

Rooting depths, lateral root spreads and below-ground/above-ground allometries of plants in water-limited ecosystems

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Summary

1 In water-limited environments, the availability of water and nutrients to plants depends on environmental conditions, sizes and shapes of their root systems, and root competition. The goal of this study was to predict root system sizes and shapes for different plant growth forms using data on above-ground plant sizes, climate and soil texture.

2 A new data set of > 1300 records of root system sizes for individual plants was collected from the literature for deserts, scrublands, grasslands and savannas with ≤ 1000 mm mean annual precipitation (MAP). Maximum rooting depths, maximum lateral root spreads and their ratios were measured.

3 Root system sizes differed among growth forms and increased with above-ground size: annuals < perennial forbs = grasses < semi-shrubs < shrubs < trees. Stem succulents were as shallowly rooted as annuals but had lateral root spreads similar to shrubs.

4 Absolute rooting depths increased with MAP in all growth forms except shrubs and trees, but were not strongly related to potential evapotranspiration (PET). Except in trees, root systems tended to be shallower and wider in dry and hot climates and deeper and narrower in cold and wet climates. Shrubs were more shallowly rooted under climates with summer than winter precipitation regimes.

5 Relative to above-ground plant sizes, root system sizes decreased with increasing PET for all growth forms, but decreased with increasing MAP only for herbaceous plants. Thus relative rooting depths tended to increase with aridity, although absolute rooting depths decreased with aridity.

6 Using an independent data set of 20 test locations, rooting depths were predicted from MAP using regression models for three broad growth forms. The models succeeded in explaining 62% of the observed variance in median rooting depths.

7 Based on the data analysed here, Walter's two-layer model of soil depth partitioning between woody and herbaceous plants appears to be most appropriate in drier regimes (< 500 mm MAP) and in systems with substantial winter precipitation.

Key-words: climate, plant growth forms, potential evapotranspiration, precipitation, root systems

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Introduction

Ecosystems in which annual evaporative demand exceeds precipitation occupy about half of the Earth's

land surface (UNEP 1992), and plant productivity in them often increases linearly with mean annual precipitation or actual evapotranspiration (Rosenzweig 1968; Chong *et al.* 1993). The availability of water to individual plants in such systems depends in part on local climatic and edaphic factors and also on the depth, lateral spread and degree of overlap of plant root systems (Casper & Jackson 1997). Actual water use also depends on plant vascular architecture and on the balance of above- and below-ground plant dimensions (West *et al.* 1999).

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Previous research in water-limited environments leaves little doubt that sizes and shapes of root systems differ among plants from arid to humid systems (Kutschera & Lichtenegger 1997). For example, plants are typically predicted to have larger root : shoot ratios in drier than in more mesic environments (Walter 1963; Pallardy 1981; Chapin *et al.* 1993). Nevertheless, absolute maximum rooting depths or lateral spreads might still be greater in wetter systems because plants are often bigger there. This distinction between absolute and relative plant dimensions is important for understanding ecological processes at different scales. For example, lateral root spreads and maximum rooting depths influence how many neighbours compete for resources and determine the potential pool of resources available to plants in an ecosystem (Caldwell & Richards 1986; Fitter *et al.* 1991; Canadell *et al.* 1996). Relationships between relative root and shoot size are important for studies of allocation and allometry in individual plants. As an example of the latter, plants of a given canopy size may need larger root systems in coarse textured soils, because such soils offer larger resistance to water flow and have smaller water-holding capacities and deeper infiltration depths (Sperry *et al.* 1998; Jackson *et al.* 2000b).

For predicting and modelling functions of natural ecosystems, plant diversity is sometimes reduced to a small number of plant functional types (Smith *et al.* 1993). Because there is little information about the functional ecology of many species, plant growth form categories are often used as proxies for such functional types (Box 1996; Sala *et al.* 1997). Data on maximum rooting depths and lateral root spreads could be useful for predicting functional differences between plant growth forms today and under future climate change scenarios. Moreover, many recent modelling studies have assumed that woody and herbaceous growth forms compete for resources in the upper soil layers, while woody plants have a larger proportion of roots in deeper layers, taking up significantly more soil water there (Jackson *et al.* 2000a). This assumption is known as the two-layer model and was first proposed by Heinrich Walter (1939) for tropical savannas, but its generality has been disputed (Seghieri 1995; Mordelet *et al.* 1997). Data on rooting depths of woody and herbaceous plants under a range of climates should be useful for determining under which climatic conditions and for which plant growth forms this model is most likely to apply.

The aim of this study, based on a new global dataset of > 1300 observations for individual plants, is to predict sizes and shapes of root systems from biotic and abiotic factors in water-limited environments. The study includes a comprehensive scaling analysis of relationships between above- and below-ground plant dimensions, to our knowledge the first such attempt.

In order to provide a framework for *a priori* predictions about relationships among climate, soil and plant dimensions, we developed a simple conceptual model

based on the assumption that roots grow only as deeply as needed to fulfil plant resource requirements. This assumption is based on the idea that shallow root systems are generally favoured over deep root systems because (a) energy costs for construction, maintenance and resource uptake are lower for shallow roots (Adiku *et al.* 2000); (b) shallow soil layers are usually less likely to be oxygen-deficient (Hillel 1998); and (c) nutrient concentrations are often greater in the upper soil layers (Jobbágy & Jackson 2001). Our conceptual model links rooting depths largely to water availability, and predicts that rooting depths increase if water is available at depth and if there is transpirational demand for it.

This simple conceptual model allows us to test a set of predictions for water-limited ecosystems. One is that maximum rooting depth will be deepest in subhumid environments where evaporative demand slightly exceeds precipitation. Shallower rooting of individual plants is predicted for both arid systems, because precipitation and water infiltration depths decline in arid systems, and for more humid ones, where water is frequently re-supplied to the upper soil layers, making deeper roots potentially less important. Another prediction for water-limited environments is that rooting depths will not be strongly related to potential evapotranspiration (PET), because water infiltration depths will be more limiting than evaporative demands. As a corollary, for a given plant size, lateral root spreads will be largest in arid environments to take advantage of relatively shallow infiltration depths in such systems.

Materials and methods

Data on rooting depths ($n = 1305$) and lateral root spreads ($n = 965$) of individual plants from water-limited ecosystems (≤ 1000 mm mean annual precipitation (MAP) and MAP : PET ratios < 1) were collected from the literature for deserts, semi-deserts, scrublands, grasslands and shrub- and tree-savannas (see Appendix 1). Within these climatic limits, the only records that were excluded from the present study were those from sites with a continuous cover of woody plants, such as forests and dense sclerophyllous shrublands, which are addressed in a separate study of rooting depths in humid to per-humid systems (Schenk & Jackson, unpublished data). We define rooting depth (D_i) of an individual plant i as the deepest soil depth reached by the roots of an individual plant (i.e. maximum rooting depth) and lateral root spread (L_i) as the maximum linear distance (one-sided) from the stem of an individual plant reached by its roots. Where available, canopy heights (H_i ; $n = 502$) and widths (W_i ; $n = 466$) were also recorded. Data were often determined from scale-drawings of whole plants or root systems. Where possible, canopy volumes were estimated assuming an ellipsoid shape: $V_i[\text{m}^3] = \pi \times H_i[\text{m}] \times (W_i[\text{m}])^2/6$. Data for D_i , L_i , H_i and W_i in the original literature almost never included error estimates, and therefore the inevitable sources of error could not be quantified.

Species were classified into seven growth forms: trees, shrubs, semi-shrubs (including suffrutescent forbs), perennial grasses, perennial herbaceous forbs, annuals and stem succulents. Shrub species that rarely reach heights above 1 m were classified as semi-shrubs, but small individuals of species that tend to grow taller than 1 m were classified as shrubs. The classifications generally followed those given in the papers; if none was provided, one was assigned based on information from local floras or databases (see below). In a few cases, some records for the same species were assigned to different growth forms because some species are polymorphic across their range, but for most species only a single record was found. Taxonomic nomenclature was updated using such databases as the IOPI Global Plant Checklist (<http://www.bgbm.fu-berlin.de/IOPI/GPC/>), the PLANTS database (USDA NRCS 2001) and local floras. We also recorded data on plant life span and growth habit (e.g. rhizomatous, stoloniferous or caespitose; stem and/or leaf succulence; prostrate or cushion habit; bulbous or tuberous morphology). For all statistical analyses, biennials and facultative annuals were lumped into their respective perennial categories and, because of limited sample sizes,

annual grasses and annual forbs were combined into one category.

