THE GLOBAL BIOGEOGRAPHY OF ROOTS

H. Jochen Schenk[1,3] and Robert B. Jackson[2]

[1]*Department of Biology, Box 90338, Duke University, Durham, North Carolina 27708 USA*
[2]*Department of Biology and Nicholas School of the Environment, Box 90340, Duke University, Durham, North Carolina 27708 USA*

Abstract. Studies in global plant biogeography have almost exclusively analyzed relationships of abiotic and biotic factors with the distribution and structure of vegetation aboveground. The goal of this study was to extend such analyses to the belowground structure of vegetation by determining the biotic and abiotic factors that influence vertical root distributions in the soil, including soil, climate, and plant properties. The analysis used a database of vertical root profiles from the literature with 475 profiles from 209 geographic locations. Since most profiles were not sampled to the maximum rooting depth, several techniques were used to estimate the amount of roots at greater depths, to a maximum of 3 m in some systems. The accuracy of extrapolations was tested using a subset of deeply (>2 m) sampled or completely sampled profiles. Vertical root distributions for each profile were characterized by the interpolated 50% and 95% rooting depths (the depths above which 50% or 95% of all roots were located).

General linear models incorporating plant life-form dominance, climate, and soil variables explained as much as 50% of the variance in rooting depths for various biomes and life-forms. Annual potential evapotranspiration (PET) and precipitation together accounted for the largest proportion of the variance (12–16% globally and 38% in some systems). Mean 95% rooting depths increased with decreasing latitude from 80° to 30° but showed no clear trend in the tropics. Annual PET, annual precipitation, and length of the warm season were all positively correlated with rooting depths. Rooting depths in tropical vegetation were only weakly correlated with climatic variables but were strongly correlated with sampling depths, suggesting that even after extrapolation, sampling depths there were often insufficient to characterize root profiles. Globally, >90% of all profiles had at least 50% of all roots in the upper 0.3 m of the soil profile (including organic horizons) and 95% of all roots in the upper 2 m. Deeper rooting depths were mainly found in water-limited ecosystems. Deeper 95% rooting depths were also found for shrublands compared to grasslands, in sandy soils vs. clay or loam soils, and in systems with relatively shallow organic horizons compared with deeper organic horizons.

Key words: biomes; climate; global ecology; global vegetation types; latitude; plant life-forms; potential evapotranspiration; precipitation; rooting depth; soil texture; vertical root distribution.

INTRODUCTION

A century since the groundbreaking work of Schimper (1898) on ''plant geography upon a physiological basis,'' ecologists have made substantial progress in understanding the factors that shape the global distribution of vegetation and its aboveground structure (e.g., Box 1981, Woodward 1987, Prentice et al. 1992, Neilson 1995). The factors that control the biogeography of belowground vegetation structure remain less clear. For example, climate, soil characteristics, and plant life-forms are all likely to be important, but quantifying that importance at regional and global scales is difficult.

Vegetation types differ in root biomass, root turnover, vertical root distributions, and maximum rooting

[3] Present address: Wrigley Institute for Environmental Studies, University of Southern California, Los Angeles, California 90089-0371 USA. E-mail: schenk@wrigley.usc.edu

depth (Stone and Kalisz 1991, Canadell et al. 1996, Jackson et al. 1996, 1997, Vogt et al. 1996, Cairns et al. 1997). These properties influence the fluxes of water, carbon, and soil nutrients and the distribution and activity of soil fauna. Roots transport nutrients and water upwards, but they are also pathways for carbon and nutrient transport into deeper soil layers and for deep water infiltration (Johnston et al. 1983, Meek et al. 1992, Smith et al. 1999, Jobbágy and Jackson 2000, 2001). Roots also affect the weathering rates of soil minerals (Bormann et al. 1998).

To our knowledge, no large-scale analysis of the relationships between climate, soil, and vegetation with rooting depths has been attempted. Previous studies of rooting depths have examined data for particular locations or, in a few cases, for geographic regions (e.g., Weaver 1919, Shalyt 1950, Coupland and Johnson 1965, Baitulin 1979, Kutschera and Lichtenegger 1982). Other studies have examined rooting depth along climatic and/ or elevational gradients without attempting to quantify the relationship of rooting depths with climate (Weaver
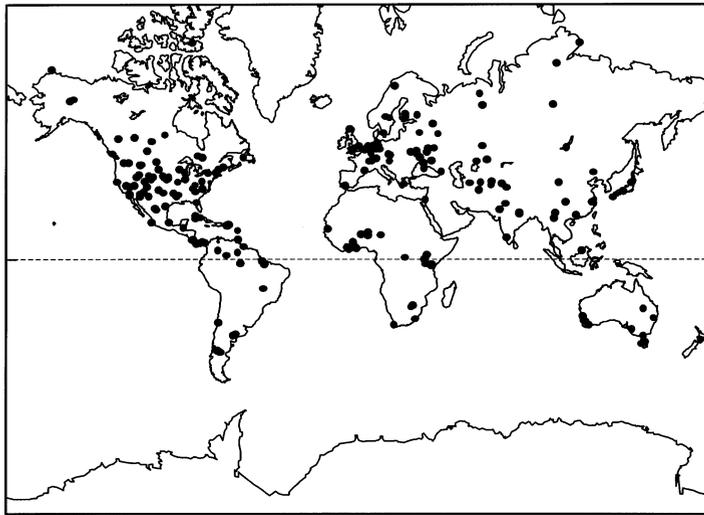
Fig. 1. Geographic locations of root profiles in the global database.

1977, Lichtenegger 1996, Schulze et al. 1996, Yanagisawa and Fujita 1999).

Regional and global data for rooting depth are also needed as inputs to global biogeochemistry and vegetation models. In the recent Project for Intercomparison of Land Surface Parameterization Schemes (PILPS), rooting depth and vertical soil characteristics were the most important factors explaining scatter for simulated transpiration among 14 land surface models (Mahfouf et al. 1996, Jackson et al. 2000a). Recently, the Terrestrial Observation Panel for Climate of the Global Climate Observation System (GCOS) identified the 95% rooting depth as a key variable needed to quantify the interactions between the climate, soil, and plants, stating that the main challenge was to find the correlation between rooting depth and soil and climate features (GCOS/GTOS Terrestrial Observation Panel for Climate 1997).

The goals of our study were two-fold: (1) to identify and, where possible, quantify biotic and abiotic factors that influence the vertical distribution of roots in the soil, and (2) to quantify vertical root distributions for global vegetation types. We examined these two questions in several contexts. One of them was the effect of plant life-form on rooting depths. Woody plants such as trees and shrubs on average tend to be more deeply rooted than grasses and forbs (Walter 1971, Jackson et al. 1996). Many vegetation and biogeochemistry models are parameterized with deeper maximum rooting depths or a greater proportion of roots at depth for woody plants (e.g., Dickinson et al. 1993, Neilson 1995, Haxeltine and Prentice 1996, Sala et al. 1997). We examined the basis for these generalizations globally, comparing the relative impact of plant life-form, soil, and climate on rooting depths. Such an analysis can help determine whether biotic or abiotic factors are better predictors of rooting depths. Another purpose of our analysis was to identify vegetation types where the

potential mismatch between typical sampling depth and actual rooting depth appears to be particularly large. This information should allow researchers to target root sampling in particular systems.

