern of resource consumption as a function of resource availability has different shapes for different species (Fig. 1B). Differences in the shapes of water uptake functions are brought about by differences in the response patterns of leaf conductance to water potential, differences in xylem conductance and vulnerability, differences in root conductance, and leaf:root ratio: in short, the overall hydraulic architecture of the plant (Smith

and Nobel 1986; Sperry et al. 2002). There appears to be a structural tradeoff between xylem conductivity and vulnerability, such that functional or structural features that protect the xylem system from embolism also tend to lower hydraulic conductivity (Hacke and Sperry 2001). As a result, more drought-tolerant species can use water over a broader range of conditions (Chapin 1991; Sperry et al. 2002), including a broader range of interpulse lengths (Sher et al. 2004). In particular, water extraction at lower soil water potentials is possible, but at the cost of lower maximum leaf conductances or reduced leaf area. By contrast, a less tolerant species achieves much higher rates of whole-plant gas exchange when soil water potential is near saturation, but loses hydraulic conductivity more rapidly as soil water potential declines. As a result, plant species that are more sensitive to the interpulses are also likely to be more responsive to increases in water availability (Novoplansky and Goldberg 2001a, 2001b; Sher et al. 2004). Whether the resulting relationship of water use for a pair of species that differ in hydraulic architecture leads to relative non-linearity, as envisioned in Fig. 5, cannot be decided categorically, but it is possible to address this question with physiological models (Sperry et al. 1998) and experimental determination of water use functions.

Relatively nonlinear resource uptake can only act as a coexistence mechanism when resource consumption by a particular species alters the temporal pattern of resource availability in a way that has a stronger negative impact on itself than on its competitors (Relative nonlinearity section above; Fig. 6). Although such effects are predicted by theory, no experimental studies have examined the effects of uptake functions on patterns of resource availability, to our knowledge, although such studies are certainly feasible. Like covariance between environment and competition, as discussed above, such effects of uptake on resource availability will be strongest for plants tapping into soil layers where transpiration dominates soil moisture depletion.

Regeneration and pulse use

The above two sections have focused on variation over time in growth or water uptake. However, as emphasized by Grubb (1977), a critical phase in the life of a plant is establishment, and coexistence mechanisms potentially operate in this phase also. Just as environmentally-dependent, temporally variable germination can promote coexistence of annual plants by the storage effect (Resource pulses and the storage effect section), so too can temporal variation in establishment of perennial plants (Chesson and Huntly 1988; Chesson 2003). However, due to their longer lifespan, the population dynamics of perennial plants tend to be responsive to environmental variation on longer timescales, being driven not by single pulses, but rather by the temporal distribution of pulses over weeks or years (Anderson and Inouye 2001).

The storage effect is likely to be a common contributor to coexistence of desert perennials, which show substantial between-season and between-year species-specific variation in seed output, germination, and establishment, which one would expect to translate into species-specific establishment patterns similar to those described above for annual plants. Seeds of perennials often germinate only after a series of rain pulses, and subsequent seedling survival is often dependent upon a series of relatively wet days, seasons, or even years (Neilson 1986; Wilson and Witkowski 1998; Weltzin and McPherson 2000). Seedling establishment is rare, not only due to water limitation, but also due to factors such as seed availability, temperature, herbivory, and fire (e.g., Grubb 1977; De Villalobos and Peláez 2001; Midgley and Bond 2001). These other factors may themselves be affected by patterns of rainfall and so may exaggerate the tendency for recruitment of perennials to be infrequent and episodic.

Like desert annuals, perennial species may differ in the rainfall sequences and thresholds that influence seed production, seed germination, and seedling survival. Thus, although species may be broadly correlated in the timing of recruitment, particular patterns of rainfall may favor seed production, germination and establishment of certain species over others. The wide interspecific variation observed in physiological (e.g., osmotic adjustment, nutrient uptake capacity) and morphological traits (e.g., seed size and seed coats, root morphology and depth distribution) is consistent with this suggestion. For instance, species differ in seed coats and rooting patterns, which results in differing patterns of germination and seedling survival in response to environmental factors (Wilson and Witkowski 1998; Brown et al. 2003; Danthu et al. 2003). Hence, much quantitative variation in the relative recruitment rates of different species is likely to occur within times when rainfall is sufficient for some recruitment of perennial species. Species can be broadly correlated in times of establishment (e.g., wet years or seasons), while still differing importantly in finer-scale temporal patterns of establishment.