Mean annual precipitation (MAP) and its seasonal distribution were recorded from each publication or, where not recorded, were estimated from the nearest available weather station. Precipitation regimes were divided into four classes: winter, summer, all year, and tropical seasonal for seasonally dry climates lacking a cold season. Temperate and subtropical precipitation regimes were classified as summer regimes when the ratio of the precipitation during the 6 warmest months of the year to that during the 6 coldest months was ≥ 1.25 , and as winter regimes when this ratio was ≤ 0.75 . Estimates for mean annual potential evapotranspiration (PET) calculated by the Penman-Monteith method were taken from the global 0.5° gridded data set of Choudhury (1997). Soil texture data were also included when provided in the papers.

Statistical analyses had to take into account several issues. Root data for different plant growth forms were not randomly distributed over the range of climates studied, some environmental variables were correlated, and certain combinations of environmental factors were underrepresented (Fig. 1). In consequence, some

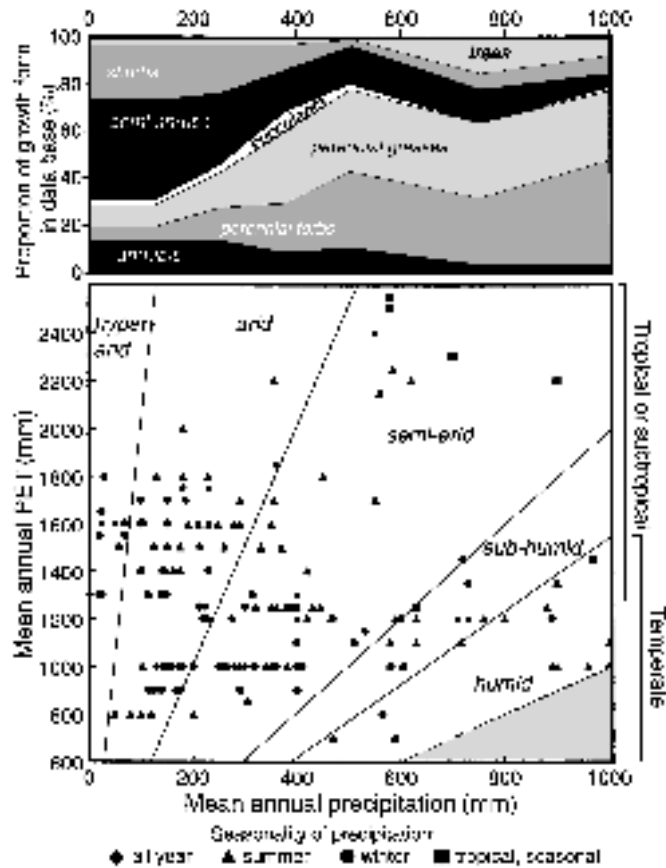


Fig. 1 Characteristics of the data base used in this study. The upper graph shows the relative proportions of plant growth forms in the data base as a function of mean annual precipitation (MAP). The bottom graph shows the distribution of root data in the data base in relation to mean annual potential evapotranspiration (PET) and MAP. Humidity zones are defined by MAP : PET ratios (UNEP 1992) as hyper-arid (MAP : PET ≤ 0.05), arid (MAP : PET > 0.05 to $= 0.2$), semi-arid (MAP : PET > 0.2 to $= 0.5$), subhumid (MAP : PET > 0.5 to $= 0.65$) and humid (MAP : PET > 0.65). The symbol shapes represent different types of seasonality as indicated in the legend.

statistical analyses were restricted to climatic ranges (as indicated below) that included a sufficient number of all categories of plant growth forms, soil texture and seasonality. Root data for all growth forms were also strongly and positively skewed (see table in Appendix 2). The data were fitted to statistical distributions using Crystal Ball software version 4.0 (Decisioneering, Denver, Colorado, USA), followed by comparisons of chi-square goodness of fit statistics between distributions. The best fits for both rooting depth and lateral root spread data were attained by fitting the data to log-normal distributions. Consequently, the best measure of central tendency for these data is the mean of the log-transformed data, or its back-transformed version, which is the geometric mean. As expected for log-normal distributions, geometric means did not differ significantly from medians (table in Appendix 2).

Statistical analyses were designed to test the effects of biotic and abiotic factors on rooting depths, lateral root spreads and their ratios. Allometric relationships between above-ground plant sizes and root system dimensions were examined by reduced major axis (RMA) regression analyses of log-transformed L_i and D_i against log-transformed canopy volumes (V_i) for growth form categories expected to differ in allometry: woody plants, forbs and grasses. The linear RMA regression procedure is recommended for allometric analyses when both the dependent and independent variables are estimated with error (Niklas 1994; Sokal & Rohlf 1995), and was calculated using the program PAST, version 0.65 (Øyvind Hammer, Palaeontological Museum, University of Oslo, Oslo, Norway).

All other statistical analyses were conducted using SYSTAT 9.0 (SPSS Science, Chicago, Illinois, USA), with data for D_i , L_i and L_i/D_i log-transformed to normalize the distributions. Data for MAP, PET and canopy volumes were also log-transformed to reduce positive skew and variance in the data. All parametric analyses of root system dimensions as a function of climate excluded the MAP * PET interaction term, because its inclusion did not significantly improve the models and caused problems of multicollinearity among MAP, PET and MAP * PET (Zar 1996). Temperature was also not included as a climatic variable because it is highly confounded with PET (Thorntwaite 1948; Budyko 1974).

To quantify relationships of root system dimensions with climate, the variables L_i , D_i and L_i/D_i were analysed in linear regressions that included either MAP or MAP and PET as independent variables. Analyses were restricted to climates with > 50 mm MAP because few data were available from extreme, drier climates. Goodness of fit for regressions containing only MAP as the independent variable was compared with regressions with both MAP and PET by comparing their adjusted r^2 values. To estimate differences in overall rooting depths between humidity zones, we combined D_i values for all growth forms for each humidity zone (Fig. 1; UNEP 1992) and calculated their geometric

means and 95% confidence intervals (CI95%). Stem succulents were not included in these analyses because data for them were available from only a very limited range of climatic conditions.

Effects of the seasonality of the precipitation regime on L_i , D_i and L_i/D_i in temperate and subtropical environments were analysed in generalized linear models containing seasonality (winter, all year, summer), growth form, MAP, PET and interaction terms (excluding MAP * PET) as independent variables. These analyses were restricted to climates with > 50 mm and < 500 mm MAP, because data sets with summer rainfall regimes were scarce from drier climates and over-represented from wetter climates. Tropical climates were excluded from these analyses because they normally lack a cold season. Significant effects of seasonality were further examined by comparing root dimensions for each plant growth form in Bonferroni adjusted multiple pairwise comparisons between seasonality categories.

The prediction that allometries between above- and below-ground plant sizes change along climatic gradients was examined in multiple, linear regressions with below-ground to above-ground size ratios as dependent variables and MAP and PET as independent variables. The two allometric ratios examined were the rooting depth/canopy volume ($D_i : V_i$) and lateral root spread/canopy volume ($L_i : V_i$) ratios for three broad growth form categories: forbs, grasses and woody plants. Both ratios were log-transformed for the analyses.

To examine effects of soil texture on the relationship between root system and canopy size, the log-transformed allometric ratios $D_i : V_i$ and $L_i : V_i$ were further analysed in generalized linear models containing the independent variables soil texture, growth form (forbs, grasses, woody plants), MAP, PET, and all interaction terms except those containing MAP * PET (see above). Soil texture classes were reduced to two broad categories (coarse = gravel, sand to loamy sand; fine = sandy loam and finer) to ensure adequate sample sizes of all growth forms over the entire climatic gradient.