METHODS

The database of root profiles

The database of 115 root profiles described in Jackson et al. (1996) was expanded to include 475 root profiles for 209 geographical locations (Fig. 1; Appendix A) with data sets included if root samples were taken in at least four depth increments. For each root profile in Appendix A, we recorded latitude and longitude, soil texture and other soil characteristics, depth of organic horizons, type of roots measured (e.g., fine or total, live or dead), sampling method, units of measurements (root mass, length, number, surface area), and sampling depth. We also recorded the presence and dominance of plant life-forms as described in the publications (including succulents, forbs, grasses, semi-shrubs, shrubs, and four categories of trees: needle-leaved vs. broadleaved, evergreen vs. deciduous). Semi-shrubs were treated separately from shrubs because many studies made this distinction and because previous studies found differences in rooting depth between shrubs and semi-shrubs (Baitulin 1979, Nechaeva 1985, Leishman and Westoby 1992). We also noted whether the vegetation was relatively ''natural'' or altered by humans (e.g., forest plantations). Where unavailable, geographic coordinates were estimated based on geographic information in the publications. The precision of these estimates varied from a few kilometers in the majority of cases to no more than 0.5° latitude or longitude in a few cases (mostly for sites in unpopulated areas in boreal or tropical zones).

Mean annual precipitation was recorded from each publication or, where unavailable, was estimated from

TABLE 1. Quantitative studies of vertical root distributions to sample depths of ≥3 m.

Source	Geographic location	Vegetation type	Sampling depth (m)
Bille (1977)	Sahel, Senegal	Dry tropical savanna	6
Carbon et al. (1980)	Southwestern Australia	Mediterranean woodland	15–18
Cerri and Volkoff (1987)	Manaus, Brazil	Tropical evergreen forest	5
Chen et al. (1994)	Southern China	Warm-temperate evergreen forest	5
Freckman and Virginia (1989)	New Mexico, USA	Semi-desert	4–13
Hertel (1999)	Northwestern Germany	Cool-temperate deciduous forest	3.6
Higgins et al. (1987)	Cape Province, South Africa	Mediterranean shrubland	3.5
Hosegood (1963)	Kenya	Dry tropical savanna	4.9–5.8
Jama et al. (1998)	Western Kenya	Tropical tree plantation	4
Lucot and Bruckert (1992)	Franche-Comté, France	Cool-temperate deciduous forest	4
Miroshnichenko (1975)	Turkmenistan	Desert	6
Nepstad et al. (1994)	Para, Brazil	Tropical evergreen forest	5.8
Popov (1979)	Southern Turkmenistan	Temperate savanna	3.2
Roupsard et al. (1999)	Southern Sudan	Dry tropical savanna	7.5
Schulze et al. (1996)	Patagonia, Argentina	Desert and semi-desert	3
Sternberg et al. (1998)	Para, Brazil	Tropical evergreen forest	4
Vandenbeldt (1991)	Southwestern Niger	Dry tropical savanna	4
Zverev and Seiidova (1990)	Turkmenistan	Desert	4

the nearest available weather station. The seasonal distribution of precipitation was estimated from 1961–1990 long-term monthly means for 0.5° grid cells recorded in the Climate Research Unit (CRU) Global Climatologies (Intergovernmental Panel on Climate Change Data Distribution Center, University of East Anglia, Norwich, UK). Estimates for mean monthly potential evapotranspiration (PET) calculated by the Penman-Monteith method were taken from the global 0.5° gridded data set of Choudhury (1997) and Choudhury and DiGirolamo (1998). To estimate PET for sites in tropical cloud forests, mean values for a grid cell were halved to account for the effects of permanent cloud cover (Bruijnzeel and Proctor 1995).

Most profiles included roots from different species and life-forms. Where data were given separately for species or life-forms they were averaged to generate an estimated profile for the community, but the individual data were retained for the life-form analyses. Data for both late and early successional vegetation were included. Root profiles for crops and from fertilized or ploughed soils were excluded because root distributions in such systems can be strongly influenced by management practices, a factor that we were unable to include in our analyses. Also excluded were root profiles from wetlands and seasonally flooded desert playas, grasslands, savannas, and forests.

Interpolation and extrapolation of root profiles

Root profiles differed in the number and depth of intervals sampled, which made standardizing them necessary so that statistical analyses could weigh each profile equally. To achieve this, profiles were interpolated by fitting a nonlinear smoothing function to each profile. Another issue was that only 9% of the 475 root profiles were sampled to a depth at which no further roots were found, with few studies sampling root profiles to depths of 3 m or more (Table 1). These

incompletely sampled profiles (those not sampled to the maximum rooting depth or to at least 3 m depth) were extrapolated using the same mathematical function used to interpolate completely measured profiles. Tests of the accuracy of interpolations and extrapolations were conducted using 76 profiles sampled to at least 0.8 m depth *and* to depths at which no further roots were found *or* which had been sampled to ≥2 m depth (hereafter termed the ''deep profiles'').

The goal of interpolations and extrapolations was to estimate the depths above which 50% of all roots (D_{50}) and 95% of all roots (D_{95}) were located in the soil. All interpolations and extrapolations of profiles were restricted to a depth of 3 m, because this should be sufficient for most vegetation types (Canadell et al. 1996) and because our data set of deep profiles did not allow us to test the accuracy of extrapolation to greater depths. Details about the interpolation and extrapolation methods and tests of their error rates are in Appendix B. The nonlinear model used in this study for interpolation of deep profiles and for the interpolation and extrapolation of all other profiles was a logistic dose-response curve (LDR), which was fitted to cumulative root profiles:

$$r(D) = \frac{R_{max}}{\left[1 + \left(\dfrac{D}{D_{50}}\right)^c\right]}. \quad (1)$$

In this equation, $r(D)$ is the cumulative amount of roots above profile depth D (in cm, including organic layers), R_{max} is the total amount of roots (i.e., total biomass, length, number) in the profile, D_{50} is the depth (cm) at which $r(D) = 0.5 R_{max}$, and c is a dimensionless shape-parameter. The LDR model was fitted to all profiles, initially allowing R_{max} to vary to obtain the best fit. To avoid excessive errors, extrapolations were restricted to a maximum sampling depth, D_{max}, of either

TABLE 2. Global vegetation types used for grouping root profile data, and the number of profiles in the database for each type. Types delimited by aridity are listed with their mean annual precipitation limits.

Climatic zone	Vegetation type	Annual precipitation (mm)	n
Arctic	Tundra		20
Boreal	Boreal forests		33
Temperate	Cool-temperate conifer forest		19
	Cool-temperate broadleaved-deciduous forests		29
	Conifer plantations in the cool-temperate broadleaved forest zone		24
	Warm-temperate forests†		27
	Heathlands		5
	Meadows and pastures in the boreal and temperate forest zone (mostly anthropogenic)		17
	Prairies	>500	19
	Semi-arid steppes	≤500	29
	Temperate shrub/tree savannas (including forest-steppe transition zones)		25
	Mediterranean shrublands and woodlands		17
	Semi-desert shrublands	>150–500	35
	Deserts	≤150	19
Tropical	Dry tropical shrub/tree savannas and grasslands	≤1000	31
	Humid tropical shrub/tree savannas and grasslands	>1000	16
	Tropical deciduous and semi-deciduous forests		16
	Tropical evergreen forests		59
High elevation	Alpine communities		9
	Tropical cloud forests		8

  † The warm-temperate category includes conifer forests and plantations, broadleaved-deciduous forests, and broadleaved, evergreen forests.

twice the sample depth or to 3 m depth, whichever was smaller, and the cumulative amount of roots at D_{max} was set to 100%. Profiles sampled to the apparent maximum rooting depth or to ≥3 m were not extrapolated. Profiles for tundra were also not extrapolated beyond the measured depth because we assumed that permafrost was free of roots. Of all profiles, 20.0% were extrapolated to ≤1 m depth, 44.3% to between 1 m and ≤2 m, 14.7% to between 2 m and ≤3 m, and 21.0% were not extrapolated.