Many desert perennials are very long-lived, which allows storage of reproductive potential over generations, and so provides the buffering of population growth required for the storage effect. Evidence suggests that most desert perennials have lifespans of a decade or more, and many have maximum lifespans of centuries to millennia (e.g., Steenburgh and Lowe 1983; Goldberg and Turner 1986; Bowers et al. 1995). For instance, Cody (2000) sampled a plot of the Mojave Desert after a 15-year interval and found that only 11% of the individuals of the 22 species present had died. Similarly, Goldberg and Turner (1986) documented that 31 of 39 species present in plots that were repeatedly mapped for 72 years had longevities of at least 20–30 years, with about half of these having longevities of more than 50–72 years, and Bowers et al. (1995) found that substantial proportions of the individuals of 14 species had survived for 100 years, as evidenced in photographic records from Arizona, USA.

The long lives of desert perennials facilitate reconstruction of past population history, which gives clues to the dynamics that have produced extant communities, and these often give evidence consistent with the storage effect. For instance, age or size structure of populations of desert plants suggests that surviving plants are the remnants of periodic bouts of establishment (e.g., Crisp and Lange 1976; Jordan and Nobel 1981; Steenburgh and Lowe 1983; Goldberg and Turner 1986; Turner 1990) and that these bouts of establishment have occurred disproportionately in different years for different species (Jordan and Nobel 1982; Goldberg and Turner 1986; Chesson and Huntly 1989; Turner 1990; Anderson and Inouye 2001). Detailed data on the population structure of even one species at many sites and years (i.e., over many spatial and temporal conditions) are rarely available, but the long-term large-scale study of saguaro conducted by Steenburgh and Lowe (1983) shows episodic establishment of the saguaros that form local populations and also shows considerable variation from place to place in the years in which establishment was successful, with some variation associated with specific environmental factors that are probably causally related. Such demography cannot be reconstructed for cases in which species differ in seasonal, rather than year-to-year, patterns of establishment, as these more subtle differences in phenology are not recorded in the annual age structure of populations. However, seasonal differences in conditions favorable for germination and establishment could contribute to the diversity of desert perennials through storage effects.

Studies of intra- and interspecific density-dependence of establishment during the course of a growing season could provide critical missing data to test for a role of seasonal separation of establishment phenology in diversity. Studies of competition during establishment are unfortunately few, and it is critical to know whether high pulses of recruitment lead to strong competition, particularly for abundant species. Such covariance between environment and competition would limit the gains that an already abundant species can make during times that are favorable for its recruitment, but less abundant species would not be as limited during their favorable times, because the absolute magnitude of recruitment would not be as great and so would not lead to as much competition. This difference in covariance between environment and competition for species of different abundances is a necessary element of the storage effect (Chesson and Huntly 1988), but failure to appreciate its importance has led to the failure to collect empirical information on this critical feature.

The question arises as to whether relative nonlinearity of competition can also have a role in regeneration. According to a general model of recruitment variation (Chesson 2003), this would occur if shorter-lived or more competitively sensitive species caused greater variation in plant density whenever they became abundant. Such a mechanism could work within perennial plants, within annual plants, or could include interactions between the two. As plausible as this might be, we are aware of no

studies that show greater density variation in a system when shorter-lived plants become more common. This lack of data probably reflects the tendency we have noted for failure to appreciate the need to measure the relationship between intraspecific competition, interspecific competition, and environmental conditions for species that co-occur over a range of environmental conditions, in space or in time.

Although regeneration processes may commonly contribute to coexistence through the storage effect and relatively nonlinear competition, their contributions via other mechanisms are not ruled out. For example, nurse plants are important to the establishment of some aridland perennials. This requirement could result in spatiotemporal dynamics of cyclic succession (Wiegand et al. 1995; Weltzin and McPherson 1999), fostering coexistence through successional mosaics (Chesson and Huntly 1997) in which facilitation by nurse plants has an important role. Unfortunately, few studies of perennials in arid environments go beyond germination and early survival to allow robust evaluation of this mechanism.