Because MAP and plant growth form are likely to be factors that are strongly related to absolute rooting depths in water-limited ecosystems, these variables were chosen to develop predictive rooting depth models. The models were tested against geometric means of rooting depths (D_i) calculated for 20 geographical test locations at which more than 15 rooting depths for individual plants of different species had been measured. Data from these test locations were not used anywhere in model development. The geometric mean (or median) of individual plant rooting depths measured in a given ecosystem may be viewed as an estimate for a geometric mean (or median) ecosystem rooting depth (D_e).

The models were parameterized by linear regression of D_i against MAP for three plant growth form categories: annuals, herbaceous perennials and woody perennials (excluding trees and succulents, which did not

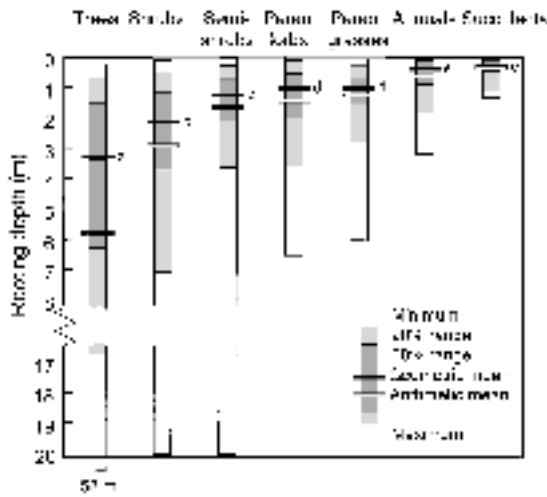


Fig. 2 Maximum rooting depths of plant growth forms. Geometric means marked by different letters were significantly different according to one-way ANOVAs (see table in Appendix 2 for statistical parameters).

occur at any of the test sites). These three categories were chosen because the limited data set ($n = 803$) used to develop these models did not allow us to distinguish between perennial grasses and forbs or between shrubs and semi-shrubs. Predicted rooting depths for the test locations were calculated for each growth form as a function of MAP, and the geometric mean ecosystem rooting depth D_e for each location was calculated by weighting the estimated D_i for each growth form by the number of replicates from that growth form originally measured at the site. Predictions and measurements were compared by calculating the r^2 coefficient to determine the percentage of the variance explained by the model. We also examined whether modelled and measured data both showed the same relationship with MAP. Modelled and measured geometric means of ecosystem rooting depths were linearly regressed against MAP, and regression slopes and intercepts were compared by analysis of covariance (Sokal & Rohlf 1995).

Data from humid sites with MAP : PET ratios ≥ 0.75 were not used for model development because data from such sites were few (Fig. 1) and because none of the 20 test locations had such a humid climate.

To test whether plants from some families are more likely to be either more shallowly or more deeply rooted than the average herbaceous or woody plant, we compared log-transformed D_i for families against log-transformed D_i for the whole data set minus the family being tested. These comparisons were conducted separately for woody and herbaceous plants and were restricted to families that had at least 20 data sets of D_i in the category (woody/herbaceous) that was analysed. Comparisons were done by t -tests and P -values were adjusted for multiple comparisons using the modified Bonferroni procedure of Jaccard & Wan (1996).

Results

Absolute rooting depths (D_i) and lateral root spreads (L_i) generally increased for plant growth forms as their size and life span increased (Figs 2 and 3, table in Appendix 2), with values greatest in trees and smallest in annuals. Perennial grasses and forbs did not differ in root dimensions, and shrubs had significantly larger D_i and L_i than semi-shrubs. Succulents had very shallow rooting depths but large lateral root spreads (Figs 2 and 3). There were also clear differences among growth forms in the shape of the root systems, with succulents having the largest ratios of lateral spread to rooting depth ($L_i : D_i$), a geometric mean of 4.5 (vs. $c. 3$ for trees, $c. 1$ for shrubs, $c. 0.5$ for semishrubs, and $0.3-0.35$ for all herbaceous plants, see table in Appendix 2).

Differences in root system sizes (D_i and L_i) were explained partly by above-ground size differences (V_i), with significant correlations for woody plants, forbs and grasses (Fig. 4). Differences in canopy sizes accounted for $c. 10\%$ of the variance of D_i in woody plants, $c. 41\%$ in forbs and $c. 24\%$ in grasses (Fig. 4), and rooting depths increased more strongly (as measured

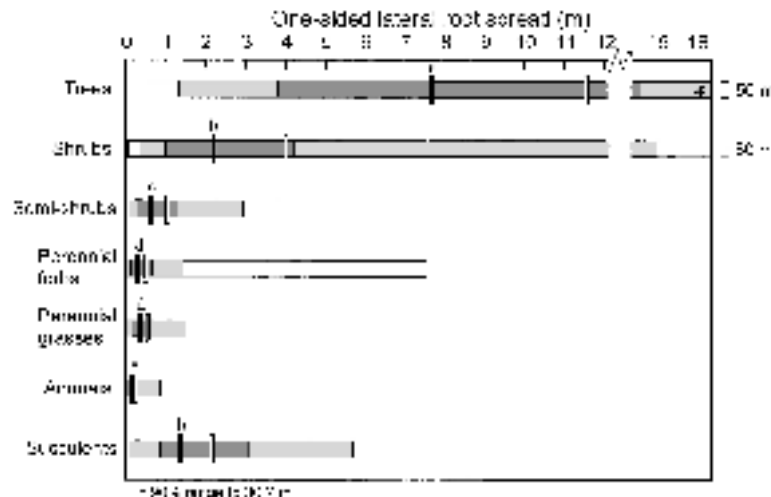


Fig. 3 Lateral root spreads of plant growth forms. Key and statistical convention as in Fig. 2.

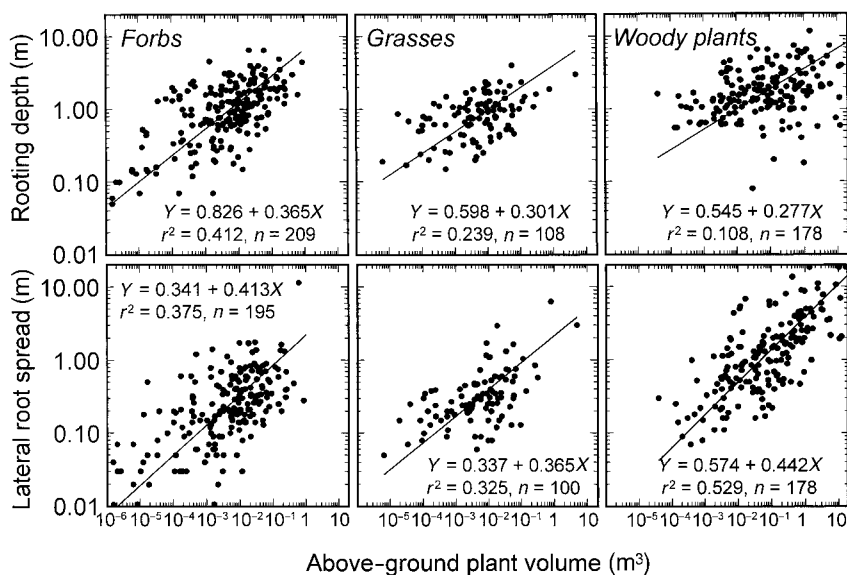


Fig. 4 Allometric relationships between above-ground canopy volume and root dimensions (maximum rooting depth and lateral root spread). The regression lines and equations are based on reduced major axis regressions performed on log-transformed data, using the general equation $\log_{10}(D_i \text{ or } L_i) = a + b \log_{10}(V_i)$, with D_i and L_i expressed in m and V_i in m³.