Seventy-six test profiles were used to derive bootstrapped estimates of the errors of mean extrapolated 50% and 95% rooting depths (see Appendix B; extrapolated rooting depths are hereafter denoted as D_{x50} and D_{x95}). To test whether vertical root distributions in the test profiles were representative of the whole data set, they were subsampled to a depth of ~1 m, a typical sampling depth for the whole data set. (If the upper meter contained less than four sample intervals they were subsampled to 1.6 m at most.) Compared to the remaining database, root distributions within these ~1 m-deep test samples did not differ from those found in other profiles measured to the same range of depths (see Appendix B). In consequence, root distributions in the upper ~1 m portions of the test profiles appear to be representative of the database as a whole, which suggests that mean extrapolation errors observed for these profiles may also be representative of the entire database.

Analyses of rooting depths as a function of climate, soil, and vegetation characteristics

Root profiles were initially grouped by location and physiognomy into 20 global vegetation types (Table 2).

Root profiles were assigned to the climatic regions (arctic, boreal, cool-temperate, warm-temperate, or tropical) using the global climate classification schemes of Walter et al. (1975), Troll and Paffen (1980), and Bailey (1998). We chose the term "warm-temperate" (Troll and Paffen 1980) instead of the largely synonymous term "subtropical" (Bailey 1998).

Mean rooting depths and their confidence intervals (95% CI) were calculated for all vegetation types with ten or more replicates. Differences among root profiles were compared within subsets of similar vegetation types along gradients of increasing temperature and/or aridity.

Profiles were also grouped by life-form (Table 3) to determine whether there were consistent differences among rooting depths of ecosystems dominated by trees, shrubs, semi-shrubs, and grasses. For this comparison, we chose two climatic ranges that encompass ecosystems dominated by all four of these life-forms, spanning from semi-deserts to dry forests in the temperate zone (>150–750 mm annual precipitation) and in the tropical zone (>250–1500 mm annual precipitation).

Rooting depths were further analyzed for their relationships with climate, soil, vegetation, and sampling method (see Table 3). Because of limited detail in most of the profiles, soil texture was reduced to three categories: sand (including loamy and clayey sand), loam (sandy loam to silt-loam), and clay (including clay-loam and sandy clay). Quantitative information about the amounts of gravel and rocks in the soil were not available for most of the sites. Vegetation was grouped

TABLE 3. Variables in correlation analyses and general linear models of rooting depths.

Category	Variable	Units	Transformation for statistical analyses
Climate	Annual precipitation (R_a)	mm/yr	log x
	Length of warm season (number of months with >45 mm PET)†	months/yr	none
	Length of dry season (number of dry months per total number of months in the warm season)	months/months	none
	Annual PET (PET_a)	mm/yr	log x
	Precipitation surplus (annual sum of monthly precipitation amounts that exceed monthly PET)	mm/yr	log(x + 1)
	Moisture index: R_a/PET_a	mm/mm	none
Soil	Depth of organic layer	cm	log(x + 1)
	Soil texture: sand/loam/clay	3 categories	
Vegetation	Life-form dominance (5 classes: trees, shrubs, semi-shrubs + grasses, grasses, shrubs/trees + grasses)	5 categories	
	Vegetation type (see Table 2)	20 categories	
Methodology	Kinds of roots measured: fine (<5 mm) or total	2 categories	
	Measurement units: mass (kg/m²), length (km/m²), or number per vertical profile area	3 categories	
	Sample depth	cm	log x

† A monthly PET of 45 mm corresponds to a mean monthly temperature of ~10°C (based on regressions performed with climate data for North American LTER sites compiled by D. Greenwald and T. Kittel and archived on the Internet at ⟨http://www.lternet.edu/documents/Publications/climdes⟩.

in five dominance categories: trees, shrubs, semi-shrubs (often co-dominant with herbaceous plants), grasses, or co-dominance of woody plants and grasses (i.e., tree–or shrub–savannas).

Climatic variables examined included precipitation and potential evapotranspiration. Effects of temperature were not examined separately, because they are strongly correlated with potential evapotranspiration. Of the various climatic parameters and indices that were tested for potential relationships with rooting depths, only those that showed significant relationships are discussed in this paper (Table 3). Correlations between D_{x50} or D_{x95} and environmental variables were examined by Spearman rank correlations in SYSTAT 8.0 (Wilkinson et al. 1998). To test whether extrapolations of rooting depths affected their relationships with environmental variables, the same correlation analyses were also conducted with the following data sets: Non-extrapolated rooting depths for the whole data set ($n = 475$), non-extrapolated rooting depths for all profiles sampled to the maximum rooting depth or to ≥2 m depth ($n = 100$), and extrapolated rooting depths of all profiles not sampled to the maximum rooting depth and sampled to <2 m depth ($n = 375$). Non-parametric correlation analysis was used to minimize the effects of unknown errors in both the dependent variable (rooting depths) and in the environmental variables. Probabilities were determined from Zar (1996).

General linear models (GLM) were constructed by backward stepwise regression to estimate the proportions of variances in rooting depths accounted for by vegetation type, life-form dominance, climate, soil, and sampling depth. Rooting depths were log-transformed to normalize their distributions. Vegetation type, life-form dominance, and soil texture were included in the models as categorical variables, and six transformed

climatic variables were included as continuous variables (Table 3). Where noted, the data set was split into four subsets (tropical forests, tropical ecosystems not dominated by trees, temperate and boreal forests, and temperate and boreal ecosystems not dominated by trees) because exploratory analyses suggested that these subsets differed in their relationships between rooting depths and climatic variables. Because there are numerous potential errors for both the dependent and independent variables used in these linear models, we report only r^2 coefficients for the models with the highest r^2. The proportion of the variance in rooting depths explained by sampling depths was estimated for each subset of the data by comparing general linear models that included sampling depth, vegetation type, life-form dominance, climate, and soil characteristics, with the best GLM that did not include sampling depth as a covariate.

