

# Water use trade-offs and optimal adaptations to pulse-driven arid ecosystems

SUSANNE SCHWINNING and JAMES R. EHLERINGER

*Department of Biology, University of Utah, 257S 1400E, Salt Lake City, Utah 84112–0840, USA*

## Summary

**1** We introduce a hydraulic soil-plant model with water uptake from two soil layers; one a pulse-dominated shallow soil layer, the other a deeper soil layer with continuous, but generally less than saturated soil moisture. Water uptake is linked to photosynthetic carbon assimilation through a photosynthesis model for C<sub>3</sub> plants.

**2** A genetic algorithm is used to identify character suites that maximize photosynthetic carbon gain for plants that experience a particular soil moisture pattern. The character suites include allocation fraction to stem, leaves and shallow root, stem capacitance and stem water storage capacity, maximal leaf conductance and sensitivity of leaf conductance to plant water potential, and a critical soil water potential at which shallow roots cease to transfer water.

**3** We find that if pulse water is a more important water source than deeper soil water in the environment, optimal phenotypes lean towards adaptations that maximize pulse water use (small root : shoot ratio, predominantly shallow root system, high leaf conductance with high stomatal sensitivity to plant water status). If deeper soil water is more important, phenotypes lean towards adaptations that maximize deeper soil water use (large root : shoot ratio, predominantly deep root system, lower leaf conductance with low stomatal sensitivity). Stem succulence is adaptive only when deeper soil water is unavailable.

**4** From among the continuum of derived phenotypes, four phenotypes are selected that resemble the character suites of winter annuals, drought-deciduous perennials, evergreen perennials and stem succulents. Under common conditions, these phenotypes reproduce many of the responses to drought and water pulse observed in their respective life-form counterparts. The comparison also highlights the differences in plant life-form sensitivity to summer and winter drought conditions.

**5** Based on these results, we discuss the possible role of annual precipitation patterns in shaping plant adaptations and determining the plant composition of arid and semi-arid environments.

*Key-words:* desert, genetic algorithm, plant functional types, whole-plant carbon gain

*Journal of Ecology* (2001) **89**, 464–480

## Introduction

It has long been suggested that distinct plant life-forms of arid and semi-arid environments utilize different components of an ecosystem's soil moisture input (Cohen 1970; Noy-Meir 1973; Cody 1986; Smith & Nobel 1986; Shmida & Burgess 1988). Support for this hypothesis has been sought primarily by comparing the

root habits and water relations of species co-occurring in the same environment (e.g. Canon 1911; Walter & Stadelmann 1974; Smith *et al.* 1997). In this paper, we take the opposite approach. Instead of asking which components of soil moisture desert plants are using the most, we ask what plants would have to be like to maximize the use of specific soil moisture patterns.

Soil moisture in arid ecosystems is extremely variable both in space and time. Moisture fluctuations are most rapid and extreme in shallow soil, and comparatively slow and more moderate at greater depths (Cable 1969; Noy-Meir 1973). In shallow soil, every rain event generates a pulse of moisture that, depending on the

Correspondence: S. Schwinning, Department of Biology, University of Utah, Salt Lake City, Utah 84112–0840, USA (tel. + 1 801-581-5927; fax: + 1 801-581-4665; e-mail: schwinning@biology.utah.edu).

Table 1 Variables and units

Symbol	Description	Unit
$A_{leaf}$	Leaf-area specific rate of photosynthesis	$\mu\text{mol C m}^{-2} \text{s}^{-1}$
$A_{plant}$	Photosynthetic carbon gain per plant per day (fitness proxy)	$\text{mmol C mol}^{-1} \text{C d}^{-1}$
$E$	Whole-plant rate of transpiration	$\text{mol H}_2\text{O s}^{-1}$
$E_i$	Whole-plant rate of water uptake from soil layer $i$	$\text{mol H}_2\text{O s}^{-1}$
$G_{leaf}$	Whole-plant leaf conductance	$\text{mol H}_2\text{O s}^{-1}$
$K_i$	Whole-plant hydraulic conductance between soil and plant	$\text{mol H}_2\text{O s}^{-1} \text{MPa}^{-1}$
$W$	Whole-plant water content	$\text{mol H}_2\text{O}$
$\Psi_{soil,1}$	Shallow soil water potential	MPa
$\Psi_{plant}$	Plant water potential	MPa
$g_{leaf}$	Leaf conductance	$\text{mol H}_2\text{O m}^{-2} \text{s}^{-1}$
$k_i$	Total hydraulic conductance between soil and plant	$\text{mol H}_2\text{O m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$
$k_{soil,i}$	Hydraulic conductance between bulk soil and root surface	$\text{mol H}_2\text{O m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$
$k_{root,i}$	Hydraulic conductance between root surface and plant	$\text{mol H}_2\text{O m}^{-2} \text{s}^{-1} \text{MPa}^{-1}$

event size and evaporative demand of the atmosphere, can last from a few hours to many weeks (Sala *et al.* 1981). Single events do not usually recharge the soil below 20–30 cm (Sala & Lauenroth 1982), but clustered rain events, especially when coinciding with colder temperatures, can infiltrate into deeper layers. Thus, deeper soil moisture is governed primarily by longer, seasonal weather patterns (Fernandez & Caldwell 1975; Reynolds *et al.* 1999), often with maximal recharge in early spring and greatest depletion in late summer (Schlesinger *et al.* 1987). Interannual components to soil moisture variation add to these patterns, through varying the total amount of summer and winter rainfall.

Plant life-forms in arid and semi-arid environments appear to specialize in taking up water from specific soil layers at certain times of the year (Walter & Stadelmann 1974; Cody 1986; Smith & Nobel 1986; Ehleringer *et al.* 1991; Flanagan *et al.* 1992; Lin *et al.* 1996), rather than converging on one generalist phenotype that can take up water wherever and whenever it becomes available. This diversification with respect to water use is repeated on a continental scale, often involving unrelated genera, for example in South America (Soriano & Sala 1983; Sala *et al.* 1989; Paruelo *et al.* 1998) and Africa (Cowling *et al.* 1994), suggesting that powerful trade-offs are associated with the use of alternative water sources in arid environments.

Here, we explore such potential trade-offs by developing a simple model of plant water transport and carbon gain in a two-layered soil environment. The study is guided by three objectives: (i) to gain a better understanding of the mechanisms that generate trade-offs in water use; (ii) to identify suites of morphological and physiological traits that are optimally adapted to exploit specific dynamic soil moisture patterns; and (iii) to compare the sensitivities of ‘pattern specialists’ to jointly experienced climatic conditions. Finally, based on the similarities between the derived ‘moisture pattern specialists’ and actual plant life-forms, we discuss how annual precipitation patterns may shape plant adaptations and life-form diversity in arid and semi-arid environments.

## Methods

### MODEL OVERVIEW

The model describes the dynamics of soil water uptake and use by plants in a pulse-driven, arid environment. We distinguish two root horizons, one in shallow soil, where water is available in pulses, and the other in deeper soil, where water availability is assumed to be constant during and between pulses. There is no exchange of water between these two layers. This simplifies the soil environment so that it includes only the two endpoints of the entire spectrum of local soil water dynamics (Noy-Meir 1973). Water uptake and transport in model plants is based on Darcy’s Law (Gradmann 1928; Cowan 1965). The rate of water loss is determined by leaf area and leaf conductance of water vapour (Cowan & Farquhar 1977). The exchange rate of CO<sub>2</sub> for water is calculated on the assumption of light-saturated, diffusion-limited (C<sub>3</sub>) photosynthetic rate (von Caemmerer & Farquhar 1981). Water uptake, loss and use depend on the partitioning of plant biomass between leaves, roots and stems, where leaves are defined as the only organs that transpire and take up CO<sub>2</sub> and roots as the only organs that can exchange water with the soil, whereas stems, which can occur above or below ground, neither transpire water vapour, nor exchange water with the soil environment, but store water. Below we give a detailed description of the model. Important variables are summarized in Table 1, parameter values are given in Tables 2 and 3.

### WATER BALANCE

Change in plant water content  $W$  is determined by the rates of water uptake from the two soil layers,  $E_1$  and  $E_2$ , and transpiration  $E$ :

$$\frac{dW_{plant}}{dt} = E_1 + E_2 - E \quad \text{eqn 1}$$

In this mass balance equation, both water uptake and loss are controlled by plant water potential  $\Psi_{plant}$ . Plant

**Table 2** Plant parameters

Symbol	Description	Value	Unit
$B_{leaf}$	Leaf biomass	Variable	mol C
$B_{root,1}$	Root biomass in soil layer 1 (shallow)	Variable	mol C
$B_{root,2}$	Root biomass in soil layer 2 (deeper)	Variable	mol C
$B_{stem}$	Stem biomass	Variable	mol C
$C_{plant}$	Whole-plant capacitance	Variable	mol H <sub>2</sub> O MPa <sup>-1</sup>
$L$	Root length density	5000 <sup>(a)</sup>	m m <sup>-3</sup>
$c_{leaf}$	Mass-specific capacitance of leaves	-19.4 <sup>(b)</sup>	mol H <sub>2</sub> O MPa <sup>-1</sup> mol <sup>-1</sup> C
$c_{root}$	Mass-specific capacitance of roots	-19.4 <sup>(b)</sup>	mol H <sub>2</sub> O MPa <sup>-1</sup> mol <sup>-1</sup> C
$c_{stem}$	Mass-specific capacitance for woody stems	Variable 1.13 10 <sup>-3</sup> (1.27 10 <sup>-4</sup> ) <sup>(c)</sup>	mol H <sub>2</sub> O MPa <sup>-1</sup> mol <sup>-1</sup> C
	for succulent stems	2.4 (6.0) <sup>(d)</sup>	mol H <sub>2</sub> O MPa <sup>-1</sup> mol <sup>-1</sup> C
$g_{min}$	Minimal leaf conductance	Variable	mol H <sub>2</sub> O m <sup>-2</sup> s <sup>-1</sup>
$g_{max}$	Maximal leaf conductance	Variable	mol H <sub>2</sub> O m <sup>-2</sup> s <sup>-1</sup>
$k_{root,max}$	Maximal root conductance	1.68 10 <sup>-2(e)</sup>	mol H <sub>2</sub> O m <sup>-2</sup> s <sup>-1</sup> MPa <sup>-1</sup>
$r_1$	Root radius in shallow layer 1	0.001	m
$r_2$	Root radius in deeper layer 2	0.0001	m
$w_{leaf}$	Water storage capacity of leaves	4.47 <sup>(f)</sup>	mol H <sub>2</sub> O mol <sup>-1</sup> C
$w_{root}$	Water storage capacity of roots	10.0 <sup>(f)</sup>	mol H <sub>2</sub> O mol <sup>-1</sup> C
$w_{stem}$	Water storage capacity of stems for woody stems	Variable 1.13 <sup>(g)</sup>	mol H <sub>2</sub> O mol <sup>-1</sup> C
	for succulent stems	21.13 <sup>(h)</sup>	mol H <sub>2</sub> O mol <sup>-1</sup> C
$\Psi_{crit,i}$	Critical soil water potential in layer i (eqn 12)	Variable	MPa
$\beta$	Stomatal sensitivity to plant water potential	Variable	MPa <sup>-1</sup>
$\lambda$	Specific leaf area	0.12 <sup>(i)</sup>	m <sup>2</sup> mol <sup>-1</sup> C
$\omega$	Specific root volume	6.0 10 <sup>-4(j)</sup>	m <sup>3</sup> mol <sup>-1</sup> C