Table 1 Regression parameters for the relationships between root system dimensions, mean annual precipitation (> 50 to ≤ 1000 mm) and mean annual potential evapotranspiration. The parameters are for the linear equations $\log_{10} Y = a_1 + b_1 \log_{10} \text{MAP}$ and $\log_{10} Y = a_2 + b_2 \log_{10} \text{MAP} + c \log_{10} \text{PET}$, where Y is the respective root variable (rooting depth (in m), lateral root spread (in m), or lateral spread/rooting depth), MAP is mean annual precipitation in mm, and PET is mean annual evapotranspiration in mm. Statistically significant parameters are marked by * ($P < 0.05$), ** ($P < 0.01$) or *** ($P < 0.001$)

	a_1	b_1	r^2	a_2	b_2	c	r^2
Rooting depth							
Annuals	-2.312	0.809***	0.265***	-0.713	0.720***	-0.449	0.267***
Perennial forbs	-1.603	0.629***	0.136***	-2.590	0.620***	0.334	0.137***
Perennial grasses	-1.053	0.409***	0.111***	-2.662	0.392***	0.543**	0.135***
Semi-shrubs	-0.316	0.178*	0.018*	1.280	0.157*	-0.504**	0.041**
Shrubs	-0.053	0.158	0.007	1.192	0.152	-0.395	0.014
Trees	1.000	-0.208	0.019	4.967	-0.086	-1.323*	0.099*
Lateral root spread							
Annuals	-3.096	0.919***	0.253***	-4.301	0.991***	0.336	0.248***
Perennial forbs	-1.029	0.196	0.009	-3.057	0.160	0.702	0.019
Perennial grasses	-0.020	-0.180	0.008	-4.304	-0.168	1.395***	0.136***
Semi-shrubs	1.273	-0.638***	0.171***	0.524	-0.646***	0.252	0.171***
Shrubs	0.279	0.020	0.000	-2.426	-0.046	0.918*	0.049
Trees	-0.089	0.383	0.057	-1.998	0.224	0.708	0.082
Lateral : depth ratio							
Annuals	-0.684	0.056	0.000	-2.026	0.136	0.374	0.000
Perennial forbs	0.585	-0.434***	0.064***	-0.448	-0.453***	0.358	0.065***
Perennial grasses	1.040	-0.589***	0.132***	-1.808	-0.581***	0.928**	0.183***
Semi-shrubs	1.316	-0.701***	0.192***	-0.414	-0.721***	0.583**	0.208***
Shrubs	0.679	-0.287	0.008	-4.286	-0.364	1.651***	0.121***
Trees	-1.405	0.747	0.108	-4.606	0.447	1.213	0.143

by the adjusted r^2 -values) with canopy size in forbs than in grasses or woody plants. Canopy sizes accounted for c . 53% of the variance of L_i in woody plants, c . 38% in forbs and c . 33% in grasses (Fig. 4). Thus in woody plants, the relationship between V_i and L_i was much stronger than the relationship between V_i and D_i .

Absolute rooting depths showed a number of significant relationships with climatic variables. Positive relationships between D_i and mean annual precipita-

tion (MAP) were observed for all growth forms except shrubs and trees (Table 1). Rainfall was a much stronger predictor for D_i than mean annual evapotranspiration (PET) in all growth forms, as adding PET into the regression models increased adjusted r^2 values by only 0.001–0.033 (Table 1). Annuals had the strongest and steepest relationships of D_i with MAP, and woody plants had the weakest. Positive relationships between PET and D_i were observed in perennial grasses

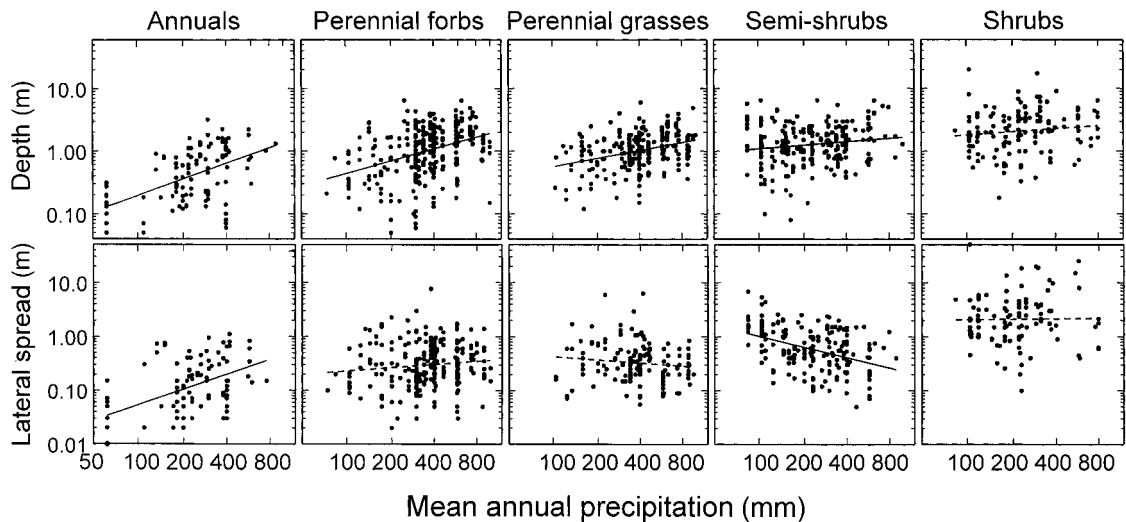


Fig. 5 Absolute maximum rooting depths and lateral root spreads for five plant growth form categories as a function of mean annual precipitation (MAP). Significant linear trends are indicated by solid regression lines, non-significant ones by dashed lines. Regression parameters are listed in Table 1. Data for trees are not shown, because the sample size for trees was rather small and because their root system sizes showed no significant relationships with MAP.

and forbs, while a negative relationship was observed in woody plants (Table 1).

Geometric means of absolute rooting depths increased from hyper-arid to the subhumid climatic zones for all growth forms combined (hyper-arid: 0.67 m, CI95% 0.46–0.93 m; arid: 0.96 m, CI95% 0.86–1.06 m; semiarid: 1.08 m, CI95% 1.00–1.17 m; subhumid: 1.63 m, CI95% 1.47–1.80 m). Geometric mean rooting depths were also more shallow in the humid zone (1.24 m, CI95% 1.02–1.48 m) than in the subhumid zone. These results support the prediction that rooting depths in water-limited ecosystems should be deepest in subhumid climates.

Lateral root spreads had generally weaker relationships with climatic variables than did maximum rooting depths (Table 1, Fig. 5). Significant relationships were not detected between L_i and MAP in perennial grasses, forbs and shrubs, but L_i increased with increasing MAP for annuals (perhaps paralleling a size increase above-ground) and decreased for semi-shrubs. Lateral root spreads increased with increasing PET in perennial grasses and shrubs (Table 1). Root system shapes also changed along climatic gradients, as $L_i : D_i$ ratios decreased with increasing MAP in perennial herbaceous plants and semi-shrubs, and increased with increasing PET in perennial grasses, semi-shrubs and shrubs (Table 1). This suggests that general shapes of root systems tend to change from relatively shallow and wide in arid climates to deeper and narrower in subhumid to humid climates.

The seasonality of precipitation affected absolute rooting depths (D_i) of shrubs very differently than other growth forms (Fig. 6). Only shrubs had shallower rooting depths in environments dominated by summer precipitation compared with non-seasonal or winter precipitation ($P < 0.05$; Fig. 6). No significant relationship between D_i and seasonality was observed for

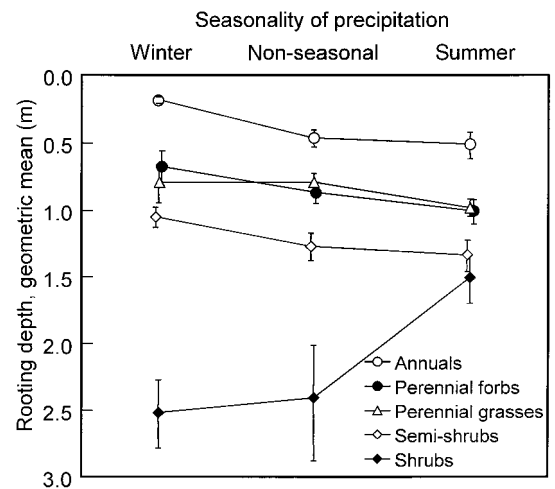


Fig. 6 Geometric means (± 1 SE) of absolute maximum rooting depths for five plant growth form categories in climates with > 50 and < 500 mm mean annual precipitation (grouped by seasonality). See Table 2 for the corresponding statistical analysis.

herbaceous perennials and semi-shrubs, while annuals were slightly more deeply rooted in summer rainfall climates ($P < 0.05$). In net effect, overall differences in rooting depths between growth forms were least pronounced in summer rainfall climates and most pronounced in winter rainfall climates, a result with implications for climate change scenarios (Fig. 6). Seasonality did not appear to have an effect on lateral root spreads or on root system shapes (Table 2).

