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Chapter 18
Water use in arid land ecosystems

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Historical development of physiological ecology within arid lands

The study of physiological ecology within arid land ecosystems has fascinated ecologists and physiologists throughout this century. Haberlandt (1914), Schimper (1898) and Warming (1909) laid the groundwork with descriptions of the morphological attributes that were thought to be of adaptive value. Early field investigations, such as those by Shreve (1923) and Walter (1931) on the metabolism of arid land plants under the natural ranges of drought and temperature, were critical to evaluating initial hypotheses of how plants were adapted to arid lands. More sophisticated instrumentation ultimately followed (Eckardt 1965), that allowed better quantification of metabolic patterns and led to new concepts, such as physiological acclimation (Mooney & West 1964), that were not obvious from previous laboratory studies. In the 1970s, field measurements moved to a new level of sophistication with the introduction of the mobile laboratory (e.g. Mooney *et al.* 1971). Of particular significance was the ability to now measure photosynthesis, transpiration and energy balance with the same precision as was previously possible only under laboratory conditions, so that investigators could better quantify the relationships between environmental shifts and metabolic adjustment (Mooney 1972; Lange *et al.* 1974). Much of the focus of these earlier studies in physiological ecology revolved around measurements of photosynthesis and gas exchange and largely ignored nutrient and water relationships.

From these field observations two decades ago, it became clear that the photosynthetic capacities of plants in low-productivity environments need not be low. In fact, under high soil moisture conditions arid land plants achieved some of the highest photosynthetic rates that had been measured for land plants (Fig. 18.1). At the same time, discussions of the functional significance of C_3 *vs.* C_4 photosynthesis had gained attention and it was becoming clear that C_4 metabolism allowed plants to achieve high rates of carbon gain with less water loss (Osmond *et al.* 1980). What was not clear was why C_4 photosynthesis is not more frequent among the taxa of arid lands if it is so advantageous (Ehleringer *et al.* 1997). Field studies in North American and South American arid lands had shown that C_4 photosynthesis

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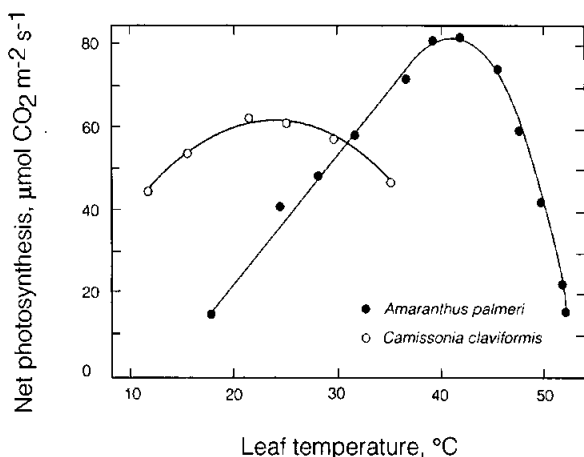[2] *Present address: Department of Biology, Keene State College, Keene, NH 03469, USA.*

Figure 18.1 Rates of photosynthetic CO_2 uptake as a function of temperature for *Camissonia claviformis* (C_3) and *Amaranthus palmeri* (C_4), two common annuals found in the arid lands of southwestern North America. Based on data from Mooney *et al.* (1976) and Ehleringer (1983).

was common only among the summer annuals and halophytic shrubs (Mulroy & Rundel 1977; Stowe & Teeri 1978; Winter 1981; Ziegler *et al.* 1981). Equivalent field studies in African and central Asian ecosystems lagged behind, although Winter (1981) had observed a number of C_4 taxa in western Asia, and this should have been further explored. It is only now that we are beginning to realize that C_4 photosynthesis may be much more common within Old World than New World deserts (P'yankov 1997; Sage & Monson 1999), suggesting that New World deserts may be too young to have reached their potential C_4 composition.

Walter (1931) established that there were wide-ranging water potentials in desert plants. Limited ecophysiological advances in arid land plant–water relations followed until the introduction of the pressure bomb (Scholander *et al.* 1965). Within the last two decades, three key observations set into motion a new way of thinking about water relations and the adaptive strategies of desert plants. These observations are hydraulic lift, cavitation and water-source partitioning.

Caldwell and Richards (1989) were among the first to report that water could 'leak' out of roots back into the soil following water potential gradients. Through hydraulic lift, plants are able to move water, from a region of higher water potential at some depth in the soil up into a shallower and drier soil layer. While this phenomenon could have been anticipated theoretically, it was not. The significance of hydraulic lift is still being debated, but it appears to play a role in enhancing gas-exchange capacity under drought and possibly enhancing nutrient cycling (Caldwell *et al.* 1998). Recently, Burgess *et al.* (1998) and Schulze *et al.* (1998) described a novel variation on this theme: inverse hydraulic lift, whereby plants move water from wetter upper soil layers to deeper dry layers. The adaptive signifi-

cance of this phenomenon remains largely unexplored, but may be associated with the ability of roots to grow through dry soil towards groundwater. If so, it could provide an explanation for the unusually deep root penetration of some desert species through soil regions too deep to be wetted by precipitation (Canadell *et al.* 1996).