(a) Value cited for *Artemisia tridentata* (Caldwell 1994); (b) approximation based on *Rhododendron* leaves (Kramer & Boyer 1995, p. 63); (c) first value applies between 0 and -3.5 MPa, second value below -3.5 MPa, based on Tyree & Yang (1990) for *Tsuga canadensis*; (d) first value applies between 0 and -1 MPa, second value below -1 MPa, based on Hunt & Nobel (1987) for *Ferrocactus acanthodes*; (e) based on primary roots of *Agave* and *Ferrocactus* (Nobel 1989), values for other species are similar (Campbell 1985); (f) corresponds to 80% (leaves) and 90% (roots) water in fresh weight (Kramer 1983) and 60% carbon in dry weight; (g) based on 60% water in fresh weight and 60% carbon in dry weight; (h) based on 95% water in fresh weight (Nobel & Sanderson 1984) and 60% carbon in dry weight; (i) average value for desert shrubs, equivalent to 60 cm<sup>2</sup> per g dry weight; (j) assuming that roots have the same density as water, 90% water content and 60% carbon in dry matter.

**Table 3** Environmental parameters

Symbol	Description	Value	Unit
$E_{pot}$	Potential evapotranspiration	82.5 <sup>(a)</sup>	mol H <sub>2</sub> O m <sup>-2</sup> d <sup>-1</sup>
$P_{atm}$	Atmospheric pressure	0.1 <sup>(b)</sup>	MPa
RH	Relative humidity	20	%
$T_{air}$	Air temperature	30	C
$e_{air} - e_{sat}$	Vapour pressure deficit in air	3.62	kPa
$k_{sat}$	Saturated hydraulic conductivity of soil	5.8 10 <sup>-3</sup>	kg s m <sup>-3(c)</sup>
$m$	Texture parameter of soil	3.67 <sup>(c)</sup>	-
$t_{day}$	Time of daylight per day	50400 <sup>(d)</sup>	s
$\Psi_e$	Air entry potential of soil	-11 <sup>(e)</sup>	kPa
$\Psi_{soil,2}$	Deeper soil water potential	Variable	MPa

(a) Based on Campbell's (1977, p. 140) formula and full sunlight (1300 W/m<sup>2</sup>), averaged over a day assuming sinusoidal time course (i.e.  $PE_{avg} = PE_{max} * 2/\pi * t_{day}$ ); (b) corresponds to sea level; (c) values taken from Campbell & Norman (1998, p. 130); (d) 14 h, corresponds to c. 15 May and 28 July at 35N, 110 W.

water potential and water content are related through whole-plant capacitance  $C_{plant}$ :

$$\frac{dW_{plant}}{dt} = C_{plant} \frac{d\Psi_{plant}}{dt} \quad \text{eqn 2}$$

$C_{plant}$  is composed of the capacitances of leaf, root and stem:

$$C_{plant} = B_{leaf}c_{leaf} + B_{root}c_{root} + B_{stem}c_{stem} \quad \text{eqn 3}$$

where  $B_{leaf}$ ,  $B_{root}$  and  $B_{stem}$  is the biomass (in mol carbon) of leaves, roots and stems, respectively, and  $c_{leaf}$ ,  $c_{root}$  and

$c_{stem}$  are the corresponding mass-specific capacitances. When fully hydrated (i.e. at  $\Psi_{plant} = 0$  MPa), leaves, roots and stems have a tissue-specific, maximal water storage capacity  $w$ . These and all other plant hydraulic parameters are summarized in Table 2.

Water uptake rates from the shallow soil layer ( $E_1$ ) and the deeper soil layer ( $E_2$ ) are governed by Darcy's Law:

$$E_i = (\Psi_{soil,i} - \Psi_{plant})K_i \quad \text{eqn 4}$$

**Table 4** Optimization parameters

Symbol	Description	Range	Unit
$P_{stem}$	Fraction of total biomass in stem	0–1	–
$P_{leaf}$	Fraction of non-stem biomass in leaf	0–1	–
$P_{root,1}$	Fraction of root biomass in soil layer 1 (shallow)	0–1	–
$C_{stem}$	Stem capacitance	0.02–2.0	mol H <sub>2</sub> O <sup>-1</sup> MPa <sup>-1</sup> mol <sup>-1</sup> C
$W_{stem}$	Storage capacity of stems	2–20	mol H <sub>2</sub> O mol <sup>-1</sup> C
$g_{max}$	Maximal leaf conductance	0.01–1.0	mol H <sub>2</sub> O m <sup>-2</sup> s <sup>-1</sup>
$\Psi_{crit,1}$	Critical soil water potential in soil layer 1	–0.1 to –7.0	MPa
$\beta$	Stomatal sensitivity to plant water potential (exponential incrementation)	10 <sup>-3</sup> –10 <sup>2</sup>	MPa <sup>-1</sup>

where  $K_i$  is the whole-plant conductance for water in the pathway from the bulk soil in layer  $i$  to the leaf, and  $\Psi_{soil,i}$  is the corresponding bulk soil water potential (MPa). Transpiration rate ( $E$ ) is determined by the product of whole-plant leaf conductance for water vapour ( $G_{leaf}$ ) and the saturation water vapour pressure gradient between leaf and air, divided by total atmospheric pressure ( $P_{atm}$ ).

$$E = \frac{e_{air} - e_{sat}}{P_{atm}} G_{leaf} \quad \text{eqn 5}$$

This formulation is based on the approximation that leaf and air temperatures are identical (hence  $e_{air} - e_{sat}$  describes the diffusion gradient).

$G_{leaf}$  and  $K_i$  are whole-plant conductances and their magnitudes depend on the amount of biomass allocated to roots and leaves and on the area-specific conductances of leaves and roots, which vary in response to environmental conditions. To distinguish between whole-plant conductance ( $G_{leaf}$ ) and area-based leaf conductance ( $g_{leaf}$ ), we use upper and lower case letters, respectively. Whole plant leaf conductance is thus:

$$G_{leaf} = \lambda B_{leaf} g_{leaf} \quad \text{eqn 6}$$

where  $\lambda$  is the specific leaf area (in m<sup>2</sup> per mol leaf carbon). Leaf conductance  $g_{leaf}$  is bounded by maxima and minima with water potential  $\Psi_{plant}$  as the only controlling variable:

$$g_{leaf} = g_{min} + g_{max} e^{(\beta \Psi_{plant})} \quad \text{eqn 7}$$

$\beta$  describes the sensitivity of stomatal aperture to  $\Psi_{plant}$ . We set a limit to the range of stomatal control by setting  $g_{min} = 0.001 g_{max}$ .

As with leaf conductance, we distinguish between whole-plant hydraulic conductance ( $K_i$ ) and area-based hydraulic conductance ( $k_i$ ). Whole-plant conductance is determined by:

$$K_i = \frac{2\omega}{r_i} B_{root} k_i \quad \text{eqn 8}$$

where  $\omega$  is specific root volume (and  $2\omega/r_i$  is specific root area). Root area-based hydraulic conductance ( $k_i$ ) is a serial combination of the pathway between the bulk

soil and the root surface ( $k_{soil,i}$ ) and between the root surface and the plant ( $k_{root,i}$ ):

$$\frac{1}{k_i} = \frac{1}{k_{soil,i}} + \frac{1}{k_{root,i}} \quad \text{eqn 9}$$

Both types of conductances decrease with decreasing water potential (Nobel & Sanderson 1984; Campbell 1985). To represent the relationship between soil hydraulic conductance and soil moisture we use Campbell's (1985) analytical approximation for cylindrical roots:

$$k_{soil,i} = \frac{k_{sat} \left( \frac{\Psi_e}{\Psi_{soil,i}} \right)^m}{A_i} \quad \text{eqn 10}$$

with

$$A_i = \frac{r_i}{2} (1-m) \ln(\pi r_i^2 L_i) \quad \text{eqn 11}$$

Here,  $k_{sat}$  (saturated conductivity)  $\Psi_e$  (air entry potential) and  $m$  (soil texture parameter) are soil-specific constants for which we adopt values that represent sand (Table 4). Sand was a practical choice, as our field sites are on sandy soil. We will address the possible effects of choosing sand over other soil types on the model results in the discussion section.  $A_i$  is a scaling factor that transforms hydraulic conductivity to hydraulic conductance, depending on root length density ( $L_i$ ; total length of root per volume of soil), root diameter ( $r_i$ ) and soil texture ( $m$ ).

Root conductance is also variable and two mechanisms have been suggested to explain why specific root conductance decreases with soil moisture: root shrinkage (Nobel & Sanderson 1984) and hydraulic failure of the root xylem (Sperry *et al.* 1998). For simplicity, we assume that root surface conductivity is constant up to a critical minimum soil water potential  $\Psi_{crit,i}$  and then decreases to zero. Water flow across the root surface then ceases.

$$k_{root,i} = k_{root,max} \quad \text{if } \Psi_{soil,i} > \Psi_{crit,i}$$

$$k_{root,i} = 0 \quad \text{if } \Psi_{soil,i} \leq \Psi_{crit,i} \quad \text{eqn 12}$$

This de-couples plant water status from that of the soil during extreme drought, consistent with observation and irrespective of the mechanism.

## CARBON GAIN

Rates of photosynthesis are calculated for leaves assuming saturating irradiances and a maximal rate of photosynthesis typical for  $C_3$  plants, using the equations developed by von Caemmerer & Farquhar (1981). Under these conditions, photosynthesis is diffusion limited:

$$A_{leaf} = \frac{g_{leaf}}{1.6}(c_a - c_i) \quad \text{eqn 13}$$

where  $c_a$  is the ambient, atmospheric and  $c_i$  is the intercellular  $CO_2$  concentration (p.p.m.). The denominator 1.6 scales the conductance for water vapour ( $g_{leaf}$ , eqn 7) into conductance for  $CO_2$ , and  $c_i$  is calculated from von Caemmerer & Farquhar (1981) using values of constants from Long (1991). The average daily whole-plant photosynthetic carbon gain (in  $mmol\ mol^{-1}\ plant\ C\ d^{-1}$ ) can then be calculated by integrating photosynthesis over time and multiplying by leaf area:

$$A_{plant} = \frac{T}{t_{day}} \lambda B_{leaf} \int_{t=0}^{t=T} \frac{A_{leaf}(t)}{1000} dt \quad \text{eqn 14}$$

where  $T$  is the total time interval considered (in seconds) and  $t_{day}$  is the number of seconds of daylight per day. The denominator 1000 scales photosynthetic carbon gain from  $\mu mol$  to  $mmol$ . Throughout, carbon gain among plant types is compared on a basis of equal total plant biomass.