Analyses of relative rooting depths showed that herbaceous plants of a given canopy size tended to have deeper roots in drier than in wetter climates. The allometric size ratios $D_i : V_i$ and $L_i : V_i$ decreased with increasing MAP in forbs and grasses. In contrast, for woody plants, $D_i : V_i$ increased with increasing MAP and $L_i : V_i$ showed no significant relationship with

Table 2 Statistical parameters of generalized linear models of root dimensions as a function of plant growth form (annual, perennial forb, perennial grass, semi-shrub, shrub), seasonality of rainfall (winter, even, summer), MAP and mean annual PET. Models were developed for climates ranging from > 50 mm to < 500 mm MAP

Model: r^2 of model	Rooting depth 0.369				Lateral root spread 0.537				Lateral root spread/rooting depth 0.300			
	SS	d.f.	F-ratio	P	SS	d.f.	F-ratio	P	SS	d.f.	F-ratio	P
Growth form	1.446	4	3.211	0.013	0.162	4	0.262	0.902	1.065	4	1.887	0.111
Seasonality	0.441	2	1.958	0.142	0.273	2	0.885	0.413	0.244	2	0.865	0.422
MAP	0.924	1	8.213	0.004	0.026	1	0.166	0.684	0.093	1	0.658	0.418
PET	0.748	1	6.648	0.010	0.015	1	0.096	0.757	1.353	1	9.582	0.002
Seasonality \times growth form	2.316	8	2.572	0.009	0.408	8	0.330	0.954	2.066	8	1.830	0.069
Growth form \times MAP	1.004	4	2.230	0.064	1.563	4	2.534	0.039	1.820	4	3.224	0.012
Growth form \times PET	1.626	4	3.612	0.006	0.473	4	0.767	0.547	0.803	4	1.422	0.225
Seasonality \times MAP	0.244	2	1.084	0.339	0.116	2	0.375	0.688	0.444	2	1.573	0.208
Seasonality \times PET	0.441	2	1.958	0.142	0.366	2	1.186	0.306	0.349	2	1.234	0.292
Seasonality \times growth form \times MAP	1.613	8	1.791	0.075	1.254	8	1.017	0.422	2.772	8	2.455	0.013
Seasonality \times growth form \times PET	2.247	8	2.496	0.011	0.446	8	0.361	0.941	2.221	8	1.967	0.048
Error	90.391	803			97.474	632			88.505	627		

Table 3 Regressions for the relationships between allometric ratios (below-ground to above-ground plant size), MAP (mm) and mean annual PET (mm). The two allometric ratios were the rooting depth to canopy volume ratio ($D_i : V_i$ in m^{-2}) and the lateral root spread to canopy volume ratio ($L_i : V_i$ in m^{-2}). The regression parameters listed are for linear equations of the format $\log_{10} Y = a + b \log_{10} MAP + c \log_{10} PET$, where Y is the respective allometric ratio. The regression coefficients a, b and c are listed with their standard errors. Allometric ratios were calculated separately for woody and herbaceous plants. Regression coefficients marked by different letters were significantly different between growth forms at $P < 0.05$. All regressions and regression coefficients were significantly different from zero at $P < 0.05$, except regression coefficient b for $L_i : V_i$ in woody plants

Allometric ratio	a	b	c	adjusted r^2	n
$D_i : V_i$					
Forbs	11.12 ^a \pm 2.64	-0.62 ^b \pm 0.23	-2.39 ^a \pm 0.78	0.046	208
Grasses	12.94 ^a \pm 3.09	-1.75 ^b \pm 0.42	-2.05 ^a \pm 0.82	0.132	108
Woody plants	7.87 ^a \pm 2.27	0.61 ^a \pm 0.22	-2.56 ^a \pm 0.69	0.129	178
$L_i : V_i$					
Forbs	12.72 ^a \pm 2.69	-0.90 ^b \pm 0.23	-2.88 ^a \pm 0.79	0.084	194
Grasses	14.73 ^a \pm 2.95	-2.11 ^c \pm 0.40	-2.47 ^a \pm 0.77	0.210	100
Woody plants	6.69 ^a \pm 1.86	0.09 ^a \pm 0.18	-1.86 ^a \pm 0.56	0.057	178

MAP (Table 3). Both of the allometric ratios $D_i : V_i$ and $L_i : V_i$ decreased with increasing PET in all growth forms (Table 3), suggesting that plants of a given above-ground size tend to have smaller root systems in warmer climates (high PET) than in colder climates. The fact that both allometric ratios changed with MAP and PET also suggests that the effects of climate on plant size differ above- and below-ground.

There was no evidence for effects of soil texture on allometric below-ground to above-ground size ratios (data not shown). Maximum rooting depths and lateral root spreads also did not differ consistently for plants of a given size growing in soils of different texture.

Regression models were developed to predict geometric mean rooting depths for plants co-occurring at each of 20 geographical locations. The regression equations were calculated from all data (sample sizes n given below) excluding those from these 20 locations (see Methods). These models included only precipitation and broad growth form categories (annual, herbaceous perennial, woody perennial) as independent variables. The equations were:

Annual forbs and grasses: $\log_{10} D_i = -1.9507 + 0.6730 \log_{10} MAP$; $n = 57$, adj. $r^2 = 0.340$.

Perennial forbs and grasses: $\log_{10} D_i = -1.6641 + 0.6621 \log_{10} MAP$; $n = 212$, adj. $r^2 = 0.150$.

Woody shrubs and semi-shrubs: $\log_{10} D_i = -0.3857 + 0.2412 \log_{10} MAP$; $n = 282$, adj. $r^2 = 0.044$.

These models predicted geometric mean rooting depths at the 20 test locations quite well (Fig. 7). The general trend of increasing rooting depths with increased precipitation was predicted accurately, as neither the slopes (ANCOVA, sum of squares 0.0081, d.f. = 1, F -ratio = 0.0698, $P = 0.793$) nor the intercepts (ANCOVA, sum of squares 0.0010, d.f. = 1, F -ratio = 0.0089, $P = 0.925$) differed between linear regressions of measured and modelled data against MAP (Fig. 7). A comparison of predicted versus modelled data by linear regressions yielded a goodness of fit of $r^2 = 0.623$ ($n = 20$; F -ratio = 29.682; $P < 0.0001$). This result provides further evidence that precipitation is an important factor governing rooting depths of plant growth forms in water-limited environments; it also suggests that these regression equations may be used to

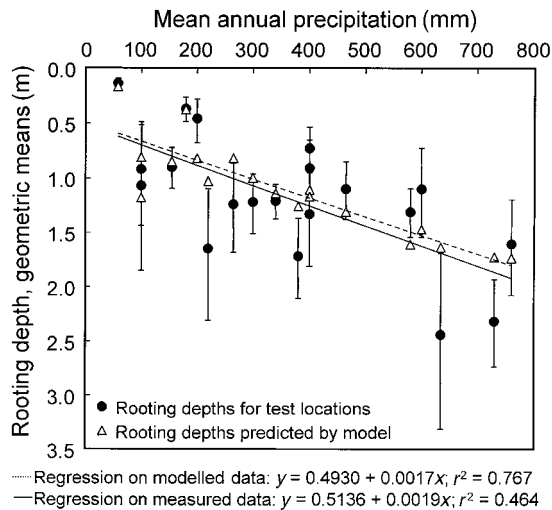


Fig. 7 Geometric means of absolute maximum rooting depths for 20 geographical locations as a function of mean annual precipitation. Error bars represent 95% confidence intervals for the geometric means. Also shown are the geometric means predicted for each site by a regression model (see Results).

predict geometric means of plant rooting depths for sites in climates with MAP : PET ratios of < 0.75 .