The study of plant–water relations under extremes received a boost with the development of methods to measure xylem cavitation on a routine basis (Tyree & Sperry 1989). Decreased water potentials lead to increased xylem cavitation and decreased hydraulic conductivity. How stomata regulate water flow so as to avoid run-away cavitation is an area of very active research. While few data are available for arid land species, it appears that variation in the capacity of xylem to avoid cavitation during drought and winter freeze events may be correlated with the geographical distributions of desert shrubs (Pockman & Sperry 1997).

Lastly, the use of stable isotope analyses of xylem water at natural abundance levels has provided a quantitative means of identifying the specific soil layers from which plants are extracting soil moisture (Fig. 18.2). The approach allows for non-destructive exploration of specific root activity, particularly in response to
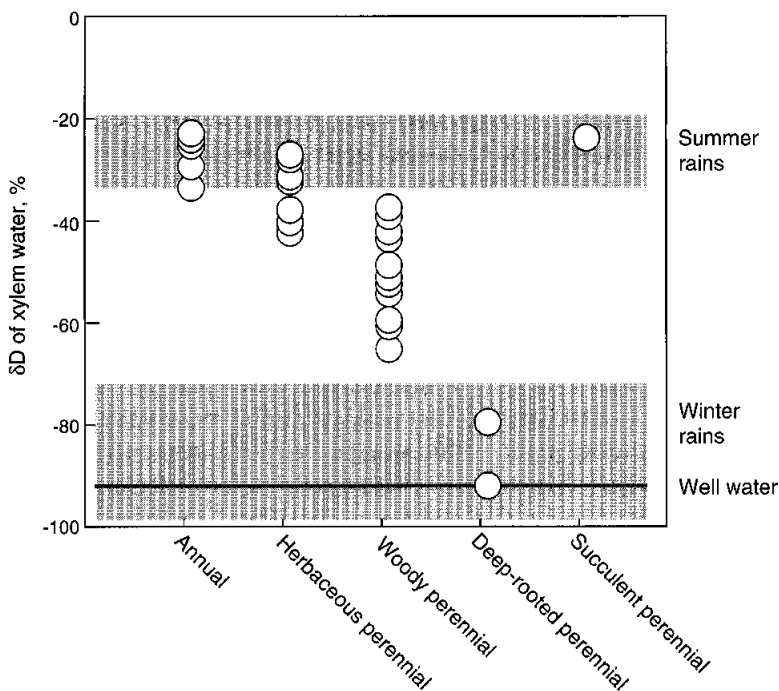
Figure 18.2 Hydrogen isotope ratios (δD) of xylem water from different species, representing contrasting life forms, following summer rains in the arid lands of the Colorado Plateau. The data show that different life forms are utilizing different water sources, even following a strong summer precipitation event. Adapted from Ehleringer *et al.* (1991).

dynamic changes in soil moisture availability (Ehleringer & Dawson 1992; Dawson & Ehleringer 1998).

Emerging linkages between ecophysiology and ecosystem-level processes

While much remains to be learned in the area of basic adaptation in arid land plants, opportunities have arisen over the past decade to extend the principles of physiological ecology from its traditional whole-plant focus to other levels of organization. Among these new research opportunities are studies addressing the molecular basis of ecophysiological functions (Chapter 1). Within arid land ecosystems, exciting progress is being made in such diverse areas as understanding the nature and significance of aquaporins for regulating water movement and in the molecular mechanisms governing photosynthetic pathway switching in response to drought. At the same time, principles of physiological ecology are being extended to higher levels of organization, such as the control of ecosystem fluxes (Chapter 19) and species composition within communities. Which ecophysiological processes are scalable and relevant at higher levels of organization remains an important and interesting challenge to the field (Ehleringer & Field 1993).

The need to address how ecological systems will respond to global change and to understand constraints on ecological systems for land management is widely recognized. However, these increased research opportunities come at a cost to the discipline of physiological ecology: fragmentation resulting from movements into new research opportunities poses a challenge for maintaining communication and integration within the whole-organism science community.

Historically, metabolism and adaptation have been approached through analysis of plant responses to constant resource levels (either high or low). Yet, realistically, arid lands are pulse driven and the focus should be directed at a consideration of how plants exploit pulse-driven resource dynamics. Variability in resource availability occurs on at least three relevant scales: pulses of moisture input within a single season, biseasonal inputs within a single year and interannual variability in precipitation. Analysis of annual precipitation patterns forms the basis for understanding how plant performance and fitness are affected by large-scale climatic phenomena (such as El Niño), which can affect regional climate patterns on a decadal basis.