## SIMULATION

The dynamics of water use by plants is simulated using a finite difference approximation with a time-step size of 50 s or less, ignoring diurnal variation in environmental parameters (Table 3). Days have a constant length of 14 h and leaf photosynthesis is light-saturated over the entire photo-period. Thus, we chose the conditions of daily peak water demand to represent the maximal hydraulic stress a plant must be able withstand. An additional assumption is that the photosynthesis rate at that time is positively correlated with daily cumulative photosynthesis, so that we can correctly rank species by carbon gain.

Temperature and relative humidity stay fixed at 30 °C and 20%, respectively. All simulation intervals start with the input of 10 mm water into the shallow soil horizon between 0 and 20 cm, creating a pulse of soil moisture in this layer, but not in the layer below. Simulations continue for between 10 and 200 days with no further input of water. During this interval, water in the upper horizon is depleted, while deeper soil moisture stays constant (there is no exchange of water between the shallow and deeper soil horizon). The rate of evaporative depletion is determined by the simplified (Linacre 1973) model for bare soil, which subdivides the shallow soil layer into a surface component (0–5 cm) and a subsurface component (5–20 cm). We assume that shallow roots occur only in the subsurface

layer. Initial evaporation depletes only the surface component; later both sublayers contribute to evaporation. Actual rates of soil moisture depletion may be faster or slower than predicted by the Linacre model, depending on the resident vegetation and initial soil water content, but this is not important for our study.

## GENETIC ALGORITHM

The ability of plants to utilize pulses of soil moisture in the shallow soil, or else in deeper soil layers, depends on a number of physiological and morphological plant characteristics. We identified eight such characteristics (Table 4) and devised a genetic algorithm to search for their optimal combinations. We follow the approach described by Schwefel (1995). Each of the eight characteristics is assigned a range of possible values. This range is divided into 64 values including the endpoints and transformed into six-digit binary numbers. The entire 'genome' of an individual consists of a string of 48 binary digits (eight parameters  $\times$  six digits). An initial population of phenotypes (i.e. character combinations) is selected at random from the parameter ranges, by sampling with replacement, and tested in simulations to determine average daily carbon gain of individuals over the entire simulation period (eqn 14). This is taken as a fitness proxy. Setting a common tolerance limit for all individuals, we assign zero fitness to all individuals that, at any time during the simulation, have a plant water potential  $\leq -6$  MPa. Throughout the optimization procedure only the phenotypes change, the simulated soil moisture pattern always stays exactly the same.

Following the tests, all members of the initial population are ranked according to 'fitness' (i.e. average carbon gain). The two fittest individuals enter the next population unaltered. This ensures that the fitness of the fittest individual in a population never declines. The remaining individuals of the next generation are randomly selected from the previous, with fitness-weighted selection probabilities. Individuals are selected in pairs and before they enter the next generation, pairs exchange binary digits ('cross-over') with a probability of 0.2. Then, additional random mutations (0 into 1 or vice versa) are imposed with a probability of 0.2. These particular cross-over and mutation probabilities have been chosen because, in preliminary optimization runs, they tended to produce the greatest fitness increase with each generation. However, the exact probability values are not critical to the optimization results.

When an optimization run is repeated with an identical soil moisture pattern, the selected phenotypes tend to converge on similar character combinations. Convergence is fast for the first five generations, but slows considerably thereafter. Larger populations converge faster, but the advantage of population size begins to diminish above 500. For the solutions presented in this paper, we chose population sizes of 1000 and optimization through 20 generations. Using this

protocol most plant characteristics converge on similar values but some variation persists. To represent the accuracy of the optimization result for each character value, we show the best three of six independently derived solutions. While larger populations and longer optimization cycles may have been desirable from a mathematical point of view (Schwefel 1995), they were unfeasible given the duration of the optimization runs. However, we found that the chosen optimization protocol resulted in sensible solutions and acceptable precision for fitness and most optimized plant characters.

## Results

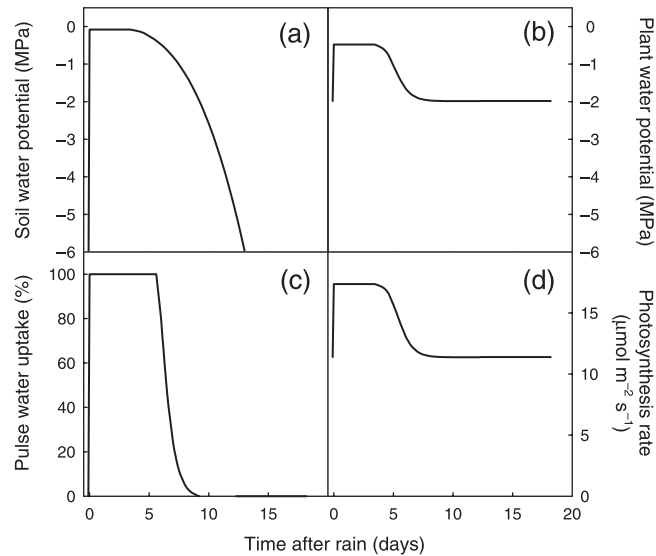
### AN EXAMPLE OF PULSE DYNAMICS AND PULSE USE

In this model, rainfall nearly saturates the shallow soil layer for *c.* 4 days, then soil water potential declines rapidly and after 12 days falls below  $-6$  MPa (Fig. 1a), the theoretical limit for water extraction by model

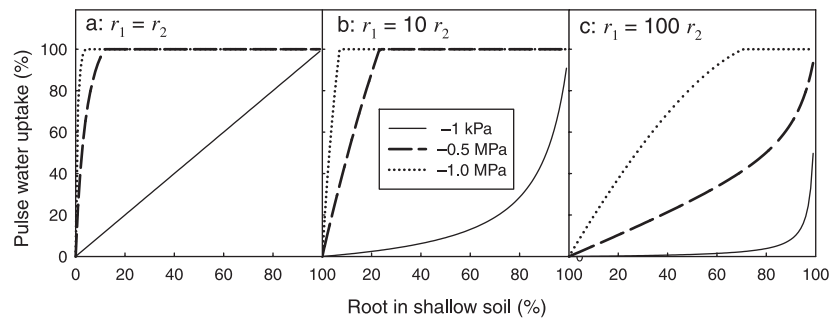
plants. However, the plant in Fig. 1 takes up shallow soil water only until day 9 (Fig. 1c) and plant water potential and photosynthesis remain elevated for only 5 days (Fig. 1b,d). Pulse and post-pulse periods are phases of quasi-steady state, separated by a brief transition period of *c.* 2 days. We begin our analysis of trade-offs in soil water use by examining the pulse and post-pulse phases separately, focusing first on allocation-mediated trade-offs.

### TRADE-OFF 1: ROOT DISTRIBUTION BETWEEN SHALLOW AND DEEPER SOIL

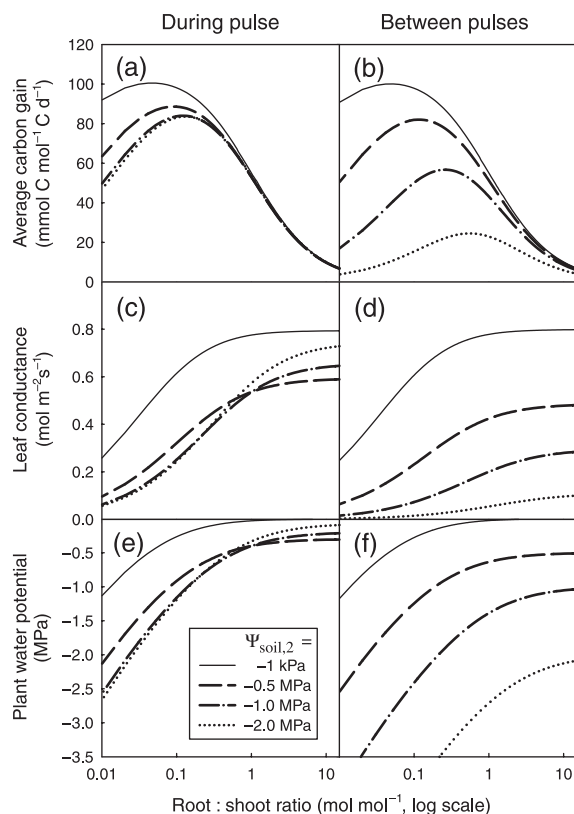
It is often tacitly assumed that the vertical root distribution of a plant informs the relative resource uptake from the corresponding soil strata. However, pulse water uptake is proportional to shallow root biomass only when both soil layers have equal water potentials (i.e. are both saturated) and all roots have identical hydraulic properties (Fig. 2a). When the shallow soil water potential is higher (almost always during pulse), comparatively



**Fig. 1** Pulse dynamics in sandy soil. (a) Soil water potential in the shallow layer between 5 and 20 cm; (b) plant water potential; (c) percentage of shallow soil water in plant transpiration stream; (d) leaf-level photosynthesis rates. Environmental conditions as in Table 3 with a deeper soil water potential of  $-1.5$  MPa. Plant parameters are  $B_{stem} = 0$  mol C,  $B_{leaf} = 0.5$  mol C,  $B_{root,1} = 0.25$ ,  $B_{root,2} = 0.25$  mol C. Shallow and deep roots are identical.



**Fig. 2** The relationship between root distribution and pulse water uptake. (a) Shallow and deep roots are identical; (b) shallow root radius is  $10 \times$  greater than deeper root radius; (c) shallow root radius is  $100 \times$  greater than deeper root radius. Holding total root biomass constant, root radius is inversely related to total root conductance (eqn 8). The root : shoot ratio is 1 throughout. Shallow soil water is saturated ( $\psi_{soil,1} = -1$  kPa) and deeper soil water potential varies as indicated.



**Fig. 3** Plant performance as a function of root : shoot ratio during and between water pulses. The deeper soil water potential is varied as indicated. Root distribution between shallow and deeper soil is 50 : 50, stem biomass is zero. Other parameters are  $g_{\max} = 0.8 \text{ mol H}_2\text{O m}^{-2} \text{ s}^{-1}$ ,  $\beta = 1 \text{ MPa}^{-1}$ . All other parameters are set to their default values (Table 2).

little shallow root biomass is needed to supply the entire transpiration flux from pulse water (Fig. 2a,b,c). This is due to the non-linear relationship between soil hydraulic conductance and soil moisture (eqn 10).