Herbaceous plants from three plant families were especially likely to be deeply rooted. The geometric mean D_i for all herbaceous plants in the data base was 0.85 m, compared with the following values for the more deeply rooted families: Fabaceae ($D_i = 1.27$ m; $n = 57$; $P = 0.0012$), Asteraceae ($D_i = 1.17$ m; $n = 17$; $P = 0.0003$), and Poaceae ($D_i = 1.02$ m; $n = 262$; $P < 0.0001$) (with P -values indicating statistical differences from the mean for all plants excluding those being tested). For woody plants, the geometric mean D_i in the entire data set was 1.47 m, and only woody plants in the Mimosaceae were significantly more deeply rooted than this value (geom. mean $D_i = 3.50$ m; $n = 38$; $P = 0.0012$). Woody plants from two families were more shallowly rooted than the geometric mean for all woody plants: Asteraceae ($D_i = 1.24$ m; $n = 132$; $P = 0.034$) and Cactaceae ($D_i = 0.29$ m; $n = 30$; $P < 0.0001$).

Discussion

This study sheds some light into the dark world of roots by finding that a large proportion of the variance in root system sizes can be predicted from above-ground plant sizes, growth form and climatic variables. The data also generally supported our predictions generated by a simple conceptual model relating rooting depths to climate: in water-limited environments rooting depths were more strongly related to mean annual precipitation (MAP) than to potential evapotranspiration (PET), and absolute rooting depths were deepest in subhumid environments. The observed relationships between root system sizes and climatic variables differed dramatically between plant growth forms.

ROOT SYSTEMS OF DIFFERENT GROWTH FORMS

Not surprisingly, maximum rooting depths (D_i) and lateral root spreads (L_i) of different plant growth forms were positively related to their typical above-ground sizes, with trees having the largest root systems and annuals the smallest (Figs 2 and 3). Root systems also differed between shrubs and semi-shrubs, two growth forms that are often not distinguished in the ecological literature, with shrubs tending to have deeper root systems with lateral spreads similar to depths, and semi-shrub root systems tending to be shallower and spreading only to about half their depths (table in Appendix 2). Perennial grasses and forbs, however, did not differ in root system dimensions (Figs 2 and 3), although the former are fibrous-rooted and the latter tend to be tap-rooted, nor in their relationships between canopy size and root dimensions (Fig. 4), nor in their responses to the environmental factors we analysed (Table 1, Fig. 5). Such generalizations notwithstanding, we observed much variability within growth forms. Locally, plant rooting depths may differ substantially from the global patterns identified here.

The data on lateral root spreads (Fig. 3, table in Appendix 2) may be useful for estimates of below-ground competition and the area over which plants interact with neighbours (Casper & Jackson 1997). Such plant 'neighbourhoods' were typically between 2 and 16 m in radius for shrubs and trees, but only 0.10–0.60 m for herbaceous plants, with semi-shrubs and stem succulents intermediate. Most (95%) herbaceous perennials have lateral root spreads of ≤ 1.5 m, and 95% of all shrubs have lateral root spreads of ≤ 15 m (Fig. 3), and plants would potentially compete below-ground with other plants of the same growth form over twice these distances.

The relatively strong allometric relationships between above-ground plant size and root system dimensions (Fig. 4) are probably largely due to the fact that larger plants need more roots to supply a greater leaf area with water and nutrients and, *vice versa*, that the maintenance of large root systems requires a larger leaf area. However, a biomechanical model developed by Ennos (1993) also predicts that superficial lateral roots are more efficient in anchoring plants with large above-ground sizes than deep, vertical roots, which fits with our observation that lateral root spreads in woody plants tended to be more strongly related to above-ground plant size than rooting depths (Fig. 4).

ABSOLUTE ROOTING DEPTHS AND CLIMATE

Maximum rooting depths showed strong, positive relationships with MAP for all growth forms except shrubs and trees (Table 1). Moreover, as predicted by our conceptual model, maximum rooting depths for all growth forms combined tended to be shallowest in arid regions and deepest in subhumid regions. The relationship

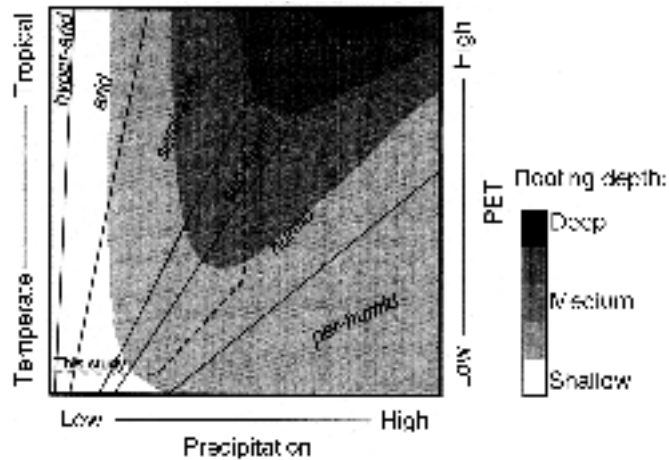


Fig. 8 Conceptual model of the hypothesized relationships between climate and absolute maximum rooting depths. The range of climates covered in this study is indicated by the dashed line, and humidity zones correspond to those in Fig. 1 (UNEP 1992).

between absolute rooting depths and MAP was strong enough that it could be used successfully in a predictive regression model explaining 62% of the variance observed among rooting depths for arid to subhumid climates. The remaining percentage of the variance is likely to be due to such factors as species composition, the long-term and seasonal variability of precipitation, soil characteristics and site history.

This increase of absolute rooting depths with MAP apparently contradicts the often-held assumption that plants tend to be most deeply rooted in the driest environments, but the distinction between relative and absolute rooting depths is critical. For a given canopy size, herbaceous plants do have deeper maximum rooting depths in drier environments (Table 3), but absolute rooting depths increase along the gradient from arid to humid environments as a result of the increasing trend in above-ground plant size. Roots, however, are not simply deeper in humid climates 'because the plants are bigger', as plant sizes above and below ground respond differently to climatic variables, and above- to below-ground allometries therefore change along the gradient from arid to humid climates (Table 3 and discussion below). Furthermore, deeply rooted shrubs and trees were found in all climates, probably due to phreatophytic species occurring wherever groundwater is within the reach of their roots, independent of climate. It should also be noted that only maximum rooting depths of individual plants were measured and that depths at which plants have 50% or 95% of their root biomass are significantly deeper in drier than in humid environments (Schenk & Jackson 2002).

The close relationship between absolute rooting depths and MAP in the environments examined suggests that infiltration depths may limit rooting depths (Dobrowolski *et al.* 1990; Breman & Kessler 1995; Reynolds *et al.* 2000). Infiltration depths depend on such soil factors as topography, texture, organic matter content and structure, as well as the seasonal distribution of rainfall. A simple calculation based on an

average field capacity of *c.* 30% for a loamy soil (Patterson 1990) suggests that long-term mean infiltration depths may rarely exceed 0.3 m in climates with about 100 mm of MAP and 2.3 m in climates with about 700 mm precipitation. This compares well with the geometric mean rooting depths observed for herbaceous perennials of 0.5 m in climates with 50–150 mm precipitation and of 2.1 m in climates with 650–750 mm precipitation. In contrast, trees and shrubs tend to have rooting depths of ≥ 2 m in all water-limited environments. Their deeper roots may tap into ground water or may access water either accumulated at depth during unusually wet years or transported laterally across the landscape (Jackson *et al.* 1999). It is important to remember, however, that root channels and macro-pores are likely to act as conduits for water recharge deeper than predicted by simple infiltration models.

The observed relationships between climate and absolute rooting depths supported our prediction that rooting depths should be greatest in subhumid climates, where there is a seasonal surplus of water that can accumulate at depth and a seasonal evaporative demand for that water during the dry season (see model in Fig. 8). Rooting depths in humid to per-humid (MAP \gg PET) environments, which lie outside the scope of this study, are likely to be more shallow, because water there tends to be available in the upper soil horizons throughout the growing season. The data also support our prediction that, for the range of water-limited environments considered in this study, absolute rooting depths would not be strongly related to PET. Positive relationships between absolute rooting depths and PET are more likely to be found in climates where precipitation equals or exceeds evaporative demands. Based on all of these considerations, one would expect the greatest rooting depths ($\gg 2$ m) to occur in sub-humid, subtropical to tropical regions (Fig. 8). Such regions were largely outside the limits of this study, but data sets of rooting depths from such regions in Africa

(Savory 1963), India (Howard 1925) and south-eastern Brazil (Villares *et al.* 1953) all support this prediction. A major problem of root studies in subtropical and tropical areas is that sample depths often appear to be insufficient for estimating maximum rooting depths there (Jackson *et al.* 1996; Schenk & Jackson 2002). One study that documented a root profile in a tropical forest to great depths (Nepstad *et al.* 1994) found roots at 18 m depth. This study was conducted in a subhumid to humid tropical forest with a 5-month-long dry season, which are conditions for which our conceptual model predicts very deep roots.