Arid land ecosystems are among the most sensitive ecosystems to change, whether this change is associated with anthropogenic land-use activities or shifting climate conditions (Schlesinger et al. 1990; IPCC 1996). Globally, arid land ecosystem structure and function have shifted towards increased desertification and biological invasions, largely because of overgrazing (Schlesinger et al. 1990; Kassas 1995). The extent and nature of invasions can alter ecosystem relationships in what appear to be irreversible directions, shifting shrublands to annual grasslands in some regions (e.g. saltbush-bunchgrass to cheatgrass conversions in the northern

Great Basin of North America), while in other locations allowing tree and herbaceous species to establish and dominate (e.g. mesquite, Russian thistle and creosote invasions into the southwestern arid lands of North America). Unfortunately, the factors influencing ecosystem functioning, sensitivity to climate change and resiliency to invasions are not well understood. We believe that advances in the understanding of the dynamics of plant distribution in desert ecosystems will depend critically upon an appreciation of the basis for variability among plants and the susceptibility of these and other ecosystem components to change by outside factors such as invasion and anthropogenic factors altering resource availability on local and regional scales.

The role of precipitation patterns in arid land ecosystems

Ecosystem primary productivity in arid land ecosystems is a highly correlated linear function of cumulative precipitation pulses, with nitrogen availability modifying the slope of the response (Le Houérou 1984; Noy-Meir, 1985; Gutierrez & Whitford 1987; Gutierrez *et al.* 1988; Sala *et al.* 1988; Ludwig *et al.* 1989; Ehleringer & Phillips 1999). The slope of the relationship between primary productivity and precipitation ('rain-use efficiency', *sensu* Le Houérou 1984) is steeper for winter-spring precipitation than for summer precipitation, most likely because of temperature-dependent differences on evaporation. Heavily grazed and degraded lands tend to have a lower rain-use efficiency than undisturbed ecosystems (Le Houérou 1984; Varnamkhasti *et al.* 1995).

Apart from the well-established effect of cumulative precipitation on productivity, there is a less well established, but potentially strong, effect of cumulative precipitation on the composition of desert plant communities. The dominance of many desert vegetation components are known to fluctuate in response to departures from mean climatic conditions (e.g. Goldberg & Turner 1986). Arid land ecosystems also respond strongly to the patterns in which resources are supplied, most importantly, the variability and timing of rainfall events (Noy-Meir 1973; Ehleringer 1999). In addition, different vegetation components may be differentially sensitive to rainfall patterns, as suggested by Ehleringer *et al.* (1991) and Ehleringer (1999). Lin *et al.* (1996) and Williams and Ehleringer (1999) tested this hypothesis in field experiments in an arid land system, simulating unusually large summer rain events (25–50 mm). They found that not all dominant perennials took up significant amounts of water from the upper 20–50 cm, although live roots were present in those soil layers.

Extreme-year types, in terms of water relations, can have significant and lasting effects on community composition. An example is the establishment and dominance of the perennial shrubs *Encelia farinosa* and *Prosopis velutina*, which replaced *Larrea divaricata* following unusually strong El Niños in 1941–43 (Turner 1990). More recently, Brown *et al.* (1997) attributed the expansion of woody perennials in southeastern Arizona to recent, unusually wet winters. There is evidence that in the last 25 years, possibly as a consequence of global change, extreme-year

types, such as El Niño, have not only become more common but also more variable in strength (Wang & Ropelewski 1995; Wang 1995). Because of the particular importance of water in the functioning of arid land ecosystems, changes in precipitation patterns are likely to play a much more prominent role in changing arid land ecosystems in the near future than other factors of global change, such as increased atmospheric CO_2 or dry deposition.

Precipitation and climate change

As our understanding of mesoscale climate processes and teleconnections increases, it is becoming increasingly clear that sea surface temperatures (SST) in the Pacific Ocean have a profound influence on both the seasonal intensity and interannual variability of precipitation in ecosystems across western North America (Carleton et al. 1990; Cayan & Webb 1992; Cayan 1996; Higgins & Schubert 1996; Zhang & Levitus 1997). Winter storms in western North America are derived from frontal systems out of the Gulf of Alaska in most years, but during El Niño years moisture originates farther south in association with higher SST. Summer monsoon precipitation events in the southwest develop as a result of land–ocean thermal differences, with moisture from the eastern Pacific and the Gulf of California. Stronger monsoons are directly related to elevated SST, which may be further amplified by strong El Niño–Southern Oscillation events (Carleton et al. 1990; Hereford & Webb 1992; Higgins et al. 1998). Studies of regional precipitation patterns in the southwest indicate trade-offs between the intensity of summer precipitation and winter snowpack from the previous season, suggesting a mechanism to decrease the strength of the monsoonal system (Cayan 1996; Higgins et al. 1998). Wetter than average winters are followed by drier than average summers and *vice versa*. One of the most often predicted early climate change events is an increase in the variance of weather and Parker et al. (1994) have reported an increased variability in eastern Pacific SST. Modelling studies predict that changes in SST are a crucial variable in climate change scenarios (Rind 1987, 1988; IPCC 1996). Small changes in the climate variability associated with elevated atmospheric CO_2 can produce relatively large changes in the frequency of extreme precipitation events (IPCC 1996). Furthermore, the thermal disequilibrium developing between the terrestrial and oceanic surfaces is increasing, leading to predictions of increased spatial and temporal variability in drought events (Rind et al. 1990). Thus, climatic changes in intra-seasonal, inter-seasonal and inter-annual precipitation patterns are predicted to occur on time scales that will influence the functioning of arid land ecosystems.