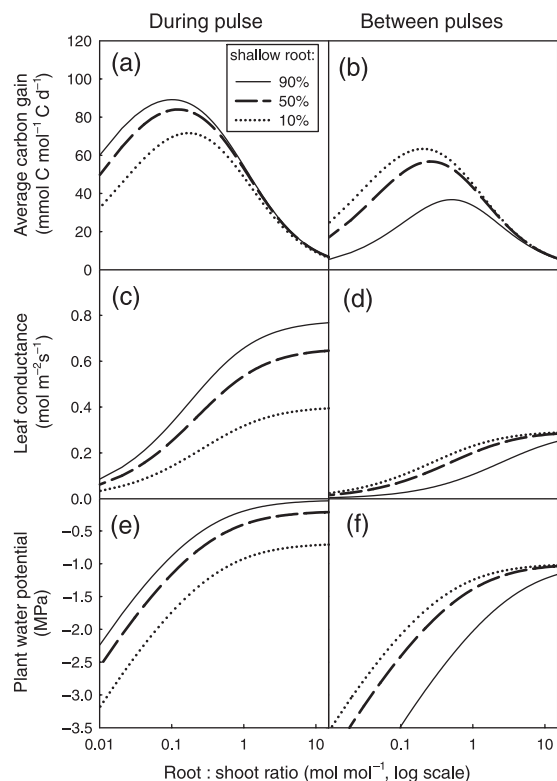
The efficiency of shallow roots is highest if the hydraulic properties of shallow and deep roots are identical (Fig. 2a). If shallow roots are, however, less efficient than deeper roots (in our example, by being thicker), more shallow root biomass is required for significant pulse water uptake (Fig. 2b,c). Differences in the specific conductance of shallow and deeper roots have been demonstrated for one desert species (Wan *et al.* 1994) and in general this is consistent with observed root distributions in relation to pulse water use by desert plants (Ehleringer *et al.* 1991; Jackson *et al.* 1996). From this point on, we take a 10-fold difference in shallow and deeper root radii, equivalent to an inverse 10-fold difference in hydraulic conductance per root biomass, to be the default (Table 2).

Based on Fig. 2, root distribution *per se* is not a major trade-off in the water use of desert plants, since comparatively little root biomass is needed to extract large amounts of water from water-saturated soils. A more important trade-off may lie between the ability of roots to persist in the environmentally harsh conditions of the shallow soil and their hydraulic efficiency (Eissenstat 1997). This would necessitate comparatively greater carbon investment for the exploitation of moisture in the shallow than in the deeper soil.

#### TRADE-OFF 2: ROOT-TO-SHOOT RATIOS

Desert plants can differ by two orders of magnitude in root : shoot ratio (Smith *et al.* 1997). A large allocation above ground, particularly to leaves, corresponds to a large potential for carbon gain, but the corresponding small root biomass may limit the capacity for water uptake and cause water stress. Conversely, a large allocation below ground may improve plant water status but limit carbon gain. This trade-off is the basis for determining the optimal root : shoot ratio in a given soil moisture condition (Fig. 3). As expected, conductance (Fig. 3c,d) does not limit whole plant carbon gain (Fig. 3a,b) when root : shoot ratios are large and leaf area then becomes critical. Small root : shoot ratios, on the other hand, decrease plant water potential (Fig. 3e,f), leaf conductance and ultimately, whole-plant carbon gain, despite the greater leaf area.

Moisture in the deeper soil affects the optimal root : shoot ratio (where whole-plant carbon gain is maximal; Fig. 3a,b). A drier deeper soil shifts the optimum towards larger root : shoot ratios, even during pulse periods (Fig. 3a), suggesting that water-saturation in the shallow soil does not fully compensate for lack of soil moisture deeper down. However, at the same moisture condition in the deeper soil, the optimal root : shoot ratio is almost always smaller during a pulse than between pulses (compare Fig. 3a,b).



**Fig. 4** Plant performance as a function of root : shoot ratio during and between water pulses. Relative allocation of total root biomass to the shallow soil is varied as indicated. Deeper soil water potential is  $-1$  MPa throughout. All other parameters as for Fig. 3.

Root distributions also affect the optimal root : shoot ratio (Fig. 4). During a pulse, plants with more shallow roots have greater carbon gain at any root : shoot ratio and maximize carbon gain at smaller root : shoot ratios than plants with fewer shallow roots (Fig. 4a). Clearly, more root allocation in the shallow soil improves plant water status during pulse periods (Fig. 4e), so that plants can benefit from a further reduction in root : shoot ratio. Between pulses these trends are reversed, because the deeper soil is then the only source of water and any increase in deeper root biomass must be beneficial.

Figures 3 and 4 illustrate the dilemma for plants that live in a dynamic and structured soil moisture environment. Should they place most roots in the shallow soil and reduce their root : shoot ratio to maximize carbon gain during pulse periods, or should they place most roots in the deeper soil and increase their root : shoot ratio to maximize carbon gain between pulses? The answer is likely to depend on the relative profitability of exploiting shallow and deeper water sources, thus, on the relationship between the frequency of pulse days and the amount of water stored in the deeper soil.

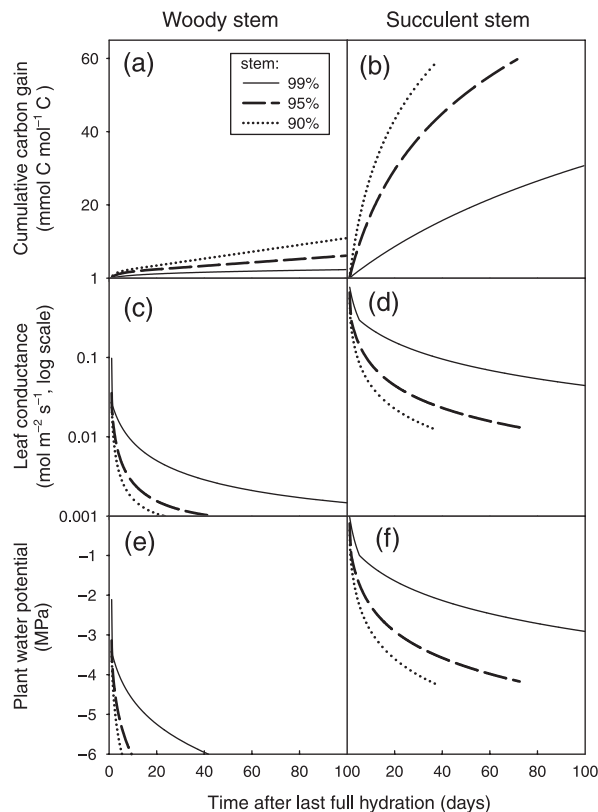
#### TRADE-OFF 3: WATER STORAGE

A large portion of perennial plant biomass is composed of tissues that neither participate in gas exchange, nor in water uptake, but transport and store water below and above ground. We now evaluate the effect of allocation to woody and succulent stems, comparing only

their water storage role in plant water relations. These two tissue types are distinguished primarily by storage capacity (in terms of water storage per unit carbon) and capacitance for water (see Table 2). Wood has little storage capacity and low capacitance. This means that stem water potential falls quickly with declining water content. In contrast, fully hydrated succulent stems (e.g. of cacti) have the highest known water content (Gibson & Nobel 1986) and a high capacitance, if scaled to a unit of stem carbon (Holbrook 1995).

Plants with woody stems, despite their smaller water storage capacity, retain water for longer than plants with succulent stems, although their water potentials soon become very negative (Fig. 5e). Leaf conductance also steeply declines (Fig. 5c) and this conserves water, but the carbon gain of woody plants is also minimal throughout the drought period (Fig. 5a). In contrast, carbon gain, leaf conductance and water potential remain much higher in succulent plants (Fig. 5b,d,f). However, unless over 95% of all biomass is allocated to stems, this amounts to rapid water loss and total desiccation after 37 days (for 90% stem) or 73 days (for 95% stem). Assuming as we did that maximal leaf conductance and stomatal sensitivity are the same for woody and succulent plants, drought survival in succulents hinges on very large allocations to stem biomass. Even so, the carbon gain of a stem succulent with 99% stem allocation exceeds that of a woody plant with 90% stem allocation by approximately three-fold (Fig. 5a,b).





**Fig. 5** Plant performance as a function of time after last state of full hydration for plants with woody and succulent stems, when soil water is unavailable. Curves break off where plant water content becomes zero. The whole-plant allocation percentage to stem is varied as indicated in the legend. Water storage capacity and capacitance for woody and succulent stems are detailed in Table 2. All other parameters are as for Figs 2 and 3.

#### OPTIMAL CHARACTER SUITES

Above, we considered three allocation trade-offs separately. We have, however, already seen that some allocation trade-offs are interdependent, so that the value of one allocation dimension affects the value of another.

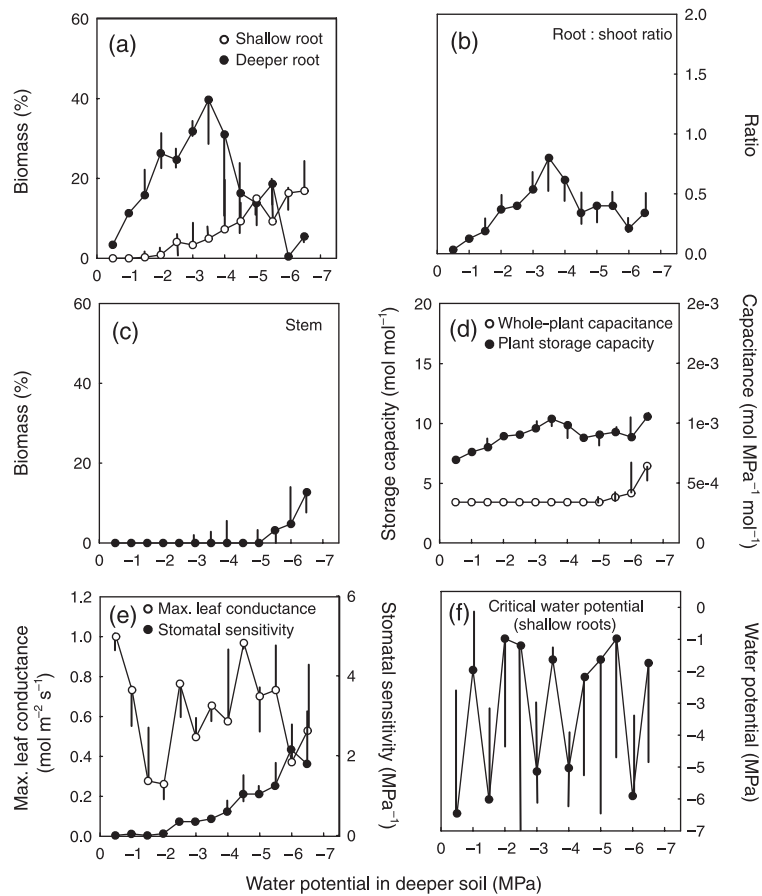
In addition, we limited our analysis to the quasi-steady state conditions of pulse and post-pulse periods, without considering that plants must be able to switch between these extremes. We will now tie these issues together by deriving optimal character combinations (Table 4) for a range of dynamic soil moisture patterns.