Effects of extrapolations on estimates of rooting depths

Rooting depths estimated by extrapolations of root distributions in the upper ~1 m of the 76 test profiles were tightly correlated with rooting depths calculated by interpolation of the whole test profiles (Fig. 2A). Not surprisingly, total errors (including interpolation and extrapolation errors) of estimated mean rooting depths decreased with the number of profiles used to derive the estimate, from up to ±40% of the mean for samples of 10 profiles to less than ±10% of the mean for samples of 60 profiles or more (i.e., the more profiles in the analysis, the smaller the error; Fig. 2B). There was a slight tendency towards underestimating mean rooting depths by ~1–3% (Fig. 2A and B). The 95% error ranges depicted in Fig. 2B were used to estimate bootstrapped 95% confidence limits (95% CL)
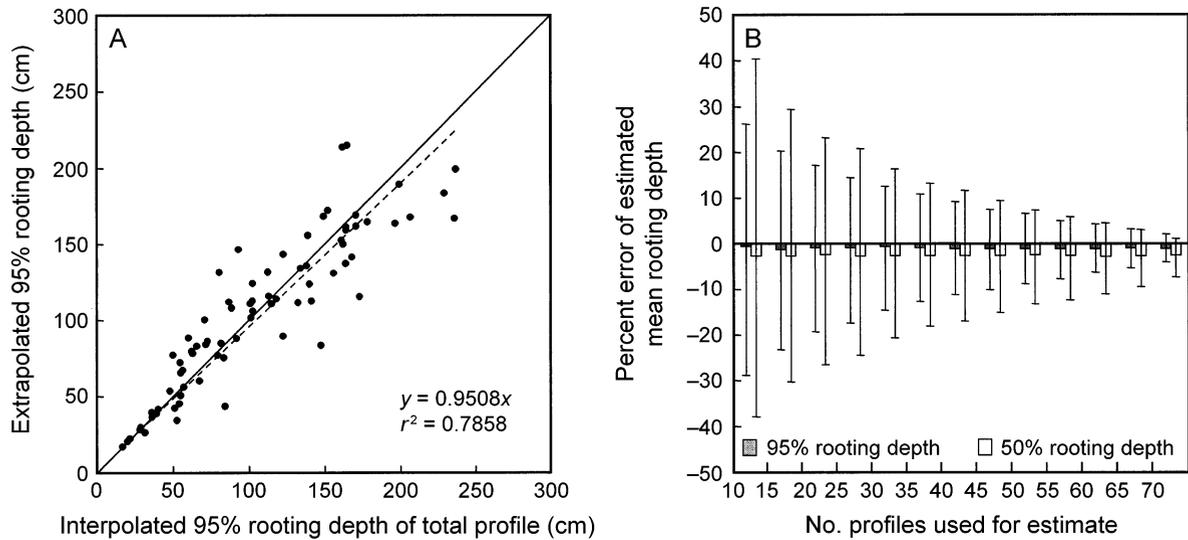
FIG. 2. (A) Comparison between 95% rooting depths estimated by extrapolation of the upper part of the root profile (~1 m depth) and 95% rooting depths interpolated for entire profiles. The data set used for this comparison consisted of 76 completely sampled test profiles. (B) Combined interpolation and extrapolation errors (%) for estimates of mean extrapolated rooting depths as a function of sample size. The error bars represent 95 percentiles of 1000 bootstrapped recalculations of mean rooting depths using subsamples of between 10 and 70 profiles.

for all mean rooting depths calculated in this study, depending on the number of profiles used to calculate the means. Confidence intervals were only calculated for sample sizes of ≥10 profiles (Fig. 2B).

The median sampling depth for root profiles was 0.88 m. In contrast, independent estimates for maximum

rooting depths of individual plants (Canadell et al. 1996; H. J. Schenk and R. B. Jackson, *unpublished data*) range from 1.7 m for temperate grasslands to 3.0 m for tropical deciduous forests (Fig. 3). In this study, extrapolation of root profiles sampled to <3 m depth added on average 31 ± 1 cm to estimates of D_{95} (cor-
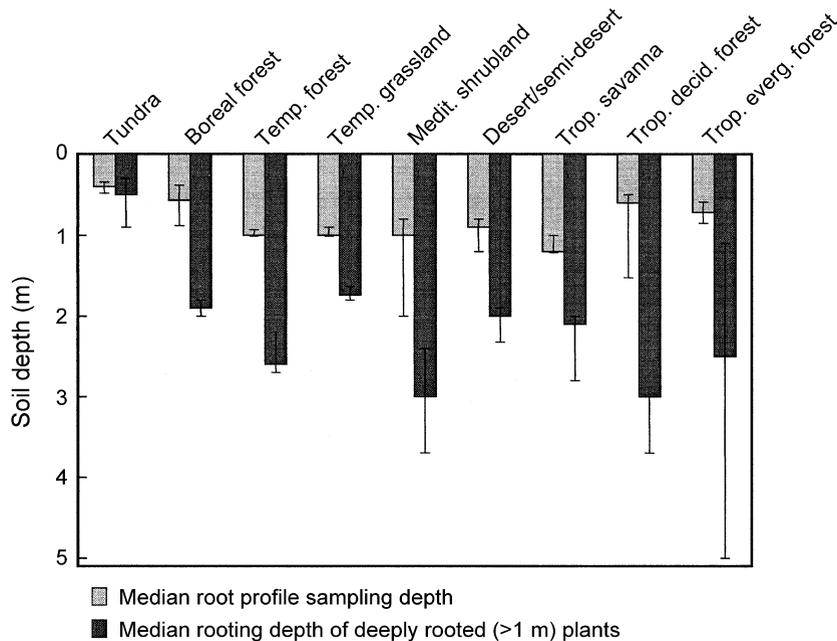

FIG. 3. Comparison between estimated rooting depths of global vegetation types and sampling depths used in quantitative studies of vertical root distributions. Rooting depths were estimated by calculating the median rooting depth of deeply rooted (≥1 m) plant species in that vegetation type from data contained in the database of Canadell et al. (1996) and Schenk and Jackson (2002). Median sampling depths were calculated from data in the global root profiles from this paper.
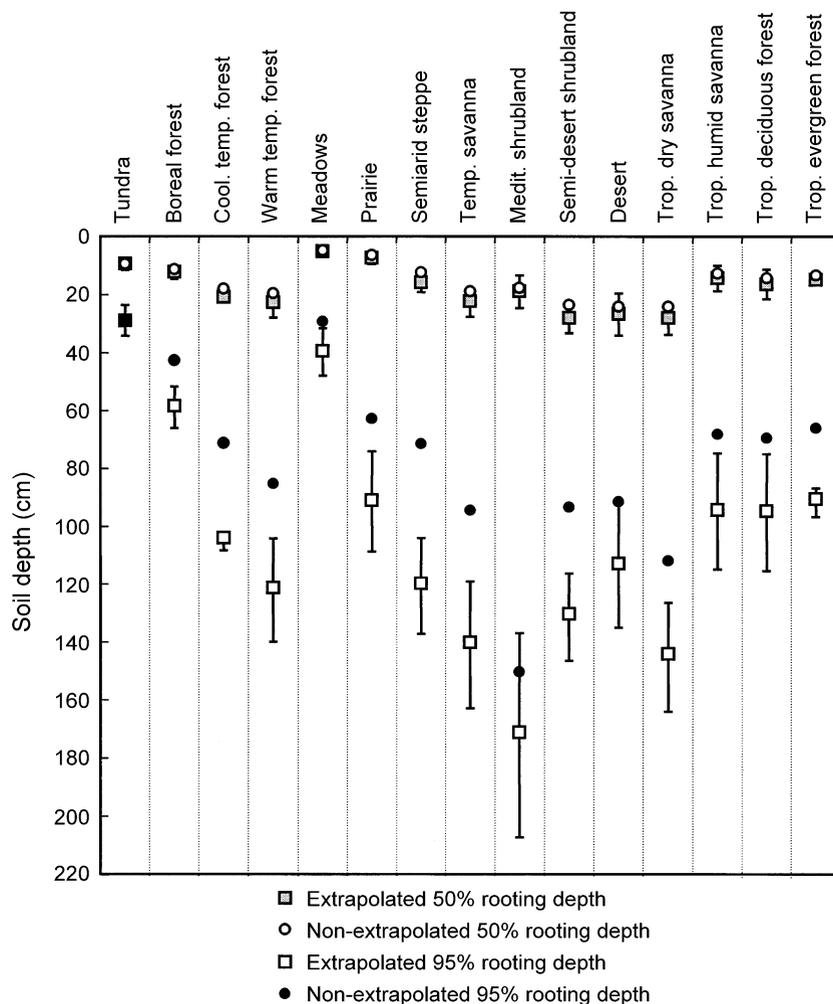
FIG. 4.   Mean extrapolated and non-extrapolated rooting depths for global vegetation types (for definitions see Table 2). Extrapolated profiles are by definition deeper than non-extrapolated profiles. The extrapolations attempt to address the problem that many researchers sampled more shallowly than the entire root profile. Error bars represent 95% confidence intervals for means, based on sample sizes (listed in Table 2) and estimates of interpolation and extrapolation errors depicted in Fig. 2B. Cool-temperate forests include conifer and broadleaved-deciduous forests, as well as conifer plantations.

responding to an increase of almost half; 48 $\pm$ 1.6%). D_{x95} values were significantly deeper than non-extrapolated D_{95} in all vegetation types other than mediterranean shrublands and woodlands, where rooting depths were extremely variable and the number of replicates was low. Extrapolations did not change 50% rooting depths substantially. They added only 3 $\pm$ 0.2 cm to estimates of D_{50} on average, and D_{x50} values were not significantly deeper than non-extrapolated D_{50} in 11 out of 15 global vegetation types (Fig. 4).