Pulse patterns, pulse utilization and water-source partitioning

This section explores how both short-term precipitation pulses and longer-term interseasonal and interannual precipitation variability might affect the performance of individual species and thus influence ecosystem structure and function.

The ecosystem that will be focused on is the Colorado Plateau in the inter-mountain region of North America (West 1983). The northern Colorado Plateau represents the dry end of a summer precipitation gradient (Fig. 18.3). While long-term statistics indicate a more or less constant precipitation input through the year, there is an extremely high degree of year-to-year variability (Ehleringer 1994). Geographically, this arises because the Colorado Plateau is located near two climatic boundaries: the southern boundary of winter, frontal-system moisture input and the northern boundary of summer monsoon moisture. The high interseasonal and interannual variability in precipitation at this site may be related to modifications of regional weather patterns that result in shifting climatic boundaries, which can enhance precipitation in some years and exclude precipitation in others. The effects of global change are most likely to be seen first here and in other ecosystems located near climatic storm-track boundaries.

Within arid lands, cumulative precipitation during a given season is usually a linear function of the number of storm events and the size–frequency distribution of individual storm events remains constant (Ehleringer 1994). Most storms are small (0–5 mm) and fewer than 8% of the storms are greater than 25 mm. El Niño and La Niña years, however, may deviate from these mean statistical trends. Cayan and Webb (1992) calculated that there were more winter precipitation days during El Niño than La Niña years (24% *vs.* 16%), and that the number of large storms and of flood events were significantly greater in El Niño than La Niña or other years (Cayan & Webb 1992; Hereford & Webb 1992; Higgins *et al.* 1998).
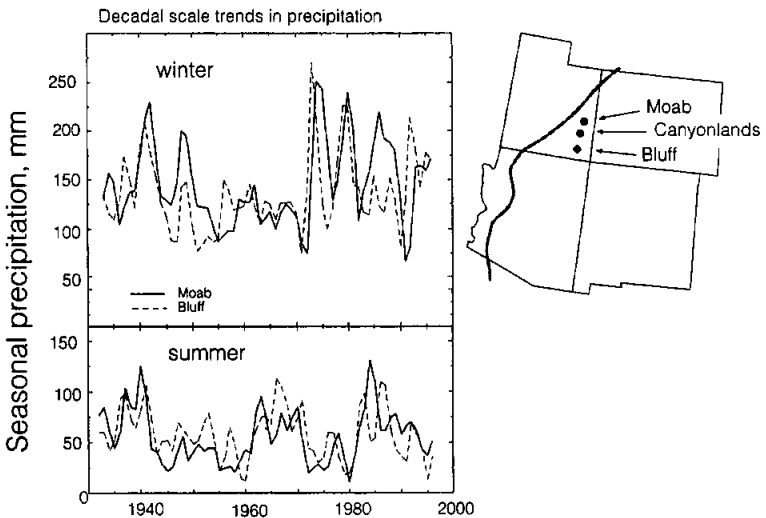

Figure 18.3 Right: a map of the Four Corners region of western North America, showing Moab, Utah, and the northern boundary of the Arizona summer monsoon. Left: a time series of the total winter precipitation and summer precipitation for Moab and Bluff, Utah, two towns located near the boundary of the Arizona monsoon system.

Winter precipitation is not utilized immediately by most plants of the Colorado Plateau, because cold winter temperatures prevent much plant activity. Instead, winter precipitation infiltrates into deeper soil layers and accumulates there during the course of the winter (Caldwell 1985; Comstock & Ehleringer 1992). By contrast, summer rain generates a brief pulse of elevated soil moisture only in shallow soil layers that persists for hours to several weeks, depending on thermal conditions and the magnitude of the pulse event (Fig. 18.4). Small pulses (<5 mm) are thought to trigger surface processes, such as surface litter mineralization and cryptobiotic crust activity, but may persist for less than a day. Larger pulses (>10–15 mm) are required in order to trigger changes in gas-exchange metabolism of plants, and still larger events (>20 mm) are required to germinate annuals (Noy-Meir 1973, 1985; Beatley 1974).