As the deeper soil water decreases from  $-0.5$  to  $-3.5$  MPa (and the pulse frequency remains constant) the optimal phenotype invests an increasing amount of biomass into deeper roots (Fig. 6a), simultaneously increasing the root : shoot ratio (Fig. 6b). Both responses compensate for the reduction in soil hydraulic conductivity, which makes it harder for plants to extract water. However, below  $-3.5$  MPa, the optimal phenotype reduces root biomass in the deeper soil, at the same time increasing shallow root biomass and decreasing the root : shoot ratio. In effect, the optimal phenotype adapts its morphology to improve exploitation of pulse water, when pulse water becomes the more profitable of the two water sources. We have already seen in Figs 3 and 4 that quite opposite allocation strategies are needed for the exploitation of shallow and deeper water sources. Figure 6 now shows

that the strategic compromise between maximizing pulse use and maximizing the use of deeper soil water shifts with the relative availability of these two water sources.

The accuracy in predicting maximal leaf conductance is fairly low compared with most other parameters (Fig. 6e). This is probably due to a strong interaction between the maximal conductance and its sensitivity to plant water status, such that a small variation in sensitivity requires a large compensation in maximal conductance. Nevertheless, there are some discernable patterns. Between  $-0.5$  and  $-2.0$  MPa, maximal leaf conductance sharply declines. This should further reduce the water demand of plants that are simultaneously reducing leaf area. However, maximal conductance picks up again below  $-2.0$  MPa. This may be an adaptation to improve pulse use, similar to the reversing trend in the root : shoot ratio. Stomatal sensitivity is rising continuously between  $-0.5$  and  $-6.0$  MPa, reflecting the increased need for down-regulation of the transpiration rate, as plants switch from pulse water to an increasingly depleted deeper water source.

From the viewpoint of water storage alone, it is not optimal to invest in stem biomass, unless the deeper soil water potential drops to  $-6.0$  MPa and below and becomes non-exploitable (Fig. 6c). The stem tissue that is added at  $-6.0$  MPa has a greater capacitance than the rest of the plant, increasing the plant's overall capacitance (Fig. 6d).



**Fig. 6** Morphological and physiological traits of optimal phenotypes as a function of water potential in the deeper soil. Simulation period is 20 days and water input occurs only once at the beginning of the simulation. Symbols indicate parameter values for the best of six independent optimization runs, vertical bars indicate their spread within the three best of six runs.

Finally, there is large variation and no trend in the critical soil water potential, at which shallow roots cease to transfer water (Fig. 6f), suggesting that the exact point of conductivity loss for roots is not very important to plant water relations. Preliminary simulations suggest that this result depends on the choice of soil texture (sandy) in this study. In sandy soil, hydraulic conductivity declines very rapidly with declining soil water potential, making additional root control over plant water status unnecessary.

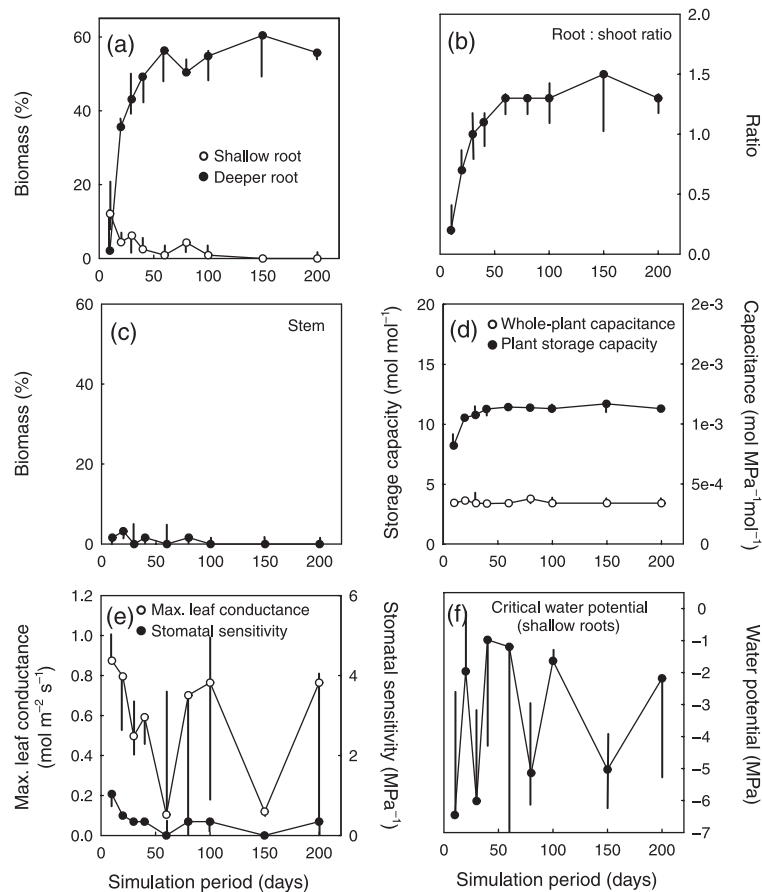
In summary, Fig. 6 shows the optimal phenotype transform, in response to declining water availability in the deeper soil, from a herbaceous plant (small root : shoot ratio, large leaf conductance) to a more xeromorphic, predominantly deep-rooted plant (larger root : shoot

ratio, smaller leaf conductance), then to a herbaceous plant with a dimorphic root system (about equal root allocation in shallow and deeper soil), and finally towards an exclusively shallow-rooted stem succulent. Many of these forms have equivalents in the real world (see discussion). For now, we pick three phenotypes from the continuum of optimal solutions in Fig. 6 to represent three contrasting life forms, which we will submit to further analysis later. To help visualize these derived abstractions, we will call the three types ‘winter annual’, ‘drought-deciduous perennial’ and ‘evergreen perennial’ (Table 5).

In Fig. 7 we consider the effects of simulation period (the inverse of pulse frequency) and hold the deeper soil water potential fixed at  $-3.5$  MPa. Simulation period

**Table 5** Four optimal phenotypes

Selection environment		Phenotype									
Simulation period (days)	$\Psi_{soil,2}$ (MPa)	Name	$B_{stem}$ (mol)	$B_{leaf}$ (mol)	$B_{root,1}$ (mol)	$B_{root,2}$ (mol)	$w_{stem}$ (mol mol <sup>-1</sup> )	$c_{stem}$ (mol/MPa mol <sup>-1</sup> )	$g_{max}$ (mol m <sup>-2</sup> s <sup>-1</sup> )	$\beta$	$\Psi_{crit}$ (MPa)
20	-0.5	Winter annual	0.0	0.97	0.00	0.03	–	–	1.00	0.002	-6.5
20	-3.5	Deciduous perennial	0.0	0.56	0.05	0.40	–	–	0.65	0.416	-1.6
20	-5.5	Evergreen perennial	0.03	0.69	0.09	0.18	0.3	$3.5 \cdot 10^{-5}$	0.73	1.250	-1.0
100	-6.5	Succulent perennial	0.41	0.46	0.13	0.00	5.2	$1.1 \cdot 10^{-3}$	0.25	2.586	-6.3



**Fig. 7** Morphological and physiological traits of optimal phenotypes as a function of simulation period. Water input occurs only once at the beginning of the simulation. Water potential in the deeper soil is  $-3.5$  MPa. Symbols and vertical bars as in Fig. 6.

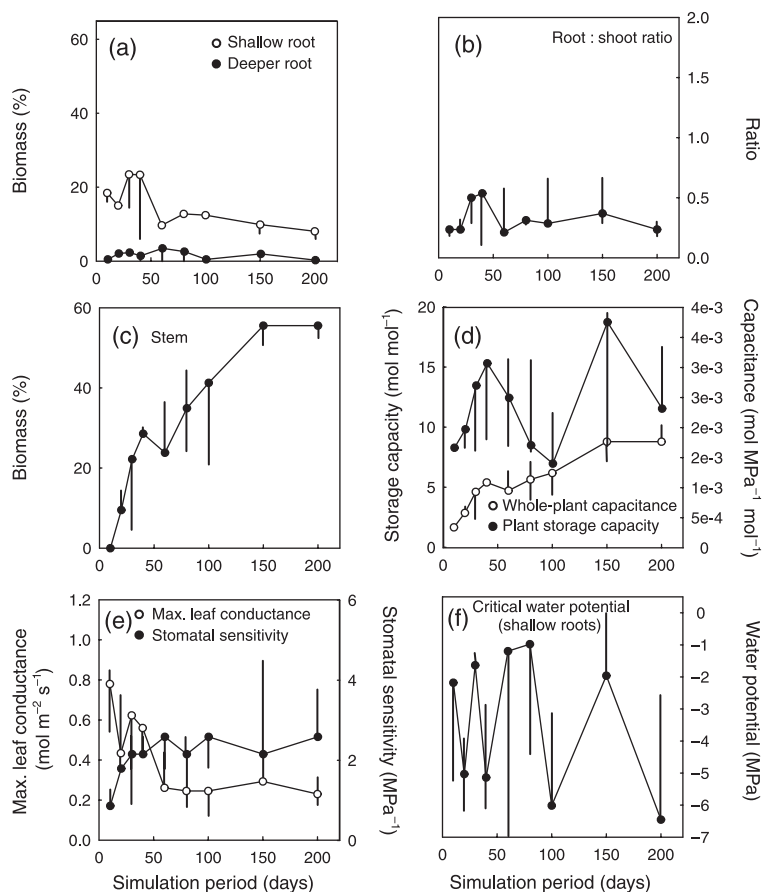
has a large effect only between 10 days (essentially zero post-pulse duration, see Fig. 1a) and *c.* 40 days (*c.* 28 days post-pulse). At 40 days, plants are so well adapted to exploiting the deeper soil that further adaptive change is unnecessary. Adaptations to long post-pulse periods include increased allocation to deep roots, loss of shallow roots (Fig. 7a), increase in root : shoot ratio (Fig. 7b) and, between 10 and 30 days, a decrease in maximal leaf conductance, coupled with a loss of stomatal sensitivity (Fig. 7e). In effect, plants become more xeromorphic. Note that the two parameters defining stomatal control (Fig. 7e) become indeterminable beyond *c.* 40 days. At this point, plants are so specialized in the exploitation of deeper soil moisture that they do not respond to the pulse of moisture in the shallow soil. Therefore, in our model, they have no need for physiological control over transpiration, and the optimization procedure cannot identify optimal solutions for the two control parameters. The adaptations to declining pulse frequency in Fig. 7 are consistent with the notion that plants shift towards a more efficient exploitation of deeper soil water, as anticipated by Figs 3 and 4.