Methodological effects on estimates of rooting depths

Of all profiles in the database, 74% were in units of mass, 16% in units of numbers, 9% in units of length, and 1% in units of surface area. All measurements were expressed on an area basis at the soil surface (e.g., kg/ m^2) with the exception of the root number data, which

were expressed as numbers per vertical profile area. Root number and root length data were common only in a subset of forest profiles. To check whether the choice of measurement units affected estimated rooting depths, we compared mean D_{x50} and D_{x95} values between profiles measured in different units for temperate forests, the only biome with enough profiles of different units.

Mean rooting depths between profiles measured in units of mass ($n = 60$), length ($n = 19$), and number ($n = 19$) for cool- and warm-temperate forests were not significantly different. However there was a tendency for profiles measured by mass to have slightly shallower D_{x95} (mean = 104 cm; 95% CL = 100, 110 cm) than profiles measured in length (mean = 115 cm; 95% CL = 94, 138 cm) or numbers (mean = 114 cm; 95% CL = 93, 137 cm).

TABLE 4. Parameters for calculating vertical root distributions within the upper 3 m of the soil profile for global vegetation types using the logistic dose-response (Eq. 1).

Vegetation type	D_{50} (cm)	D_{95} (cm)	c
Tundra	9	29	-2.621
Boreal forest	12	58	-1.880
Cool-temperate forest, including plantations	21	104	-1.835
Warm-temperate forest, including plantations	23	121	-1.757
Meadows in the forest zone	5	40	-1.448
Prairie	7	91	-1.176
Semi-arid steppe	16	120	-1.452
Temperate savanna	23	140	-1.602
Mediterranean shrubland/woodland	19	171	-1.336
Semi-desert shrubland	28	131	-1.909
Desert	27	112	-2.051
Dry tropical savannas	28	144	-1.798
Humid tropical savannas	14	94	-1.561
Tropical semi-deciduous and deciduous forest	16	95	-1.681
Tropical evergreen forest	15	91	-1.632

Notes: The parameters are based on the mean extrapolated 50% and 95% rooting depths (D_{x50} and D_{x95}, respectively) for the vegetation types (see Fig. 4). Parameters D_{50} and the shape parameter c are for use in Eq. 1.

Studies for woody vegetation often differed in whether fine roots, coarse roots, or total roots were measured (Appendix A). (Measurements of "total" roots usually excluded large skeletal roots in most profiles.) Simultaneous measurements of fine and coarse roots were available for 32 forest profiles. To compare distributions for fine and coarse roots in these profiles, we analyzed rooting depths for fine roots (<2 or 3 mm diameter), coarse roots (>2 or 3 mm), and total roots in paired t tests (fine vs. coarse and fine vs. total) using log-transformed data. To exclude any potential effects of extrapolation errors, non-extrapolated rooting depths D_{50} and D_{95} were used.

Forest root profiles for coarse roots differed in having deeper D_{50} and shallower D_{95} than fine root profiles. On average, D_{50} for coarse roots were $54 \pm 20\%$ deeper than those for fine roots ($P < 0.01$), while D_{95} for coarse roots were $12 \pm 5\%$ shallower than those for fine roots ($P < 0.01$). These results suggest that coarse woody roots, which have large effects on measurements in units of mass, tend to be concentrated in soil layers of shallow to medium depth, while the proportion of fine roots increases with depth. Many studies in the database lump fine and coarse roots (excluding large skeletal roots) into a measure of "total" roots. In forests, D_{50} for total roots were $37 \pm 13\%$ deeper than those for fine roots ($P < 0.01$), while D_{95} for total roots were similar to those of fine roots ($5 \pm 4\%$ deeper; $P = 0.08$).

RESULTS

Rooting depths of global vegetation types

Mean 50% rooting depths (D_{x50}) for global vegetation types varied mostly between 5 cm and 28 cm (18 ± 1 cm, global mean ± 1 SE; Fig. 4, Table 4). This result suggests that, on average, at least half of root biomass is found in the upper 30 cm of soil for all systems globally. Meadows and pastures in the forest zone, prairies, boreal forests, and tundra had the shallowest D_{x50}

(Figs. 4 and 5). Only 40 profiles in the database had D_{x50} values of >40 cm, and the deepest D_{x50} for the whole data set was 78 cm for a desert in Turkmenistan (Miroshnichenko 1975).

Mean D_{x95} varied mostly between 40 cm and 150 cm (Fig. 4), with a global mean of 102 cm (± 4 cm SE). Tundra, boreal forests, and meadows in the temperate forest zone had mean D_{x95} of <60 cm, while mediterranean shrublands and woodlands, temperate savannas, and dry tropical savannas had the deepest mean D_{x95} of >140 cm. Individual D_{x95} values of >200 cm depth were observed in 8% of all profiles in the database, primarily in deserts and semi-deserts, mediterranean shrublands and woodlands, temperate savannas, and tropical systems.

In general, boreal forests were much more shallowly rooted than temperate forests (Fig. 5A). Warm-temperate forests had slightly deeper D_{x95} values than cool-temperate forests, but rooting depths for all temperate forests were similar (Figs. 4 and 5A). No differences were found within these vegetation types for comparisons of deciduous and evergreen trees, broadleaved and needle-leaved trees, or plantations and natural forests. Rooting depths for meadows and pastures in the temperate and boreal forest zone, prairies, and semi-arid steppe increased in depth along an aridity gradient from wet to dry (Fig. 5B).

Mediterranean shrublands and woodlands had the deepest mean D_{x95} values of all vegetation types (Fig. 4), but this result was largely due to two root profiles of *Eucalyptus marginata* woodlands in southwestern Australia measured to 15 m and 18 m (Carbon et al. 1980). Without these two profiles, the mean D_{x95} was reduced to 109 cm with a 95% confidence interval for the mean of about ± 22 cm. Mediterranean shrublands and woodlands had higher proportions of roots at shallow depths than semi-deserts or deserts (Fig. 5C).