Plant traits and vertical partitioning

In addition to differing in water use over time, the plant species of arid and semiarid environments differ in maximum rooting depths and in distributions of root biomass with depth (Schenk and Jackson 2002b), suggesting vertical partitioning of soil moisture. Walter (1971) first saw the potential for niche separation by vertical soil moisture distribution in his classic two-layer model explaining the coexistence of grasses and woody species in savanna ecosystems. Later, Cody (1986) expanded the idea of the two-layer model and suggested that spatial partitioning may be a ubiquitous mechanism for the coexistence of plant species in water-limited ecosystems, conceiving multiple fine-graded niches for species whose root distributions differ only by degrees.

Vertical partitioning of soil moisture may have important spatio-temporal aspects that depend on pulsed resource supply: although shallow-rooted species intercept soil water first and, if at high density, may prevent the penetration of some precipitation events to deeper soil layers, in general they cannot prevent the penetration of water from large precipitation events to greater depths where it might be used by other species. Walter (1971) used these ideas to explain the variation in the regional characteristics of summer-rain savannas, which change from shallow-rooted grass-dominated ecosystems to deeper-rooted woodland with increasing summer rainfall.

The isotopic identification of xylem water from different soil depths allows direct tests of the hypothesis of vertical water partitioning (White et al. 1985; Dawson 1993). In general, isotopic studies suggest considerable overlap in the use of surface water from recent rainfall events (e.g., Ehleringer et al. 1991; Lin et al. 1996), although some species are clearly differentiated in their ability to use deeper water sources, particularly ground-water (e.g., Schulze et al. 1996; Dodd et al. 1998; Midwood 1998). Effective water partitioning appears to be most likely when annual rainfall is large enough (or evapotranspiration during the rainy season low enough) to allow infiltration to a depth that could be considered "deep" by aridland standards, e.g., below 80 cm (Reynolds et al. 2000) and if species have large differences in rooting depth. Thus, Walter's hypothesis (1971) was confirmed for species with large differences in rooting depth. However, the many species in a community with similar rooting depths use virtually identical water sources for much of the time, questioning the extent to which vertical water partitioning contributes to their coexistence (Reynolds et al. 2004).

In the majority of studies, species coexistence by vertical partitioning of water has been assessed only by one-time measurements, but such measurements are only adequate if the distributions of moisture and of active roots within the soil profile remain constant over time. Instead, soil moisture profiles and root distributions are temporally dynamic (Fernandez and Caldwell 1975; Reynolds et al. 1999) and so measurements at one time cannot reveal the full range of possible species differences in vertical water use. A better understanding of the spatio-temporal dynamics of water use by different species is needed, and consideration of temporal variation in the extraction of soil moisture by plant species from different soil layers would be fruitful to consider. There is also a need for mathematical models that reveal the kinds of spatio-temporal water-use differences between species that are most conducive to coexistence, because existing models of horizontal spatial partitioning (e.g., the spatial storage effect; Chesson 2000b) do not apply well to vertical partitioning of soil moisture.

Discussion

Arid environments, in which rain occurs sporadically, leading to pulse-interpulse cycles of resource availability and so pulsed opportunities for plant growth and reproduction, provide serious challenges to plants and other organisms. These challenges have caused the evolution of many different adaptations to take advantage of opportunities as they arise and for persistence through harsh times. Theory says that the ways in which species are differentiated by adaptations to exploit opportunities and to persist and avoid losses, are the keys to maintenance of species diversity. Such adaptation and differentiation appear common in aridland plant communities that experience the pulsed resource availability that limited and periodic rainfall entails.

The direct and indirect responses of species to the varying environment of deserts both reflect and generate opportunities for coexistence mediated by environmental variation. Species respond directly to their environment, changing patterns of such physiological processes as resource uptake, growth, reproduction, and dormancy; and they also affect the environment, most notably through

their consumption of resources, which alters the patterns of resource availability for other organisms. Theory says that differences between species in their phenology of activities, or in their relatively non-linear responses to and effects on resources, can maintain diversity. Pulsed resource availability offers many opportunities for such differentiation in species' behaviors, and our review suggests that such differences between species in patterns of resource use, growth, reproduction, and establishment are ubiquitous in arid ecosystems. This, in turn, suggests that the pulsed rainfall of arid environments has made widespread contributions to diversity maintenance. Unfortunately, there are few adequately detailed studies of differentiation between co-occurring species with which to test this idea and measure its importance. Instead, there has been a strong focus on how the intensity of competition varies in space and time, with little consideration of species differences. As interesting as such studies are, they have limited value in the understanding of species coexistence, as understanding of coexistence requires information on the relative strengths of intra- and inter-specific competition. Species coexistence is not promoted by weakness of competition, but instead by an excess of intraspecific over interspecific competition or, more generally, by an excess of intraspecific over interspecific density dependence.