Finally, in Fig. 8, we explore the response of the optimal phenotype to simulation period, when deeper soil water is unavailable. The longer the drought that follows the initial pulse, the more biomass is allocated to

stems (Fig. 8c) and the less to shallow roots (Fig. 8a). Root and leaf biomass decline in about the same proportion, so that root : shoot ratios change little (Fig. 8b). Maximal conductances become smaller and stomatal sensitivity to water potential increases (Fig. 8e), which indicates increasingly conservative water use of the remaining leaf area. Plant capacitance for water increases in parallel with stem biomass (Fig. 8d), indicating that the added stem biomass is of the 'succulent' type, but storage capacity shows no obvious trend, suggesting that capacitance is more important than storage capacity for water to conservative water use (however, in the real world these two characteristics are closely associated). Increasing drought length transforms the optimal phenotype from an essentially herbaceous phenotype with some stem succulence into a full-blown stem succulent with extremely conservative water use. From Fig. 8, we pick a fourth phenotype, which we call 'succulent perennial' (Table 5).

#### THE WATER USE OF OPTIMAL PHENOTYPES IN COMMON ENVIRONMENTS

We now compare the performances of the four selected phenotypes (Table 5) in common environments, in analogy to what is done in many field experiments. Although all phenotypes respond to a decline in water



**Fig. 8** Morphological and physiological traits of optimal phenotypes as a function of simulation period. Water input occurs only once at the beginning of the simulation. Water potential in the deeper soil is  $-6.5$  MPa (= non-exploitable by plants). Symbols and vertical bars as in Figs 6 and 7.

availability with a decline in carbon gain, there are substantial differences in the maximal carbon gain that phenotypes achieve in the wettest environment and in the magnitude of their responses to declining water availability (Fig. 9).

Phenotypes in their own selection environment always have the greatest carbon gain, as is to be expected. The overall greatest carbon gain is achieved by the winter annual (phenotype 1), due to its very small root : shoot ratio and large leaf conductance, but these same traits make it impossible for this phenotype to survive the drying of the deeper soil even to  $-3.5$  MPa (Fig. 9b,f,j). Under conditions of moderate water availability in the deeper soil, the drought-deciduous perennial (phenotype 2) has the highest carbon gain, with comparatively large values, even when pulses are infrequent (Fig. 9j), whereas the evergreen perennial (phenotype 3) needs a high pulse frequency to gain as much carbon (Fig. 9b). We have called phenotype 2 'drought-deciduous', because it operates at its tolerance limit at the deeper soil water potential of  $-3.5$  MPa. Below this value, the evergreen perennial gains more carbon (Fig. 9c,g,k) than the only other surviving phenotype, the succulent perennial (phenotype 4), whose carbon gain can exceed that of other phenotypes only when deeper soil water is unavailable

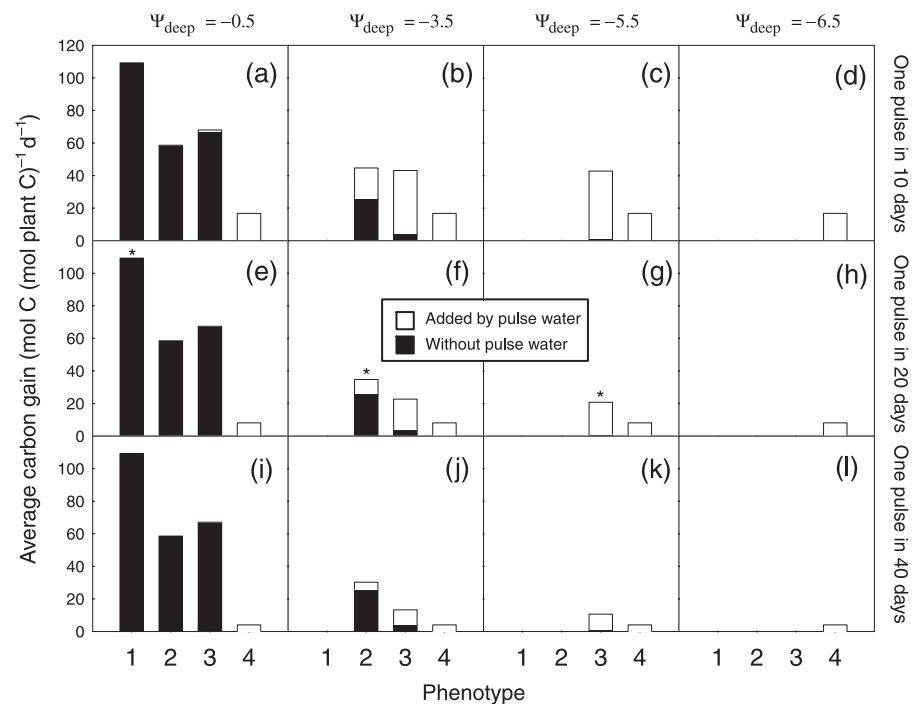
(Fig. 9d,h,l). Under these conditions, only succulents can maintain carbon gain for long after pulse (Fig. 5).

In terms of water use, phenotypes may be grouped into three categories: (i) those plants that depend predominantly on deeper soil water for carbon gain (e.g. the winter annual and drought-deciduous perennial); (ii) those that depend exclusively on pulse water (e.g. the succulent perennial); and (iii) those that exploit whichever water source is most available at the time (e.g. the evergreen perennial).

The winter annual and the drought-deciduous perennial (phenotypes 1 and 2) are more sensitive (in terms of carbon gain) to a reduction in deeper soil moisture than to a reduction in pulse frequency. The succulent perennial (phenotype 4) is sensitive only to a reduction in pulse frequency. The evergreen is sensitive to a reduction in pulse frequency only when deeper soil water is highly limiting, and to a reduction in deeper soil moisture only when pulses are rare.

## Discussion

We derived a family of plant phenotypes, each optimally adapted to a different soil moisture pattern. These predicted phenotypes have many similarities with actual desert plants, reproducing not just major



**Fig. 9** The average whole-plant carbon gain of four optimal phenotypes in a variety of environments. Deeper soil moisture declines left to right. Pulse frequency declines top to bottom. Phenotype 1 = winter annual, 2 = drought-deciduous perennial, 3 = evergreen perennial, 4 = stem succulent (see also Table 5). Solid bars designate contributions of deeper soil water to average carbon gain, open bars designate the pulse contribution to carbon gain. The pulse contribution to carbon gain is calculated by determining the difference in the average carbon gain for plants that did and did not receive pulse water. A missing bar indicates that this type did not tolerate the conditions of the simulation. \*Indicates that the respective phenotype is in its selection environment. The selection environment for phenotype 4 (one pulse in 100 days) is not included.

biomass allocation and root distribution patterns, but also many empirical phenomena of pulse use and water relations in a range of environmental conditions. This constitutes new and independent evidence for the hypothesis that plants in arid and semi-arid environments may be moisture pattern specialists. More importantly, the analysis allows us to further improve our understanding of plant water use strategies by examining morphology and physiology as integrated units of selection in a pulse-driven environment.

The modelling philosophy employed here is similar to that of Tilman (1988), in that allocation trade-offs are linked to trade-offs in the optimal exploitation of different environments. Some conclusions are also similar, for example that greater availability of below-ground resources generally favours increased above-ground allocation. However, we also consider adaptations in physiological control functions at the leaf-level, which are an indispensable part of the overall strategy in rapidly fluctuating environments.

#### CAVEATS REGARDING THE INTERPRETATION OF THE OPTIMIZATION RESULTS

Any optimal solution can only be as good or as detailed as its underlying model. We chose simplicity over completeness in describing plants in an arid environment. Three simplifications in particular warrant a cautious interpretation of the results. First, the soil was divided

into only two compartments, which we address as shallow and deep soil, but which really signify contrasting dynamics of soil water. 'Deep-rootedness' in this context does not literally refer to the absolute extent of the rooting system below the soil surface, but to the relative allocation to roots that exploit a more 'stable' water source, wherever it may be. For example, during a cold desert spring, the 'stable' water source may be located just centimetres below the soil surface, while during the summer of a winter-rain desert, the only 'stable' water source may be several metres down at the water table.

The second major simplification is the assumption of fixed biomass allocation to leaves and roots. Although plants are constrained to stay within some range of a gross morphology, they also have some fine control. For example, droughted plants may shed leaves (Comstock & Ehleringer 1988), or shift the production and maintenance of fine roots from the ephemeral to the more reliable moisture sources in the soil (Fernandez & Caldwell 1975). Our model does not have this flexibility and the predicted plant strategies can be seen only as the momentarily optimal solution to a given environment.

The third simplification lies in the choice of the objective function itself. Without assigning carbon costs for growth and maintenance, we were constrained to choose whole-plant photosynthetic carbon gain as a basis for comparing the success of alternative phenotypes. Technically, it would not have been difficult to

include carbon costs in the analysis, but the difficulty of assigning meaningful values to the growth and maintenance costs of roots, stems and leaves discouraged us from taking this course (Thornley & Cannell 2000). Unless plants are stressed, whole-plant respiration is strongly correlated with whole plant photosynthesis (Amthor 1994). Differences in whole-plant photosynthetic carbon gain among plants in the same environment may be an adequate first approximation of species differences in productivity.

#### THE HYDRAULIC SPECIALIZATIONS OF DESERT PLANTS

We likened the first phenotype to a winter annual, on the grounds of small root : shoot ratio in combination with large leaf conductance (Mooney *et al.* 1976; Ehleringer & Mooney 1983; Werk *et al.* 1983; Forseth *et al.* 1984), relative insensitivity of leaf conductance to plant water potential (Forseth *et al.* 1984), and relative intolerance to declining deeper soil moisture status, which for winter annuals determines the end of the growing season (Ehleringer 1985). Summer annuals share many of the same characteristics (Forseth *et al.* 1984), but instead of relying on winter water near the soil surface, they depend on large summer storm events that deliver water into deeper soil layers where it can remain available long enough for plants to complete their life cycles (Sala *et al.* 1981). There is a well-documented division in the dominant photosynthetic pathways between summer and winter annuals, the former being  $C_3$ , the latter predominantly  $C_4$  (Mulroy & Rundel 1977; Ehleringer 1985). We did not differentiate between the alternative photosynthetic pathways, but each may be the result of a strong selection pressure to maximize the instantaneous rate of photosynthesis under different temperature regimes, when water is abundant but time is limited. In both types of annuals, the strong effect of a few precipitation events, and their timing, on fitness may explain their high year-to-year variability (Guo & Brown 1996). Furthermore, the relief and orientation of the soil surface and the degree of perennial cover can further modify, over multiple scales, the effect of any one event on infiltration depth and pulse duration, contributing perhaps to the positive relationship between spatial abundance and distribution noted by Guo *et al.* (2000). In contrast, species that rely more on the accumulation of many precipitation events should be more strongly buffered against year type or site variation.

We pictured the second phenotype as a drought-deciduous shrub, based on larger root : shoot ratios, but not necessarily smaller leaf conductance (Ehleringer & Mooney 1983; Smith & Nobel 1986) and moderate tolerance of declining soil water potentials, which when exceeded sets the signal for leaf loss (Szarek & Woodhouse 1977; Comstock & Ehleringer 1986). The model suggests that root : shoot ratios primarily determine drought tolerance and therefore the timing of leaf

loss. Although in our simulations pulses increased the carbon gain of this phenotype very little (Fig. 9), pulse water was taken up (result not shown). The replacement of deeper soil water with pulse water, whenever it is available, may help these phenotypes conserve winter water and delay leaf loss.