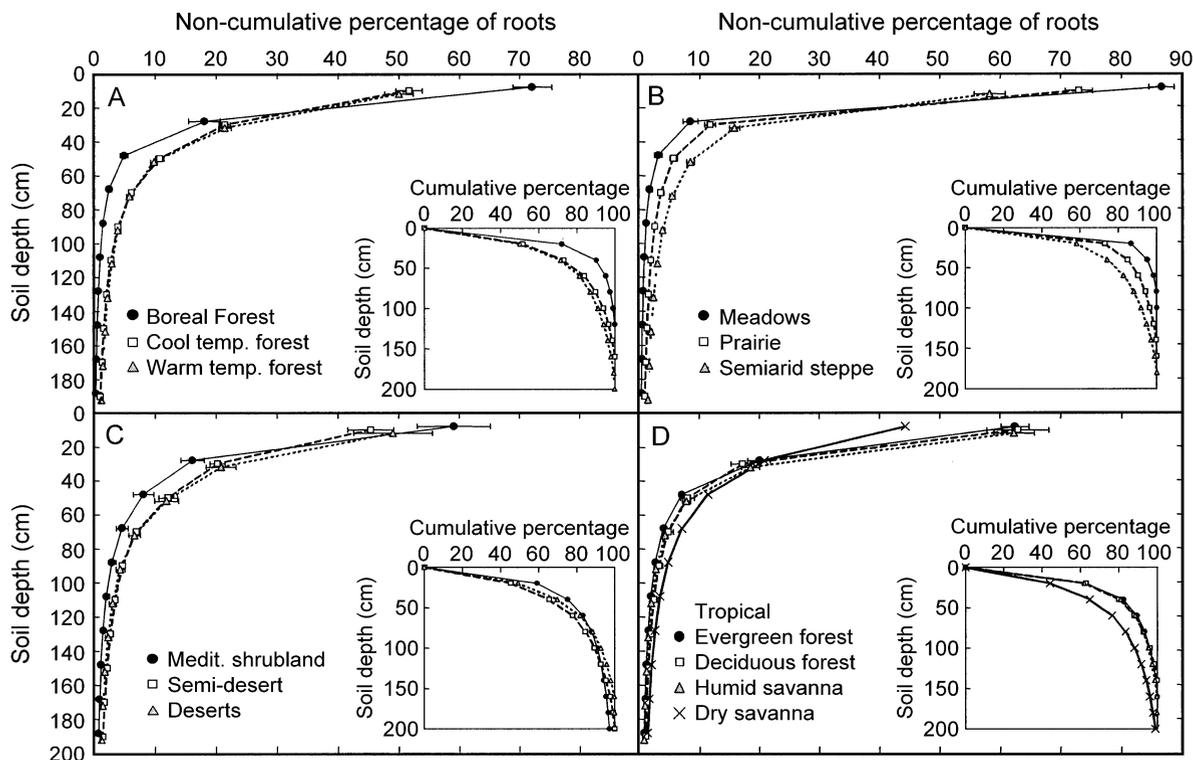Dry tropical savannas had much deeper profiles than

FIG. 5. Extrapolated root profiles for 13 global vegetation types. The large graphs are non-cumulative profiles, and the insets are cumulative profiles. For sample sizes see Table 2. Error bars represent ±1 SE. No differences in rooting depths were found among cool-temperate broadleaved forests, conifer forests, and conifer plantations, and these three categories were combined into one global vegetation type termed "cool-temperate forests" in panel (A).

the three more humid tropical types, which had similar root profiles (Fig. 5D). Tropical cloud forests ($n = 8$; mean $D_{x50} = 7$ cm; mean $D_{x95} = 46$ cm) were more shallowly rooted than tropical lowland forests.

Rooting depths for additional vegetation types were determined only for a few profiles, which does not allow calculation of confidence limits for mean rooting depths. Heathlands appear to be shallowly rooted ($n = 5$; mean $D_{x50} = 11$ cm; mean $D_{x95} = 73$ cm) as are alpine communities ($n = 9$; mean $D_{x50} = 9$ cm; mean $D_{x95} = 71$ cm).

Rooting depths of vegetation dominated by different life-forms

The comparisons of life-form rooting depths were restricted to two climatic ranges that encompass ecosystems dominated by trees, shrubs, semi-shrubs, and grasses. These ranged from semi-deserts to dry forests in the temperate zone (>150–750 mm annual precipitation) and the relatively dry tropical zone (>250–1500 mm annual precipitation). In the temperate zone, communities dominated by grasses had a mean D_{x95} of 89 cm (95% CL 81, 100 cm, $n = 38$), while communities dominated by woody plants (including semi-shrubs, shrubs, and trees) had a significantly deeper mean D_{x95} of 123 cm (as suggested by the bootstrapped confidence

limits of 123 and 126 cm, $n = 79$). There were no significant differences in rooting depths among woody life-forms within this climatic range.

In the tropical zone, communities dominated by grasses had a mean D_{x95} of 123 cm (95% CL = 97, 151 cm; $n = 15$), while communities dominated by woody plants (mostly trees) had a mean D_{x95} that was only slightly and not significantly deeper (mean = 139 cm; 95% CL = 105, 175 cm; $n = 12$). These data suggest that rooting depths of the same life-form across different climatic regions can be as pronounced as the difference between life-forms within a climatic region.

Relationships between climatic variables and rooting depths

On average, D_{x95} values increased with decreasing latitude between 80° and ~30° north or south latitude (amidst much variation) but showed no clear trend for tropical latitudes between 0° and 30° (Fig. 6). There was a conspicuous lack of shallow D_{x95} of <40–50 cm between ~20° and 32° latitude, a zone encompassing mostly dry ecosystems (Bailey 1998). With the exception of this latitudinal belt, shallow D_{x95} values were common throughout the data set independent of climate (Figs. 6 and 7). However maximum D_{x95} values increased with decreasing latitude, warm season length,
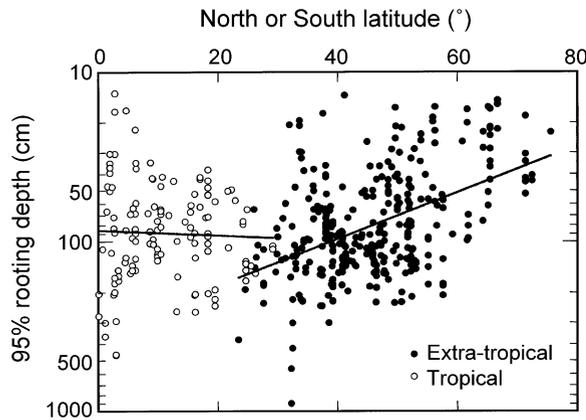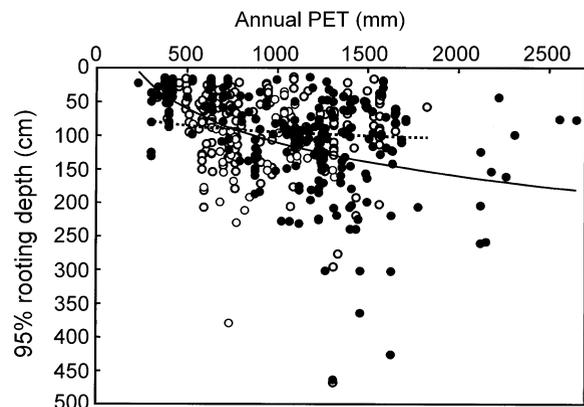
FIG. 6. Extrapolated 95% rooting depths ($n = 475$) as a function of latitude.

FIG. 7. Extrapolated 95% rooting depths ($n = 475$) for global forests and non-forest vegetation (grasslands, shrublands, and savannas) as a function of annual potential evapotranspiration. The trend lines were calculated by logarithmic equations of the form ($y = a \ln x - b$). The r^2 coefficients for the two trend lines are: forests (dashed line) = 0.007, non-forest vegetation (solid line) = 0.146.

and increasing annual PET (Tables 5 and 6). These two patterns caused a roughly fan-shaped relationship of rooting depths with annual PET (Fig. 7).