Shrubs were found to be more deeply rooted in climates with substantial winter precipitation than in climates with summer rainfall regimes. This supports a prediction that a significant proportion of roots should be located more deeply in the soil in winter- than in summer-rainfall climates (Fernandez & Caldwell 1975; Ehleringer *et al.* 1999; Schwinning & Ehleringer 2001). It is perhaps not surprising that this effect was only apparent in shrubs, whose maximum rooting depths exceed those of semi-shrubs and herbaceous plants (Fig. 2). Winter precipitation tends to infiltrate more deeply than summer rainfall, which is subject to immediate evaporative demand. Our data suggest that it may be mainly shrubs that access deep water stored during the cold season, and that soil depth partitioning between growth forms may be least pronounced in summer-rainfall regimes (Fig. 6).

Climate change may affect soil water availability, rooting depths and vegetation structure. For example, a change from largely monsoonal summer rainfall to a climate with predominant winter precipitation could potentially convert vegetation dominated by grasses and shallowly rooted woody species to one dominated by more deeply rooted woody species. There is some evidence for such vegetation change in the southwestern USA (Turner 1990; Brown *et al.* 1997), but it is difficult to disentangle the diverse causes of such changes. Sudden shifts in species dominance in response to changes in the precipitation regime are most likely where species that differ greatly in rooting depths are already present in the vegetation.

BELOW-GROUND/ABOVE-GROUND ALLOMETRIES AND ENVIRONMENTAL FACTORS

Rooting depths and lateral root spreads increased with above-ground canopy size, but the allometric relationship between above- and below-ground plant sizes varied along climatic gradients. Herbaceous plants of a given size had larger root systems in dry climates than in wet climates, in contrast to woody plants (Table 3). A common prediction in the ecological literature about the relationship between root : shoot (R : S) ratios and climate is that R : S ratios increase with increasing aridity (e.g. Walter 1963; Pallardy 1981; Chapin *et al.* 1993). This prediction is based partly on the observation

from experiments that relative carbon allocation to roots tends to increase with decreasing water supply (Wilson 1988), and partly based on optimization models (e.g. Thornley 1972; Friedlingstein *et al.* 1999). Our data support this prediction only for herbaceous plants (Table 3).

Herbaceous plants of a given canopy size had larger lateral root spreads in dry than in more mesic environments (Table 3). Absolute lateral root spreads of semi-shrubs also increased with decreasing MAP (Table 1). Large lateral root spreads in dry environments may be related to the low plant densities found there. Lateral roots could explore the soil in interspaces between plants, which would enable plants to maximize uptake of shallow soil water from small rainfall events (Walter 1963; Sala & Lauenroth 1982).

Plants in warmer climates with higher PET tended to have smaller root systems for a given canopy size than plants in colder climates with lower PET (Table 3). Previous studies also found that root biomass per surface area and root : shoot biomass ratios tended to be lower in tropical than in temperate regions (Cairns *et al.* 1997; Jackson *et al.* 1997). This pattern may be more due to direct effects of temperature rather than via PET. Root : shoot biomass ratios tend to be high under suboptimal growing temperatures (Davidson 1969), and freezing is more likely to reduce canopy sizes above ground than below ground (Woodward 1988; Nilsson & Orcutt 1996), as frost in temperate regions rarely extends deeply into the soil. Furthermore, root turnover tends to increase exponentially with temperature (Gill & Jackson 2000), suggesting that root system sizes in warmer climates may be limited by shorter root life spans.

Soil texture did not appear to affect below-ground : above-ground size ratios as predicted (data not shown). Root systems may respond to soil texture by changes in root density rather than by changing maximum depths and lateral spreads. In a previous study we found that sandy soils had a larger proportion of roots at depth than loamy or clayey soils in water-limited environments, including semi-desert shrublands, deserts and dry tropical savannas (Jackson *et al.* 2000b; Schenk & Jackson 2002). Rather than shifting maximum rooting depths downwards as texture changes from fine to coarse, plants in water-limited environments may shift the zone of maximum root activity downwards in the profile.

ECOSYSTEM ROOTING DEPTHS ALONG A PRECIPITATION GRADIENT

In water-limited environments, rooting depths (D_r) within plant growth forms tend to increase along a gradient of increasing rainfall (Fig. 5), but ecosystem-level rooting depths may also be affected by the change in the proportion of deeply and shallowly rooted growth forms along such a gradient. An increasing proportion of shrubs and semi-shrubs with increasing

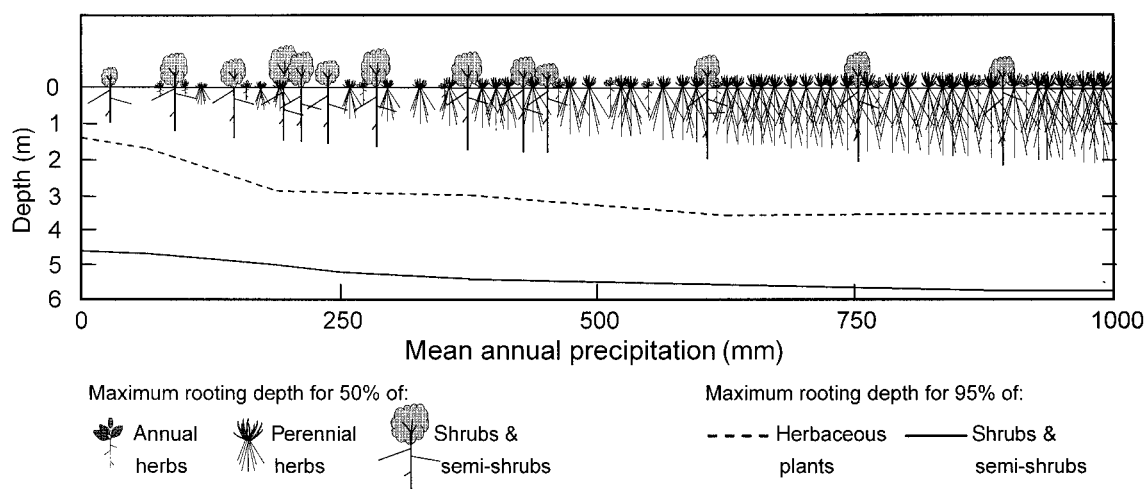


Fig. 9 Schematic diagram of the relationship between mean annual precipitation (MAP) and ecosystem-level rooting depths (D_e). The rooting depths that are illustrated as schematic drawings of individual plants approximate median ecosystem rooting depths for three broad growth form categories along the MAP gradient. Estimates of maximum rooting depths were calculated for five precipitation ranges: ≤ 125 mm, > 125 to ≤ 250 mm, > 250 to ≤ 500 mm, > 500 to ≤ 750 mm, and > 750 to ≤ 1000 mm, and only 5% of plants in that category had deeper roots than indicated by these lines. Also shown are the changing plant density and changing proportions of annual herbs, perennial herbs and semi-shrubs/shrubs along the gradient, from deserts and shrublands dominated by woody plants to grasslands dominated by herbaceous plants.

aridity has been observed in many biogeographical studies (e.g. Raunkier 1934; Arroyo *et al.* 1988; Paruelo & Lauenroth 1996; Paruelo *et al.* 1998) and is reflected in our data base (Fig. 1). Large-scale patterns in ecosystem-level rooting depths (D_e) resulting from changes in maximum rooting depths (D_i) of individual plants and in growth form dominance along a hypothetical precipitation gradient are illustrated in Fig. 9. Along this precipitation gradient, shrubs and semi-shrubs tend to dominate the driest ecosystems, where they are typically more deeply rooted than herbaceous plants. Their proportion in the vegetation generally decreases with increasing precipitation. Rooting depths of herbaceous plants are on average shallower than those of woody plants, but this difference decreases along the gradient from arid to more humid environments. Thus, at the humid end of the gradient, where herbaceous plants are more abundant, their geometric mean rooting depth may almost be as deep as that of woody plants (Fig. 9) and median ecosystem rooting depths ($D_{e, median}$) may not change significantly, as deeply rooted plants dominate at either end of the gradient (Fig. 9).