We called the third phenotype evergreen, based on increased drought tolerance, which would allow plants to maintain leaves throughout the year (Smith & Nobel 1986). Examples are *Larrea tridentata* (Odening *et al.* 1974; Ho *et al.* 1996; Reynolds *et al.* 1999) and from a cold desert, *Coleogyne ramosissima* and *Gutierrezia sarothrae* (Ehleringer *et al.* 1991; Donovan & Ehleringer 1994; Lin *et al.* 1996). Although these species are not really 'evergreen' (but winter-deciduous), they often maintain leaves until late fall. Perennial grasses also share many of the same water-use characteristics (Sala *et al.* 1989; Burgess 1995). These plants all have the capacity for rapid recovery from water-stress conditions after rain (Sala & Lauenroth 1982; Ho *et al.* 1996; Lin *et al.* 1996; Reynolds *et al.* 1999). They also tend to increase pulse water use as deeper soil water potential declines, for example between spring and summer, or between years with wet and dry winters (Ehleringer & Cook 1991; Ehleringer *et al.* 1991; Dodd *et al.* 1998). It may be this opportunistic water-use strategy that makes this type of plant so common in deserts and semi-deserts with summer rain, as suggested by Ehleringer & Dawson (1992).

The correspondence between the succulent perennial phenotypes and actual succulents includes the combination of large allocation to succulent stem, high capacitance and relatively small maximal leaf conductance, sensitive to declining water status (Nobel 1988; Nilson *et al.* 1990). These characteristics allow plants to maintain a high water potential and hold flux rates relatively constant for months after rain (Nobel 1988). Many, but not all, stem succulents are CAM plants (for exceptions see Nilson *et al.* 1990), a photosynthetic strategy that further enhances the extremely conservative water use of this plant life-form.

The selection environments for the phenotypes in this study are not those in which they achieve maximum carbon gain, but those which take them to the limit of their physiological tolerance (where non-optimal phenotypes are either dead, dormant or inefficient, Fig. 9). Differences in the carbon gain of contrasting phenotypes in the same environment are often less pronounced than differences within phenotypes in contrasting environments, which complicates the empirical study of species diversity in water use. This is because of the overriding importance of water availability in arid environments and flexibility in water use, common to most plants (Fernandez & Caldwell 1975; Sala *et al.* 1981). Species differences in water use should be more clearly exposed by quantifying their sensitivity to declining water availability in the different soil horizons, i.e. to winter or summer drought, which, as we have seen, can reverse their carbon gain rankings.

## NOT ALL DROUGHTS ARE THE SAME

In our study, the tolerance for low water potential in the deeper soil declines from the succulent plant to the winter annual in the sequence succulent > evergreen > drought-deciduous > winter annual. This ranking coincides with that for the general attribute of 'drought tolerance' for these plant types (Ehleringer & Mooney 1983). Although this correspondence is reassuring, the more important result of this study is that there are different kinds of drought events, which select different kind of plants.

Winter drought reduces the recharge of the deeper soil (Reynolds *et al.* 1999). In our model, increasing the severity of winter drought led to a character shift from a predominantly deep-rooted phenotype towards a phenotype with both deep and shallow roots (Fig. 6). A similar shift (in reverse) was observed by Turner (1990) following years of unusually high winter precipitation. After the strong El Niño years of 1941–42, a dominant population of *Larrea divaricata* (evergreen) was replaced by *Encelia farinosa* (drought-deciduous) and the deep-rooted *Prosopis velutina*. Similarly, Brown *et al.* (1997) attributed the expansion of deep-rooted woody plants in south-eastern Arizona to unusually wet winters. Just as our model predicts, increased winter rain appears to favour plants with reduced root allocation to shallow soil, even though summer precipitation did not change. The adaptive advantage of this character shift lies not necessarily in the expansion of the deep root system (after all, wetter soil requires less root for its exploitation), but more probably in the increase in leaf area, which is associated with the redistribution of roots.

Under the most extreme drought conditions (winter drought + summer drought), our analysis predicts that succulents should be the best-adapted phenotypes (Fig. 8). Yet, woody plants are found in the most arid environments on earth. The drought tolerance of woody plants is in part due to a strategy that we did not account for, namely the shedding of leaves and fine roots to isolate themselves from the environment. However, for a population of woody perennials to remain viable in this way, long periods of dormancy must be balanced by occasional substantial rainfall events that allow new growth above that needed to restore lost leaves and roots. In contrast, cacti should be able to persist on much smaller precipitation events, provided they occur consistently (e.g. dew? Malek *et al.* 1999). Clearly, there is no one definitive suite of drought adaptations, as long as drought is seen as a single variable of ecosystem water balance. What constitutes an effective drought adaptation depends largely on rain and drought patterns, e.g. whether drought occurs in winter or summer, and whether drought release is slight and brief or substantial and lasting.

## PULSE WATER USE AND ITS COST

Water near the soil surface, just after rain, is the most freely available form of water in the soil. In addition,

soil hydraulic conductivity is maximal, which further accelerates water transport. This is true for all soil textures, although sand does represent an extreme, in releasing the greatest amount of water per initial drop in soil water potential. This led to the prediction that much less shallow root biomass (but possibly slightly more in soils of finer texture) is needed to extract shallow soil water than water stored in deeper soil layers (Fig. 2a). On this basis, it seems reasonable to expect that all desert plants should use this readily available form of water. However, field observations of pulse use tell a different story. First, even though the first few cm of soil are wetted by rain more frequently than any other soil layer, unshaded, shallow desert soil contains hardly any plant roots (Nobel 1989). Secondly, some desert perennials do not take up pulse water, even after large events (Flanagan *et al.* 1992). Thirdly, even among plants that do take up pulse water, many derive only a fraction of transpiration water from the shallow soil (Ehleringer *et al.* 1991). To simulate this behaviour, we gave shallow roots a smaller conductance per unit root biomass than deeper roots, but left the mechanistic explanation open. It is possible that roots near the surface have reduced conductivity because of the extreme variation in soil water potential to which they are regularly exposed. Roots may employ costly adaptations to prevent root xylem embolism, such as a greater suberization of shallow roots observed by Wan *et al.* (1994) in *Gutierrezia sarothrae*. Alternatively, shallow roots may allow embolism and accept the consequent loss of root conductivity (Tyree & Sperry 1989). Additionally, the high temperature of shallow soil in summer can greatly increase the respiration cost of growth, maintenance and repair of shallow roots (Eissenstat 1997). Either way, reduced conductance or increased maintenance costs translate directly into an increased cost for the acquisition of shallow soil water and would generate a bias for deeper roots in desert plants.

## FINAL REMARKS

Although we used an 'evolutionary' or 'genetic' algorithm to derive the vegetation types we describe above, our approach is not intended as a model of plant evolution. Actual desert plant populations evolve while experiencing a wide range of environmental conditions, whereas our derived phenotypes experienced only one condition, precisely repeated from generation to generation. So why do the derived phenotypes seem so realistic? One interpretation is that new arrivals to an arid region fine-tune pre-existing environmental preferences and thereby become 'specialists' for a select range of conditions (Rosenzweig 1995). Our approach should produce reasonable approximations to actual desert plants, as long as the environmental conditions we simulated are common enough in an ecosystem. Equally important, our approach does not downplay the role of competition and co-evolution. Even though



we did not explicitly address the effects of vegetation on soil water dynamics, these clearly exist (Schlesinger *et al.* 1987). Resident vegetation can influence the survival and consequent evolution of arrivals by modifying the pattern of water depletion from soil. The continuation of this modelling exercise will address how contrasting phenotypes compete for water and attempt to elucidate the role of rainfall variation in maintaining life form diversity in arid and semi-arid regions.

### Acknowledgements

We thank Professor D. Robinson, Dr A.J. Parsons and two anonymous reviewers for their detailed comments on earlier drafts. This work was sponsored by the Department of Energy (DEFG0395ER62123).

### References

- Amthor, J.S. (1994) Plant respiratory responses to the environment and their effects on the carbon balance. *Plant-Environment Interactions* (ed. R.E. Wilkinson), pp. 501–554. Marcel Dekker, New York.
- Brown, J.H., Valone, T.J. & Curtin, C.G. (1997) Reorganization of an arid ecosystem in response to recent climate change. *Ecology*, **94**, 9729–9733.
- Burgess, T.L. (1995) Desert grassland, mixed shrub savanna, shrub steppe, or semidesert scrub? The dilemma of coexisting growth forms. *The Desert Grassland* (eds M.P. McClaran & T.R. Van Devender), pp. 31–67. The University of Arizona Press, Tucson.
- Cable, D.R. (1969) Competition in the semidesert grass-shrub type as influenced by root systems, growth habits, and soil moisture extraction. *Ecology*, **50**, 27–38.
- Caldwell, M.M. (1994) Exploiting nutrients in fertile soil microsites. *Exploitation of Environmental Heterogeneity by Plants* (eds M.M. Caldwell & R.W. Pearcy), pp. 325–347. Academic Press, San Diego.
- Campbell, S.G. (1977) *An Introduction to Environmental Biophysics*. Springer Verlag, New York.
- Campbell, S.G. (1985) *Soil Physics with Basic Transport Models for Soil-Plant Systems*. Elsevier, Amsterdam.
- Campbell, S.G. & Norman, J.M. (1998) *Environmental Physics*, 2nd edn. Springer, New York.
- Canon, W.A. (1911) *The Root Habits of Desert Plants*. Carnegie Institution of Washington, Washington, D.C.
- Cody, M.L. (1986) Structural niches in plant communities. *Community Ecology* (eds J. Diamond & T.J. Case), pp. 381–405. Harper & Row, New York.
- Cohen, D. (1970) The expected efficiency of water utilization in plants under different competition and selection regimes. *Israel Journal of Botany*, **19**, 50–54.
- Comstock, J. & Ehleringer, J.R. (1986) Canopy dynamics and carbon gain in response to soil water availability in *Encelia frutescens* Gray, a drought-deciduous shrub. *Oecologia*, **68**, 271–278.
- Comstock, J.P. & Ehleringer, J.R. (1988) Seasonal patterns of canopy development and carbon gain in nineteen warm desert shrub species. *Oecologia*, **75**, 327–335.
- Cowan, I.R. (1965) Transport of water in the soil-plant-atmosphere system. *Journal of Applied Ecology*, **2**, 221–239.
- Cowan, I.R. & Farquhar, G.D. (1977) Stomatal functions in relation to leaf metabolism and environment. Integration of activity in the higher plant. *Proceedings of the Symposium of the Society of Experimental Biology*, **31**, 471–505.
- Cowling, R.M., Esler, K.J., Midgley, G.F. & Honig, M.A. (1994) Plant functional diversity, species diversity and