The relationships of climatic variables with maximum rooting depths within a given climatic range were clearer than with mean rooting depths (Table 6). Deep D_{x95} values of >1.5 m were only found in climates with warm seasons of six months or longer and never in climates with annual precipitation >3000 mm. The deepest D_{x95} values of >2.4 m were found at latitudes below 39° in climates with eight warm months and <1800 mm annual precipitation.

Length of the warm season, annual PET, precipitation, precipitation surplus, latitude, and the depth of the organic layer were significantly ($P < 0.05$) correlated with rooting depths of arctic, boreal, and temperate vegetation (Table 5). Grasslands, shrublands, and savannas had rooting depths that were strongly correlated with almost all of these same variables, but the relationships for forests were weaker. The length of the dry season was correlated with rooting depths

TABLE 5. Spearman rank correlation coefficients for correlations of extrapolated 50% and 95% rooting depths (D_{x50} and D_{x95}) with environmental variables (see Table 3 for definitions of variables).

	Warm season	Annual PET	Annual precipitation	Dry season	Precipitation surplus	Organic layer	Latitude
All temperate and boreal ($n = 335$; organic layer: $n = 315$)							
D_{x50}	**0.388**	**0.369**	0.001	0.074	−0.109	**−0.233**	**−0.359**
D_{x95}	**0.423**	**0.422**	0.092	0.075	−0.034	**−0.340**	**−0.374**
Temperate and boreal forests ($n = 149$; organic layer: $n = 132$)							
D_{x50}	**0.342**	**0.257**	**0.257**	−0.111	*0.196*	**−0.306**	**−0.305**
D_{x95}	**0.284**	**0.237**	*0.195*	−0.005	**0.236**	**−0.295**	**−0.248**
Temperate and boreal grasslands and shrublands and savannas ($n = 186$; organic layer: $n = 183$)							
D_{x50}	**0.444**	**0.490**	**−0.301**	**0.419**	**−0.448**	**−0.332**	**−0.454**
D_{x95}	**0.488**	**0.509**	−0.026	**0.265**	**−0.307**	**−0.503**	**−0.455**
All tropical ($n = 135$; organic layer: $n = 130$)							
D_{x50}	*0.192*	0.011	**−0.364**	**0.363**	**−0.306**	−0.101	−0.075
D_{x95}	*0.216*	0.161	**−0.364**	**0.392**	**−0.363**	**−0.373**	0.013
Tropical forests ($n = 86$; organic layer: $n = 82$)							
D_{x50}	*0.219*	0.037	*−0.232*	*0.244*	−0.167	0.033	−0.001
D_{x95}	*0.242*	*0.246*	**−0.264**	**0.353**	**−0.330**	**−0.393**	0.121
Tropical grasslands and shrublands and savannas ($n = 49$)							
D_{x50}	NA	−0.158	**−0.377**	*0.304*	*−0.317*	NA	−0.154
D_{x95}	NA	−0.095	−0.145	0.090	−0.069	NA	−0.151

Notes: Models including the depth of organic layers as independent variables excluded all profiles that had no information on the depth of the organic layer but included profiles without organic layers. Coefficients marked in boldface are statistically significant at $P < 0.01$; those marked in bold italics are significant at $P < 0.05$. Significance levels are not adjusted for multiple comparisons.

TABLE 6. Climatic limits for the occurrence of 95% rooting depths exceeding 0.3, 0.6, 0.9, 1.2, 1.5, 2.1, and 2.4 m.

95% rooting depth (m)	Latitude	Annual PET (PET$_a$) in mm	Growing season (mo)	Annual precipitation (R_a) in mm	R_a/PET$_a$
>0.3	<72°30′	>300	≥3		
>0.6	<65°30′	>300	≥4		<4.0
>0.9	<62°00′	>300	≥4		<4.0
>1.2	<58°00′	>300	≥4	≤3000	<3.3
>1.5	<58°00′	>575	≥6	≤3000	<2.5
>2.1	<58°00′	>725	≥6	≤1800	<2.5
>2.4	<39°00′	>725	≥8	≤1800	<2.5

Note: For definitions of environmental variables see Table 3.
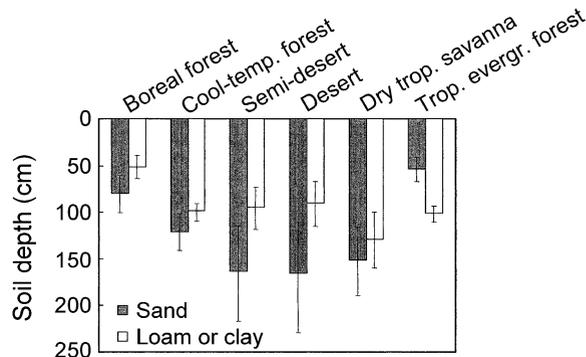

FIG. 8. Extrapolated 95% rooting depths for six global vegetation types with measurements in both sandy and fine-textured (loam to clay) soils. Error bars represent 95% confidence intervals for means, based on sample sizes and estimates of interpolation and extrapolation errors depicted in Fig. 2B.

in non-forest vegetation. For temperate, boreal, and arctic systems in general, rooting depths increased significantly with increasing length of the warm season and annual PET and decreased with increasing latitude and depth of the organic layer (Table 5). Rooting depths in forests increased with increasing annual precipitation and precipitation surplus, but generally showed the reverse trend in non-forest vegetation.

Relationships of rooting depths with environmental variables were generally weaker for tropical vegetation, especially with annual PET and the length of the warm season (Table 5). These results may reflect the narrower range of these variables in the tropics. In contrast, annual precipitation was generally more strongly correlated with rooting depths in tropics than outside the tropics. Rooting depths in the tropics were negatively correlated with annual precipitation and mostly positively correlated with the length of the dry season. Tropical forests showed a strongly negative correlation of D_{x95} with the depth of the organic layer, but no effects of the organic layer on D_{x50}.

Rooting depth and soil characteristics

Of the six vegetation types in Table 2 with enough replicates to compare rooting depths and soil texture, sandy soils had deeper D_{x95} values than loam or clay soils in boreal forests, cool-temperate forests, semi-desert shrublands, deserts, and dry tropical savannas (Fig. 8). The only system where this was not the case was tropical evergreen forest, which apparently had shallower rooting depths in sandy soils.

Organic horizons contained substantial amounts of roots in all forest types. Forest profiles had an average of 16 ± 3% of fine roots in organic horizons (*n* = 92), and 17 ± 2% of total roots (*n* = 142). Mean depths of the organic horizons containing roots (usually excluding the L layer of undecomposed litter) were 11.0 ± 1.9 cm (*n* = 29) for boreal forests, 4.0 ± 0.7 cm (*n* = 60) for cool-temperate forests, 0.7 ± 0.3 cm (*n* = 20) for warm-temperate forests, and 3.9 ± 0.9 cm (*n* = 80) for tropical forests. Rooting depths decreased in all

forest systems as the depth of organic horizons increased (Table 5).