Stable isotope analyses are a key to unravelling the response patterns to pulses (Chapter 21). Plants do not fractionate against ^2H (D) or ^{18}O during water uptake, and therefore the isotopic composition of water in roots and suberized stem tissues is an integrated measure of the water-uptake patterns of the roots (Dawson & Ehleringer 1991, 1993; Ehleringer et $al.$ 1993). Moisture pulses derived from winter and summer precipitation events have a different isotopic composition. Therefore analysis of stable isotope ratios of xylem sap provides a quantitative measure of the water sources currently used by plants. This approach was used to study a wide range of species with contrasting life histories in a Colorado Plateau desert scrub ecosystem. The study showed that pulse utilization patterns may be correlated with
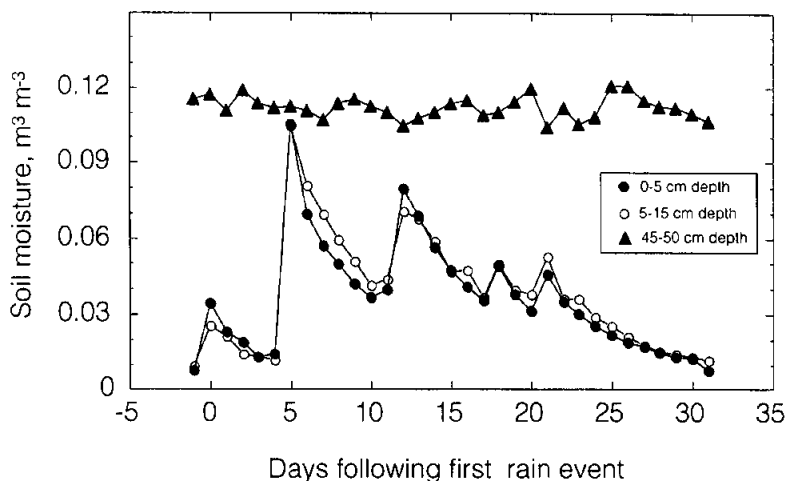

Figure 18.4 Soil water content near the surface and at an intermediate depth during the summer for Canyonlands National Park, Utah. Note the rapid dynamics and changes in soil moisture in the upper soil layers (J.R. Ehleringer, R. Gebauer & S. Schwinning, unpublished data).

broad life history characteristics (Ehleringer *et al.* 1991 and Ehleringer 1999). For example, several woody perennial shrub species were using little of the moisture which saturated the upper soil layers after a 50-mm storm event. Other woody perennials derived 20–45% of their transpiration water from the upper soil layers, whereas the succulent CAM (crassulacean acid metabolism), annual and herbaceous perennial components fully utilized moisture derived from summer rains. Similar studies have confirmed that herbaceous perennials utilized summer moisture inputs more extensively than did woody perennials, for example in Patagonia shrublands (Sala *et al.* 1989), the Arizona savannah (Weltzin & McPherson 1997), New Mexico rangelands (McDaniel *et al.* 1982) and sagebrush steppe (Donovan & Ehleringer 1994).

Desert species are astonishingly variable in their ability to utilize pulses of water and plant-available nitrogen. Gebauer and Ehleringer (1999) have shown that there is considerable diversity, not just in the amount of water and nitrogen taken up by plants during a pulse event, but also in the season in which plants are best able to utilize pulses (Fig. 18.5). They examined the *in situ* ability of six dominant woody perennials to utilize pulses presented at different times (May, July and September) by simulating a heavy 25-mm pulse event. Stable isotope tracers (^2H and ^{15}N) were used to follow nitrogen and water uptake. In late May all species derived less than 10% of stem water from the simulated rain event, even though the upper 25 cm was saturated by this pulse (data not shown). At other times, a larger fraction of plant water was absorbed by surface roots (up to 65%), and large differences in the amount and timing of summer rain utilization became apparent among perennials (Gebauer & Ehleringer 1999). Interestingly, although the occurrence of water and plant-available nitrogen are highly correlated in time, their uptake is not. For example, in July only *Artemisia* took up appreciable amounts of water and
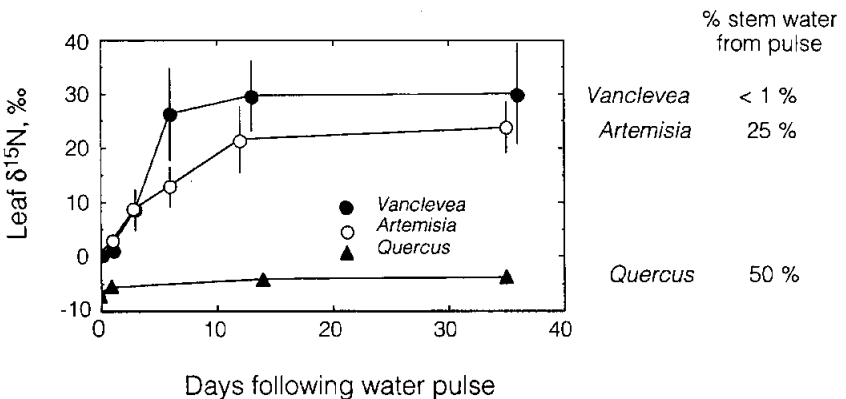

Figure 18.5 Variations in the ability of desert shrubs to take up either water or nitrogen during July following a pulse label application to the upper soil layers (Gebauer & Ehleringer 1999).

nitrogen. Water, but not nitrogen, uptake occurred in *Quercus*, while *Vanclevea* took up nitrogen but not water. Earlier studies have established that independent uptake patterns for water and nutrients occur naturally (Schulze & Bloom 1984).