- climate in arid and semi-arid southern Africa. *Journal of Arid Environment*, **27**, 141–158.
- Dodd, M.B., Lauenroth, W.K. & Welker, J.M. (1998) Differential water resource use by herbaceous and woody plant life forms in a shortgrass steppe community. *Oecologia*, **117**, 504–512.
- Donovan, L.A. & Ehleringer, J.R. (1994) Water stress and use of summer precipitation in a Great Basin Shrub community. *Functional Ecology*, **8**, 289–297.
- Ehleringer, J.R. (1985) Annuals and perennials of warm deserts. *Physiological Ecology of North American Plant Communities* (eds B.F. Chabot & H.A. Mooney), pp. 162–180. Chapman & Hall, New York.
- Ehleringer, J.R. & Cook, C.S. (1991) Carbon Isotope Discrimination and Xylem Hydrogen Isotope Ratios in Desert Plants. *International Symposium on the Use of Stable Isotopes in Plant Nutrition, Soil Fertility and Environmental Studies*, pp. 489–497. International Atomic Energy Agency, Vienna.
- Ehleringer, J.R. & Dawson, T.E. (1992) Water uptake by plants: perspectives from stable isotope composition. *Plant, Cell and Environment*, **15**, 1073–1082.
- Ehleringer, J.R. & Mooney, H.A. (1983) Productivity of desert and Mediterranean-climate plants. *Encyclopedia of Plant Physiology: Physiological Plant Ecology IV* (eds O.L. Lange, P.S. Nobel, C.B. Osmond & H. Ziegler), New Series, Volume 12d, pp. 205–231. Springer-Verlag, Berlin.
- Ehleringer, J.R., Phillips, S.L., Schuster, W.S.F. & Sandquist, D.R. (1991) Differential utilization of summer rains by desert plants. *Oecologia*, **88**, 430–434.
- Eissenstat, D.M. (1997) Trade-offs in root form and function. *Ecology in Agriculture* (ed. L.E. Jackson), pp. 173–199. Academic Press, San Diego.
- Fernandez, O.A. & Caldwell, M.M. (1975) Phenology and dynamics of root growth of three cool semi-desert shrubs under field conditions. *Journal of Ecology*, **63**, 703–714.
- Flanagan, L.B., Ehleringer, J.R. & Marshall, J.D. (1992) Differential uptake of summer precipitation among co-occurring trees and shrubs in a pinyon-juniper woodland. *Plant, Cell and Environment*, **15**, 831–836.
- Forseth, I.N., Ehleringer, J.R., Werk, K.S. & Cook, C.S. (1984) Field water relations of Sonoran Desert annuals. *Ecology*, **65**, 1436–1444.
- Gibson, A.C. & Nobel, P.S. (1986) *The Cactus Primer*. Harvard University Press, Cambridge, Massachusetts.
- Gradmann, H. (1928) Untersuchungen über die Wasserverhältnisse des Bodens als Grundlage des Pflanzenwachstums. *Jahrbuch für wissenschaftliche Botanik*, **69**, 1–100.
- Guo, Q. & Brown, J.H. (1996) Temporal fluctuations and experimental effects in desert plant communities. *Oecologia*, **107**, 568–577.
- Guo, Q., Brown, J.H. & Valone, T.J. (2000) Abundance and distribution of desert annuals: are spatial and temporal patterns related? *Journal of Ecology*, **88**, 551–560.
- Ho, M., Roisman, R.E. & Virginia, R.A. (1996) Using strontium and rubidium tracers to characterize nutrient uptake patterns in creosotebush and mesquite. *Southwestern Naturalist*, **41**, 239–247.
- Holbrook, N.M. (1995) Stem water storage. *Plant Stems: Physiology and Functional Morphology* (ed. B.L. Gartner), pp. 151–174. Academic Press, San Diego.
- Hunt, E.R. Jr & Nobel, P.S. (1987) Non-steady-state water flow for three desert perennials with different capacitances. *Australian Journal of Plant Physiology*, **14**, 363–375.
- Jackson, R.B., Canadell, J., Ehleringer, J.R., Mooney, H.A., Sala, O.E. & Schulze, E.D. (1996) A global analysis of root distributions for terrestrial biomes. *Oecologia*, **108**, 389–411.
- Kramer, P.J. (1983) *Water Relations of Plants*. Academic Press, San Diego.



- Kramer, P.J. & Boyer, J.S. (1995) *Water Relations of Plants and Soils*. Academic Press, San Diego.
- Lin, G., Phillips, S.L. & Ehleringer, J.R. (1996) Monsoonal precipitation responses of shrubs in a cold desert community on the Colorado Plateau. *Oecologia*, **106**, 8–17.
- Linacre, E.T. (1973) A simpler empirical expression for actual evapotranspiration rates: a discussion. *Agricultural Forest Meteorology*, **11**, 451–452.
- Long, S.P. (1991) Modification of the response of photosynthetic productivity to rising temperature by atmospheric CO<sub>2</sub> concentrations: has its importance been underestimated? *Plant, Cell and Environment*, **14**, 729–739.
- Malek, E., McCurdy, G. & Giles, B. (1999) Dew contribution to the annual water balances in semi-arid desert valleys. *Journal of Arid Environments*, **42**, 71–80.
- Mooney, H.A., Ehleringer, J.R. & Berry, J.A. (1976) High photosynthetic capacity of a winter annual in Death Valley. *Science*, **194**, 322–323.
- Mulroy, T.W. & Rundel, P.W. (1977) Annual plants: adaptations to desert environments. *Bioscience*, **27**, 109–114.
- Nilson, E.T., Sharifi, M.R., Rundel, P.W., Forseth, I.N. & Ehleringer, J.R. (1990) Water relations of stem succulent trees in north-central Baja California. *Oecologia*, **82**, 299–303.
- Nobel, P.S. (1988) *Environmental Biology of Agaves and Cacti*. Cambridge University Press, New York.
- Nobel, P.S. & Sanderson, J. (1984) Rectifier-like activities of roots in two desert succulents. *Journal of Experimental Botany*, **35**, 727–737.
- Nobel, P.S. (1989) Temperature, water availability, and nutrient levels at various soil depths. Consequences for shallow-rooted desert succulents, including nurse plant effects. *American Journal of Botany*, **76**, 1486–1492.
- Noy-Meir, I. (1973) Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics*, **4**, 25–51.
- Odening, W.R., Strain, B.R. & Oechel, W.C. (1974) The effect of decreasing water potential on net CO<sub>2</sub> exchange of intact desert shrubs. *Ecology*, **55**, 1086–1095.
- Paruelo, J.M., Jobbagy, E.G., Sala, O.E., Lauenroth, W.K. & Burke, I.C. (1998) Functional and structural convergence of temperate grassland and shrubland ecosystems. *Ecological Applications*, **8**, 194–206.
- Reynolds, J.F., Virginia, R.A., Kemp, P.R., Soyza, A.G. & Tremmel, D.C. (1999) Impact of drought on desert shrubs: effects of seasonality and degree of resource island development. *Ecological Monographs*, **69**, 69–106.
- Rosenzweig, M.L. (1995) *Species Diversity in Space and Time*. Cambridge University Press, Cambridge.
- Sala, O.E., Golluscio, R.A., Lauenroth, W.K. & Soriano, A. (1989) Resource partitioning between shrubs and grasses in a Patagonian steppe. *Oecologia*, **81**, 501–505.
- Sala, O.E. & Lauenroth, W.K. (1982) Small rainfall events: an ecological role in semiarid regions. *Oecologia*, **53**, 301–304.
- Sala, O.E., Lauenroth, W.K., Parton, W.J. & Trlica, M.J. (1981) Water status of soil and vegetation in a shortgrass steppe. *Oecologia*, **48**, 327–331.
- Schlesinger, W.H., Fontayn, P.J. & Marion, G.M. (1987) Soil moisture content and plant transpiration in the Chihuahuan Desert of New Mexico. *Journal of Arid Environment*, **12**, 119–126.
- Schwefel, H.-P. (1995) *Evolution and Optimum Seeking*. John Wiley & Sons, New York.
- Shmida, A. & Burgess, T.L. (1988) Plant growth form strategies and vegetation types in arid environments. *Plant Form and Vegetation Structure* (eds M.J.A. Werger, P.J.M. v.d. Aart, H.J. During & J.T.A. Verhoeven), pp. 211–241. SPB Academic Publishing, The Hague.
- Smith, S.D., Monson, R.K. & Anderson, J.E. (1997) *Physiological Ecology of North American Desert Plants*. Springer-Verlag, Berlin.
- Smith, S.D. & Nobel, P.S. (1986) Deserts. *Photosynthesis in Contrasting Environments* (eds N.R. Baker & S.P. Long), pp. 13–62. Elsevier, Amsterdam.
- Soriano, A. & Sala, O. (1983) Ecological strategies in a Patagonian arid steppe. *Vegetatio*, **56**, 9–15.
- Sperry, J.S., Adler, F.R., Campbell, G.S. & Comstock, J.P. (1998) Limitation of plant water use by rhizosphere and xylem conductance: results from a model. *Plant, Cell and Environment*, **21**, 347–359.
- Szarek, S.R. & Woodhouse, R.M. (1977) Ecophysiological studies of Sonoran Desert plants. II. Seasonal photosynthesis patterns and primary production of *Ambrosia deltoidea* and *Oleña tesota*. *Oecologia*, **28**, 365–375.
- Thornley, J.H.M. & Cannell, M.G.R. (2000) Modelling the components of plant respiration: representation and realism. *Annals of Botany*, **85**, 55–67.
- Tilman, D. (1988) *Plant Strategies and the Dynamics and Structure of Plant Communities*. Princeton University Press, Princeton, New Jersey.
- Turner, R.M. (1990) Long-term vegetation change at a fully protected Sonoran Desert site. *Ecology*, **71**, 464–477.
- Tyree, M.T. & Sperry, J.S. (1989) Vulnerability of xylem to cavitation and embolism. *Annual Review of Plant Physiology and Plant Molecular Biology*, **40**, 19–38.
- Tyree, M.T. & Yang, S. (1990) Water-storage capacity of *Thuja*, *Tsuga* and *Acer* stems measured by dehydration isotherms. *Planta*, **182**, 420–426.
- von Caemmerer, S. & Farquhar, G.D. (1981) Some relationships between the biochemistry of photosynthesis and the gas exchange of leaves. *Planta*, **153**, 376–387.
- Walter, H. & Stadelmann, E. (1974) A new approach to the water relations of desert plants. *Desert Biology* Volume 2 (ed. R. Brown), pp. 213–310. Academic Press, New York.
- Wan, C., Sosebee, R.E. & McMichael, B.L. (1994) Hydraulic properties of shallow vs. deep lateral roots in a semi-arid shrub, *Gutierrezia sarothrae*. *Plant and Soil*, **153**, 11–17.
- Werk, K.S., Ehleringer, J.R., Forseth, I.N. & Cook, C.S. (1983) Photosynthetic characteristics of Sonoran Desert winter annuals. *Oecologia*, **59**, 101–105.

Received 22 September 2000

revision accepted 8 January 2001