That the intensity of competition varies in space and time has one critical consequence: to understand diversity maintenance, one must consider the larger scales of time and space. A high ratio of intraspecific to interspecific competition at local scales (particular times and places) implies that mechanisms that maintain diversity do operate on such small scales, as was often suggested by traditional equilibrium models of coexistence. However, when competition varies in time and space, it is essential to integrate over time and space. Differences between species in local patterns of effect on, and response to, resources and other environmental factors can lead to an excess of intraspecific relative to interspecific competition on the larger spatial and temporal scales over which these differences occur. The primary mechanisms that can promote such larger-scale coexistence are the two discussed here, the storage effect and relative nonlinearity of competition. Measures of mechanism strength as discussed here, and detailed in Chesson (1994, 2000a, 2000b, 2003), show how integration of time and space is done in models to bring out largescale differences between intra- and interspecific competition arising from these mechanisms. Melbourne et al. (2004) and Huntly et al. (in review) give examples of integration over time and space using empirical data from field studies.

Although our focus here has been on the plant trophic level, the fauna of arid environments is diverse too, and pulsed resource availability may also play an important role in this diversity. Granivorous rodents are particularly well studied in North American deserts (Brown et al. 1979), where many studies show that rodent populations tend to increase after pulses of seed production. The responses of rodent populations to precipitation pulses are similarly diverse to those of plant populations, both seasonally and on longer, multi-year timescales (Brown and Zeng 1989; Ernest et al. 2000; Brown and Ernest 2002). These varied patterns of response suggest opportunities for coexistence mediated through different phenologies of foraging and through nonlinearities in resource consumption that are essentially equivalent to the mechanisms discussed here for plants. Recent studies suggest that seasonal resource pulses may in part underlie the often high diversity of granivorous rodents in deserts: both the storage effect, realized through different seasonal activity patterns (Brown 1989a), and relative nonlinearity of competition, due to different resource thresholds for dormancy (Brown 1989b), are implicated. Thus, the mechanisms that are the topic of this paper are not restricted to the plant trophic level, and should be considered in studies of the diversity of any trophic level or of entire food webs.

The linkages that we have discussed between organisms, environment, and diversity maintenance have implications for understanding the effects of global environmental and land-use changes on ecological communities. It is widely expected that changes in seasonality or rainfall patterns, associated with global warming, will cause a profound restructuring of local communities (e.g., Schwinning and Sala 2004): however, we cannot predict community change without a clear understanding of the mechanisms that retain species in their present or future communities. Through the mechanisms discussed here, climatic shifts are likely not only to change species' average fitness, but also to change the patterns with which inter- and intraspecific competition vary in space and time, thus the persistence and coexistence of species and sets of species. A focus on diversity maintenance, as elucidated here, should be valuable not merely for basic science, but also for anticipating the likely impacts of climate change on the biodiversity of arid and semiarid lands, and the socio-economic challenges they may entail.

Appendix: the simulation models

The simulations depicted in this article are particular illustrations of general principles developed elsewhere (Chesson 1994, 2000a; Chesson et al. 2001). The illustrative simulations are all for annual plant communities in which some fraction of the seed bank of a species germinates when a pulse occurs, and the fraction not germinating in any particular year experiences a survival rate s_i (for species i) over a year. However, in the case of relative nonlinearity, the equations have been reinterpreted in the figures for perennials with a bud bank or simply dormant biomass taking the place of the seed bank. Such

reinterpretation is possible in other cases too, at least qualitatively.