The diversity of pulse utilization suggests that niche differentiation may be an important component of ecosystem function and that competition, past or present, is a key factor in the structuring of desert communities. First, the differential use of pulse events may translate into differential sensitivity to interannual and interdecadal variations in moisture input. Ehleringer *et al.* (1991) and Ehleringer (1999) suggest that shifts in precipitation input patterns may move communities away from current species composition. For example, a northerly shift of the monsoon boundary, resulting in increased summer precipitation, should favour primarily those species that utilize summer rain the most and should increase their dominance in the community. Second, and perhaps more importantly, versatility in the exploitation of soil moisture, as exhibited by those species that were equally able to extract soil from the shallow and from the deep soil, may alter the competitive relationships among members of a community. For example, species capable of utilizing both pulse and deeper soil moisture may compete more strongly for water with deep-rooted species during dry summers, when pulses are scarce. Conversely, the same species may compete more strongly with shallow-rooted species in wet summers or following dry winters. Such a reorganization of competitive structure in a community may have complex and much less obvious effects on community composition.

Theoretical considerations concerning adaptation to pulse-driven resource supply

Functional aspects of water relationships within the soil–plant–atmosphere continuum have been well described by models, such as that of Sperry *et al.* (1999). To gain a better understanding of the trade-offs associated with the observed diverse patterns of pulse utilization by desert plants, we developed a generalized water transport model for plants. This model describes shoot and root function as a function of soil depth in sufficient detail to simulate variation in both absolute and relative pulse utilization by plants. It is assumed that plants have a limited capacity for long-term water storage, and thus do not utilize the adaptive solution of cacti and other succulents (Nobel 1997). Three variable resistances are considered in the transport pathway for water between the soil and the atmosphere: roots in upper soil layers, roots in deeper soil layers and leaves. Leaf resistance to water vapour loss in conjunction with the atmospheric water vapour deficit and leaf area determine the total water loss rate, while the root resistances in conjunction with soil water potential and soil hydraulic characteristics determine how transpiration flux is divided between shallow and deeper soil water sources. The most critical aspect of this model is the identification of the physiological or morphological plant characteristics that determine the three resistance values.

A few general principles have emerged:

1 The ability to utilize pulses is associated with a number of fundamental trade-offs in plant physiology and architecture.

2 Some character combinations work better than others, suggesting that pulse utilization is not determined by isolated characters such as, say, rooting depth, but by entire suites of characters integrating root and shoot function.

3 Plant types with contrasting degrees of pulse utilization have differential sensitivities to year type.

4 Although less explored at this point, diversity in pulse utilization may lead to complex competitive relationships within communities.

Some of the interdependencies between the character trade-offs important to pulse utilization are summarized in Fig. 18.6. To maximize pulse utilization, a plant must, quite obviously, commit a large fraction of its root system to shallow soil. Less obviously, such a plant must also maintain functional roots, despite potentially low soil water potential, and to be able to take up water as soon as it becomes available. Furthermore, a pulse user must be able to support high rates of gas exchange during a pulse, partly through decreased root:shoot ratios and partly through high maximal stomatal conductance. Lastly, pulse users must also be able to avoid desiccation at the end of a pulse event and thus should exhibit a high degree of stomatal sensitivity to declining water status. Modelling results predict that the converse holds for plants that specialize in exploiting water in deeper soil

functional type	strategy	root/shoot ratio	leaf conductance	increase in carbon gain from pulse
	water uptake from deeper soil	high	low	low
	ability to switch water source	high	moderate	moderate
	water uptake from pulse	low	high	high

Figure 18.6 General patterns emerging from a model of plant–water relations and dynamics in response to moisture pulses (S. Schwinning & J.R. Ehleringer, unpublished).

layers. Interestingly, versatile water users, with significant root biomass both in shallow and deeper soil layers (dimorphic roots), have some characteristics in common with deeper-rooted plants, for example higher root:shoot ratios, but are predicted to be more like shallow-rooted plants in other characteristics such as stomatal sensitivity.

The costs and benefits of specific allocation strategies vary with the intensity and the duration of a pulse, with pulse frequency, and with temperature, all of which should vary within and between seasons, and between years. As no plant form can perform equally well under all possible conditions, the evolution of distinct functional types specializing in the utilization of specific components of resource variability in time and space is favoured.