Maximum ecosystem rooting depths, however, increase strongly from the arid to the humid end of the gradient (Fig. 9). Maximum ecosystem rooting depth ($D_{e, max}$) is defined here as the depth exceeded by only 5% of all individual rooting depths within a plant growth form category. Maximum ecosystem rooting depths for herbaceous plants tend to be found at less than 2 m depth in the most arid environments and at almost 4 m depth in climates with > 750 mm of precipitation (Fig. 9). The deepest roots of shrubs and semi-shrubs are likely to reach greater depths of about 5 m in climates with > 125 mm precipitation, but slightly less

in drier climates. If water is found at such depths, it could potentially be made available to more shallowly rooted plants by hydraulic redistribution (Richards & Caldwell 1987; Caldwell *et al.* 1998).

APPLICABILITY OF WALTER'S TWO-LAYER MODEL

Our findings suggest that the two-layer model of soil depth partitioning between woody and herbaceous plants (Walter 1939; Walker & Noy-Meir 1982) is most likely to be applicable in the drier half of the precipitation gradient (Fig. 9) and in climates with substantial precipitation during the cold season (Fig. 6). Furthermore, niche partitioning between woody plants and grasses may be more likely in cold than in warm climates, because absolute rooting depths of woody plants tend to decrease with increasing PET, while absolute rooting depths of perennial grasses increase (Table 1). This does not mean that Walter's original two-layer model does not apply to the tropical savanna systems for which it was originally proposed (Walter 1939), but our data suggest that a two-layer model may be more common in drier climates of the temperate zone. This seems to be supported by field studies in temperate, subtropical and tropical regions (Table 4 and Appendix 3). All studies in temperate ecosystems found at least some evidence for soil depth partitioning between woody and herbaceous plants, although many studies found that only certain woody species were more deeply rooted than coexisting herbaceous plants. In contrast, about half of the studies conducted in subtropical and tropical ecosystems found no evidence for below-ground partitioning of soil resources between woody and herbaceous plants.

Table 4 Tests of the two-layer hypothesis of soil depth partitioning between woody and herbaceous plants from studies in water-limited ecosystems. Partial support for the hypothesis is indicated if only a few woody species were more deeply rooted than the herbaceous ones

Geographic location	Vegetation type	Growth form		Rainfall (mm)	Seasonality of rainfall	Support for two-layer hypothesis	Methods	Reference
		Herbaceous	Woody					
<i>Temperate</i>								
Gobi Desert, Mongolia	Temp. desert	PF, PG	SS, S	100	Summer	Yes	R	1
Karakum, Turkmenistan	Temp. desert	PG	T	110	Winter	Yes	R	15
Utah, USA	Temp. semidesert	A, PF, PG	SS, S	150	Not seasonal	Partial	W	8
Patagonia, Argentina	Temp. semidesert	PG	SS	160	Winter	Partial	R	23
Central Kazakhstan	Temp. semidesert steppe	PF, PG	SS, S	160	Not seasonal	Partial	R	26
Washington, USA	Temp. shrub steppe	A	S	160	Winter	Yes	R	21
Patagonia, Argentina	Temp. semidesert steppe	PG	SS	170	Winter	Yes	W, rem.	22
Central Kazakhstan	Temp. semidesert	A, PF, PG	SS	200	Not seasonal	Partial	R	24
S Turkmenistan	Temp. semidesert	A, PF, PG	SS, S	220	Winter	Partial	R	18
Patagonia, Argentina	Temp. shrub steppe	PG	SS	290	Winter	Partial	R, W	23
Arizona, USA	Temp. tree savanna	PG	T	300	Summer	Yes	R	10
Colorado, USA	Temp. shrub steppe	PG	SS, S	320	Summer	Yes	W, rem.	7
La Pampa, Argentina	Temp. shrub steppe	PG	S	340	Not seasonal	Partial	W, R	19
Saskatchewan, Canada	Temp. steppe	PF, PG	SS	340	Summer	Yes	R	5
Utah, USA	Temp. semidesert	PG	SS	470	Not seasonal	Yes	R	6
<i>Subtropical/tropical</i>								
S New Mexico, USA	Subtrop. semidesert	PG	S	230	Summer	No	W	20
Durango, Mexico	Subtrop. semidesert	PG	S	260	Summer	Partial	W, R	16
Chihuahuan Desert, Mexico	Subtrop. semidesert	PG	S	260	Summer	No	R	3
SE Arizona, USA	Subtrop. grassland	A, PG	SS	350	Summer	Yes	W, R	4
Tsavo National Park, Kenya	Trop. tree savanna	PG	T	450	Seasonal	Yes	R, rem.	2
Belize	Trop. tree savanna	PG	T	500	Seasonal	No	R	11
N. Province, South Africa	Trop. tree savanna	PG	T	630	Seasonal	Yes	W, R, rem.	12
S Texas, USA	Subtrop. tree/shrub Savanna	PG	SS, S	720	Summer	No	W, R	14
Tsavo National Park, Kenya	Trop. tree savanna	PG	T	770	Seasonal	No	R, rem.	2
S Kenya	Trop. tree/shrub savanna	PG	S	790	Seasonal	Yes	W	9
Zimbabwe	Trop. tree savanna	PG	T	840	Seasonal	No	W, R	25
S Kenya	Trop. tree/shrub savanna	PG	S, T	1030	Seasonal	Yes	W	9
Cote D'Ivoire	Trop. shrub savanna	PG	S	1200	Seasonal	No	W, R	13, 17

Growth forms: A = annual herbs, PF = perennial forbs, PG = perennial grasses, SS = semishrubs, S = shrubs, T = trees.

Methods: W = water use (including measurements of soil or plant water potentials, soil water content and stable isotope ratios), R = rooting depths, rem. = removal experiments. For references see Appendix 3.

PLANT TRAITS AND ROOTING DEPTHS

Differences in the shapes and sizes of root systems may also be caused by physiological, anatomical or morphological traits that are specific to a species or plant family. For example, the stem succulents included in this study all use the CAM photosynthetic pathway, and these plants had shallow and widely spreading root systems (Figs 2 and 3). However, we found no evidence for differences in rooting depths between C_3 and C_4 plants in the water-limited environments that were the subject of this study (data not shown). Certain plant families are more likely to include either shallowly or deeply rooted plants. Many legumes (woody Mimosaceae, herbaceous Fabaceae) in water-limited environments are apparently deeply rooted. Plants in the Asteraceae tend to be deeply rooted compared with other herbaceous plants, but shallowly rooted compared with other woody plants. Woody Asteraceae in our data base were mostly semi-shrubs (86%), which raises the intriguing question of whether they may be shallowly rooted because the plants tend to be small or whether the plants tend to

be small because they are unable to develop deep roots. It is also noteworthy that the fibrous-rooted grasses are more deeply rooted than the average herbaceous plant. The depth record of 6 m for a grass in our data base was for *Achnatherum splendens* (Trin.) Nevski from the semi-deserts of Kazakhstan (Baitulin 1979), close to the depth records of 6.5 m for tap-rooted perennial forb species *Karelinia caspia* (Pallas) Less. (Asteraceae) and *Zygophyllum fabago* L. (Zygophyllaceae) from the same environment (Baitulin 1979). Fibrous root systems may not always be shallower than tap-rooted ones.

Our study demonstrates that the sizes and shapes of root systems tend to differ among plant growth forms and to vary predictably along climatic gradients in water-limited systems. Some of the statistical relationships discussed in this study may be useful for predicting median root system sizes of individual plants in water-limited ecosystems and will also serve as a frame of reference for future studies. It would be especially desirable if some of these relationships could be tested in such regions as South America and Australia, from which few root data are available.

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Supplementary material

The following material is available from <http://blackwell-science.com/products/journals/suppmat/JEC/JEC683/JEC683sm.htm>

Appendix 1 List of references containing the root data used in this study.

Appendix 2 Summary table of absolute root dimensions for plant growth forms.

Appendix 3 References to Table 4.

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