The biomass arising from the germination of one seed is the unit of biomass, which grows according the differential equation

$$\frac{dB_i}{dt} = [c_i f_i(R) - m_i]B_i \tag{1}$$

between germination and flowering. Here R is resource availability (soil water content), $f_i(R)$ is the rate of resource uptake per unit biomass as a function of resource availability, c_i is conversion of uptake into new biomass, and reflects water use efficiency, and m_i is the per unit loss rate of biomass due to respiration, tissue death, and herbivory. The resource uptake rate, $f_i(R)$, is given by the equation

$$f_i(R) = \frac{a_i R^{\theta_i}}{1 + a_i d_i R^{\theta_i}} \tag{2}$$

where a_i controls the rate at which uptake increases as the resource increases, d_i controls the rate at which uptake saturates ($1/d_i$ is the maximum uptake rate) and θ_i controls the shape of the uptake curve, as illustrated in Fig. 1B. The total biomass of a species remaining at flowering was converted to new seed and added to the seedbank at the beginning of the next year at the rate ϕ_i per unit biomass.

In order to produce easily understood graphs, only one pulse of rain arriving at a point in time was allowed each year. In general, this restriction is highly conservative with respect to the mechanisms illustrated here because multiple pulses, and broad pulses that arrive continuously over an interval of time, simply increase the opportunities for partitioning. The timing of the rain pulse in a year was determined by a random draw from the beta distribution with parameters p and q (Johnson et al. 1995), and the amount of rain was a random draw from the log-normal distribution with parameters μ and σ^2 for the mean and variance, respectively, of the natural log of the amount of rain. After the beginning of a pulse, soil water content declines due to uptake and evaporation according the equation

$$\frac{dR}{dt} = -\sum_{i=1}^{n} f_i(R)B_i - \varepsilon R \tag{3}$$

with no carry-over of soil water permitted from one year to the next.

In simulations in which germination depends on the time of year when the pulse occurs, germination occurs at the beginning of the pulse with a fraction of the seed bank germinating given by the Gaussian curve

$$G_i e^{-h(t_p - \tau_i)^2}, \tag{4}$$

where G_i defines the maximum possible germination, t_p is the time of the pulse, τ_i is the time giving maximum germination of species i, and h controls the rate at which germination declines as the pulse time deviates from the optimum for the species. These curves are depicted in Fig. 1A. For germination timing relative to the beginning of the pulse, germination at the rate G_i was assumed to occur at time τ_i after the arrival of the pulse.

In all simulations depicted here, a species-specific difference in resource use was chosen according to the mechanism to be illustrated (timing independent of the pulse, timing relative to the beginning of the pulse, differently shaped uptake curves). Water use efficiency was adjusted, if necessary, to reduce average fitness differences between species until stable coexistence was found. The particular parameters chosen for these simulations were simply the first we happened upon that gave clear illustrations. Broad parameter ranges in fact give stable coexistence according the general principles discussed in Chesson (2000a). For each specific difference in timing of resource use, and for values of the parameters allowing the qualitative mechanistic features described in this article, there is always a range of average fitness differences between species supporting stable coexistence provided each species is capable of persisting in the modeled environment in monoculture.

For the simulations depicted here, the specific parameters used were $G_1=G_2=0.5$, $s_1=s_2=0.8$, $\phi_1=\phi_2=0.05$, $a_1=a_2=20$, $d_1=d_2=1$, $\theta_1=\theta_2=1$, $c_1=c_2=12$, $m_1=m_2=0.05$, $\varepsilon=1$, $\tau_1=0.35$, $\tau_2=0.4$, $h=100$, $\mu=\ln(2)$, $\sigma=0.2$, $p=q=2$ (Fig. 2). For Fig. 3, some of these parameters changed as follows:

$G_1=G_2=0.25$, $\phi_1=\phi_2=0.12$, $a_1=a_2=20$, $d_1=d_2=0.5$, $c_1=7$, $c_2=10.7$, $\tau_1=0$, $\tau_2=0.05$. The relative nonlinearity figure, Fig. 5, differed from Fig. 2 in having $a_1=40$, $a_2=5$, $d_1=1$, $d_2=0.05$, $\theta_1=1$, $\theta_2=4$, $c_1=c_2=0.5$, $\tau_1=\tau_2=0.35$, $\mu=\ln(1.5)$, $\sigma=1$, $p=4$, $q=8$.

All simulations were performed using Gauss 6.0 (Aptech Systems), with the simulation module Simgauss.

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