Looking at water as a resource, year types are largely characterized by the timing of rainfall events, the time between events and the amount of rain deposited. For example, a dry summer may be characterized by few rain events and thus long intervals between events and/or small event size. A first step in exploring the effect of year types on functional types is, therefore, to look at the effect of a single pulse and interpulse period on functional types. An example of this is shown in Fig. 18.7, where we evaluate the effect of a single pulse, solely on the basis of the average carbon gain achieved during the pulse and interpulse period, in this case a period of 20 days at typical summer temperatures (40°C daily maximum). We identified a 'dry summer' with a small pulse size (6 mm) and a 'wet summer' with a larger pulse size (12 mm). A 'wet winter' (i.e. with a high degree of recharge in deeper soil layers) is identified by a high soil water potential below 20 cm soil depth (−0.5 MPa) and a 'dry winter' by a lower soil water potential (−1.5 MPa). The calculation of carbon gain is based either on Farquhar et al. (1980) equations for C_3 plants
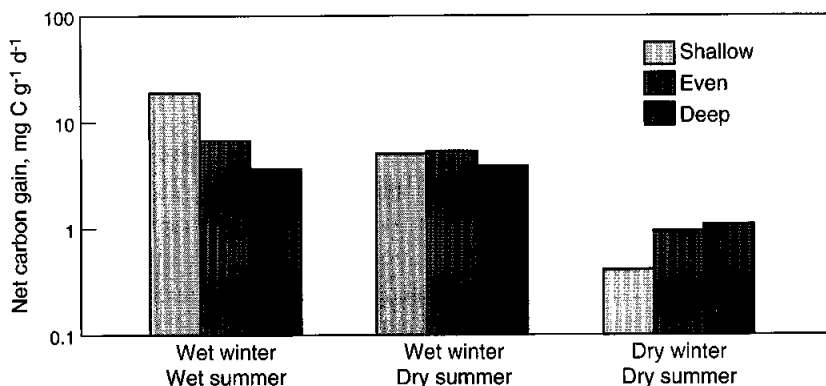

Figure 18.7 Simulation predictions for differences in carbon gain by the three fundamental life forms in deserts based on root distribution. Carbon gain is averaged over the pulse interval of 20 days and expressed per unit total carbon above and below ground (S. Schwinning & J.R. Ehleringer, unpublished).

(applied to even- and deep-rooted plants) or Collatz *et al.* (1992) simplified equations for C_4 plants (applied to shallow-rooted plants).

In these and other simulations we generally found that the wetter the summer, the greater the carbon gain of shallow-rooted plants, as may be expected. These plants, with their low root:shoot ratios, low stem fraction and often C_4 photosynthesis, can achieve the highest carbon gains under favourable conditions. However, when summers are dry, they suffer the greatest carbon losses, and may even senesce between pulses. In this case, even-rooted plants with a greater ability to exploit deeper and wetter soil layers have the advantage. Winter and summer drought can favour the deepest-rooted plants (Fig. 18.7). Although deep-rooted plants rely the most on water stored in deeper layers, they are also better able to tolerate low water potentials, because of their high root allocation to that layer. Note that differences in carbon gain, here expressed on the basis of total plant carbon, indicate only one aspect of the advantages and disadvantages of functional types. For example, there may be large differences between functional types in the costs of growth and maintenance: deep-rooted plants allocate a large amount to wood, which is cheap to maintain, whereas shallow-rooted plants may pay a high price to maintain their total biomass. These differences may greatly enhance the year-type trade-offs indicated in Fig. 18.7.

Competition for pulsed resources

It is generally accepted that arid land plants compete for water, although the contributions of pulse and inter-pulse periods to the competitive relationships among plants remain poorly understood (Casper & Jackson 1997; Goldberg & Novoplansky 1997). However, having gained some conceptual clarification of the processes involved, more specific questions about competition in pulse-driven systems can now be asked. Foremost in the context of this chapter: to what extent do plants compete for summer moisture pulses *vs.* water deposited in the winter and stored in deeper soil layers? Cohen argued as early as 1970 that competition for water should primarily occur in deeper soil layers, because shallower soil layers are depleted not by plant uptake but predominantly by evaporation. This should exclude competition for all but the largest summer pulses. However, Cohen (1970) did not consider that summer pulses may alleviate the competition for deep soil moisture when species with dimorphic root systems constitute a significant portion of the plant community. Thus, summer pulses may influence the strength of competition for water indirectly. This mechanism forms the basis for considering the shifting competitive relationships that were mentioned earlier.

Experimentally, our initial efforts were to examine the role of competition for water in the simplest possible, yet most realistic and important, vegetation type. This was *Coleogyne ramosissima*, which usually forms large nearly monospecific stands on southern portions of the Colorado Plateau, extending west to California (Ehleringer & Phillips 1999). The experiment involved adding 50 mm of winter or summer precipitation each year to target plants that did or did not have their

neighbours removed. Distinct ecophysiological differences were observed in response to these treatments, but here only the growth response is shown (Fig. 18.8). Increasing winter moisture and/or removing neighbours significantly increased plant water status, gas exchange and growth, but the impact of a summer pulse was minimal. This was surprising because *C. ramosissima* is unusual among woody perennials in that it derives about half of its transpiration flux from surface layers following a large summer rain event. However, summer pulse utilization did not translate into an immediate growth response. Apparently, only a small fraction of the additional carbon gain derived from the added summer pulse carried over to next year's growth.

The study does suggest that the strength of competition, as reported in the growth disparity between competing and isolated plants, may be strongly affected by single precipitation events. In the case of *C. ramosissima*, the additional water pulse had the greatest effect on the strength of competition when it was administered in winter, suggesting once again that only 'storable' water input can be competed for. However, while plants may not compete for pulse water, they may compete for plant-available nitrogen compounds that are released in shallow soil by a moisture-induced stimulation of microbial metabolism. Unlike water, nitrogen is storable in the shallow soil, so that whatever nitrogen remains unused becomes available to others.

Towards the integration of ecophysiology with community ecology and ecosystem ecology

It could be said that plant physiological ecologists think of communities as species assemblages selected primarily by climatic constraints and modified by ecological interactions, whereas population ecologists think of communities as organized primarily by ecological interactions and modified by environment. These opposing views are not trivial, because they may lead to very different expectations concerning the sensitivity of ecosystems to change. The study of desert ecosystems provides an opportunity for a more objective appraisal of the relative importance of climate *vs.* population interactions. Moreover, it integrates such diverse research areas as physiological ecology, productivity and fluxes at the ecosystem level, impacts of global circulation patterns on regional climate, and an area of theoretical ecology that is concerned with mechanisms of community stability. Theoreticians have long suggested that environmental variability, in conjunction with niche differentiation and certain forms of competition–environment interactions (Chesson & Huntly 1997), should be crucial for maintaining species diversity and for deciding the ultimate fate of newcomers to a community (Turelli 1981). For unknown reasons, physiological ecologists have largely ignored this hypothesis, which would have obliged them to focus more on the dynamic aspects of resource supply and utilization.

Today, several advances have made it possible to contribute to the conceptual unification of ecology in a substantial way. We have at our disposal long-term
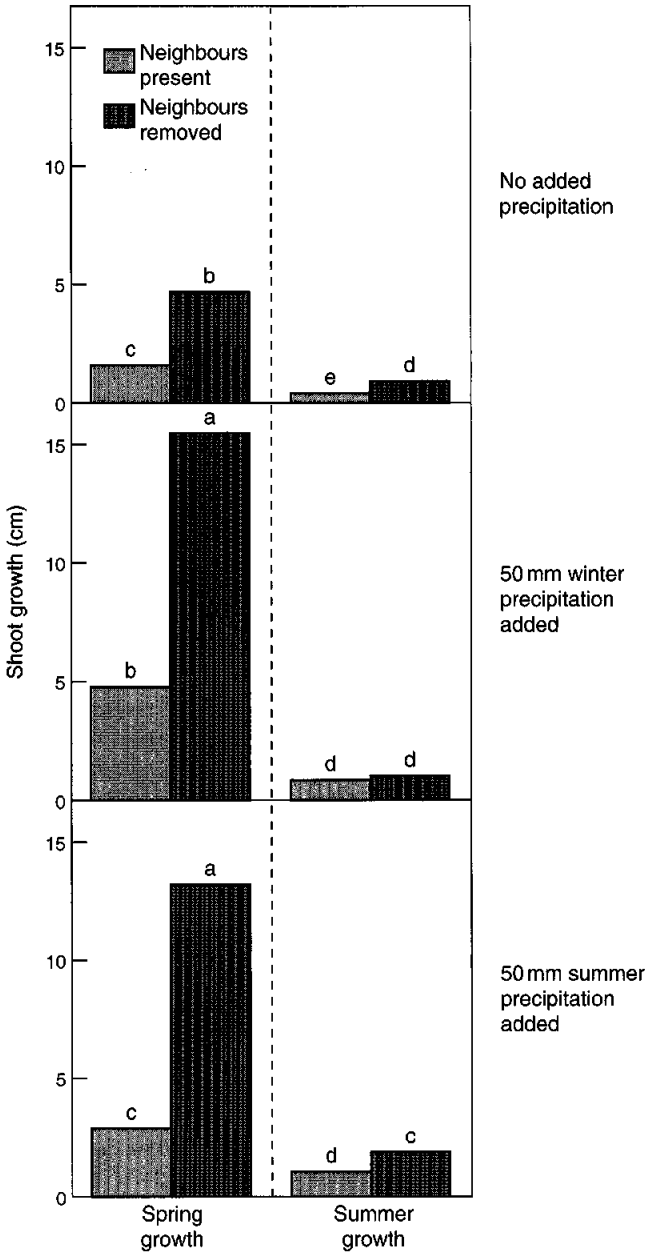
Figure 18.8 Total shoot growth on target *Coleogyne ramosissima* shrubs under various supplemental precipitation and neighbour removal treatments. Shoot growth is partitioned into spring (March to June) and summer (July to October) periods. Bars not sharing a common letter differ significantly. From Ehleringer and Phillips (1999).

records of climate factors and are increasingly able to reconstruct past, and hypothesize on future, climate. With respect to arid ecosystems, the discipline has made major advances in understanding the impact of dynamic climate patterns on various community members. Lastly, with advances in experimental technology, particularly the use of stable isotopes, estimation of the partitioning of limiting resources among competing plants *in situ* is now possible. Thus, we are in a much better position to quantify the three cornerstones of community dynamics — environmental variability, species functional diversity and competition — and we can begin to test ideas about the origin and the persistence of arid ecosystems and speculate on their future.

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