General Linear Models of rooting depths

Of the variables examined globally, climatic variables explained the greatest proportion of variation for rooting depths in the general linear model (GLM) analysis (Table 7). Climate variables explained ~20% of the variance in D_{x50} and D_{x95} on average, explaining substantially more variance for vegetation not dominated by trees (>30%) than for tree-dominated vegetation (Table 7). Globally, soil characteristics were correlated relatively weakly with rooting depths, and effects were stronger in vegetation not dominated by trees. The most important soil factor globally was the depth of the organic horizon for 95% rooting depths, with soil texture contributing little globally (and in contrast to the strong effects of texture within systems; Fig. 8). Life-form dominance classes also had low correlation coefficients with rooting depths globally. The strongest influence of life-forms was on D_{x50} values outside the tropics, which reflected the strong difference in D_{x50} between grasslands and forests (Fig. 4). The combination of life-form dominance with climate and soil variables explained ~30% of the variance in rooting depths on average. Vegetation type alone explained almost as much of the variance in rooting depths as the combination of life-form dominance class with climate and soil, probably because ecosystems within vegetation types tend to share climate and soil characteristics. Models including both vegetation type and climatic variables on average had the strongest correlations with rooting depths, explaining 35–51% of the variance in 95% rooting depths for all vegetation types except tropical forests.

Extrapolations of rooting depths had no effect on the strengths of their relationships with environmental variables. Correlation coefficients were not significantly different for correlations using extrapolated rooting

TABLE 7. Proportion of the variances explained in general linear models of extrapolated 50% and 95% rooting depths as functions of six climatic variables, two soil variables, and life-form dominance classes (Table 3), vegetation types (Table 2), and sampling depths.

Variables used in general linear models	n	Climate	Soil	Life-form	Life-form + climate + soil	Vegetation type	Vegetation type + climate	Life-form + climate + soil + sample depth
50% rooting depths								
Global: all	475	0.12	0.05	0.15	0.24	0.20	0.25	**0.30**
Global: no trees	235	**0.31**	0.07	0.23	**0.40**	**0.41**	**0.43**	**0.40**
Global: trees	240	0.06	0.06	⋯	0.11	0.25	0.27	0.17
Non-tropical: all	339	0.14	0.04	0.23	**0.33**	0.18	0.26	**0.36**
Non-tropical: no trees	186	**0.31**	0.06	0.30	**0.46**	**0.42**	**0.45**	**0.46**
Non-tropical: trees	153	0.11	0.06	⋯	0.11	0.25	0.26	0.25
Tropical: all	136	0.22	0.11	0.09	0.22	0.24	0.30	**0.33**
Tropical: no trees	49	0.26	0.00	0.03	**0.37**	0.20	0.26	**0.43**
Tropical: trees	87	0.19	0.13	⋯	0.27	0.18	0.29	**0.39**
95% rooting depths								
Global: all	475	0.16	0.17	0.05	0.26	0.26	**0.31**	**0.55**
Global: no trees	235	**0.34**	0.24	0.09	**0.34**	**0.43**	**0.45**	**0.61**
Global: trees	240	0.12	0.13	⋯	0.22	**0.31**	**0.39**	**0.56**
Non-tropical: all	339	0.25	0.18	0.08	**0.39**	0.30	**0.37**	**0.59**
Non-tropical: no trees	186	**0.38**	0.24	0.10	**0.50**	**0.44**	**0.46**	**0.62**
Non-tropical: trees	153	**0.31**	0.14	⋯	**0.37**	**0.42**	**0.51**	**0.62**
Tropical: all	136	0.15	0.17	0.08	0.20	0.15	0.15	**0.58**
Tropical: no trees	49	0.00	0.00	0.00	0.13	0.20	**0.39**	**0.65**
Tropical: trees	87	0.21	0.17	⋯	0.26	0.13	0.21	**0.57**

Notes: Models were developed for the whole global data set, for non-tropical data only, and for tropical data only. The proportions listed are the r^2 values for the best-fit models. Models that explained >30% of the variance in rooting depths are highlighted in bold.

depths than for those using non-extrapolated ones (Fig. 9; Appendix C, Table C1). Non-extrapolated rooting depths in the subset of profiles that were sampled to the maximum rooting depth or to ≥2 m largely showed the same correlations with environmental variables as did the extrapolated rooting depths of that subset of profiles that did not fit these criteria (Appendix C, Table C2). One notable exception was the lack of a correlation between extrapolated 95% rooting depths and latitude, which apparently was caused by the scarcity ($n = 8$) of deep (>2 m) D_{x95} in this data set of 375 extrapolated profiles.

Effects of sampling depths on extrapolated estimates of rooting depths were examined using the differences between r^2 coefficients of GLMs that did and did not include sampling depth. In boreal and temperate ecosystems, sampling depths explained 11–12% of the variance in D_{x95} in addition to the proportion explained by abiotic and biotic variables, which ranged from 39% to 51% (Table 7). In tropical ecosystems, sampling depths explained a far greater proportion of the variance in D_{x95}, between 26% and 31%, suggesting a fairly strong methodological bias in the estimates of tropical rooting depths. This result and the evidence that tropical samples are often under-sampled with respect to depth (Fig. 3) highlight the need for better estimates of rooting depth in tropical systems.

DISCUSSION

Of all the biotic and abiotic factors examined, climate explained the largest proportion of global varia-

tion in rooting depths (Table 7). A large part of that variation correlated strongly with climatic variables that characterize supply and evaporative demand for water. Differences in life-forms between sites accounted for the next largest proportion of the observed variation. This proportion may also be due in part to climate, because differences in the life-form dominance of ecosystems are driven in part by climatic factors (Woodward 1987, Box 1996). Differences in soils explained very little of the variation in rooting depths globally, but this may be due in part to a lack of detailed information on soil characteristics. They were quite important for results within ecosystems or vegetation types (Fig. 8).

Extrapolations of rooting depths did not affect their relationships with environmental variables (Fig. 9), which suggests that extrapolation of shallowly sampled profiles did not add additional random or systematic error. If it had, we would expect a weakening of the relationships between environmental variables and rooting depths, because the extrapolation errors should not be correlated with environmental variables. In fact, the correlations were weaker for the subset of shallowly sampled profiles that were extrapolated than for the subset of more deeply sampled profiles that were not (Appendix C, Table C2). This may have been partly caused by our conservative extrapolation procedure, which limited extrapolations to twice the sampling depth or to a maximum depth of 3 m. That the overall relationships with environmental variables were similar
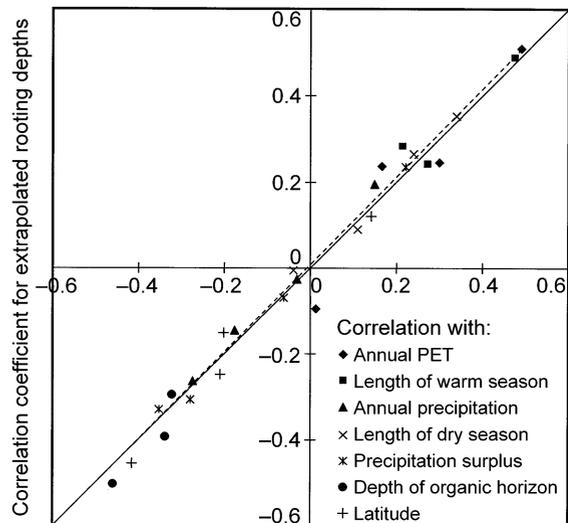
FIG. 9. Comparison of Spearman rank correlation coefficients between correlations of non-extrapolated 95% rooting depths and correlations of extrapolated 95% rooting depths with environmental variables. The data points are the coefficients listed for extrapolated 95% rooting depths in Table 5 and for non-extrapolated 95% rooting depths in Table B1 (Appendix B). Included in the graph are the coefficients for temperate and boreal forests, temperate and boreal grasslands, shrublands, and savannas, tropical forests, and tropical grasslands, shrublands, and savannas. The solid line depicts the one-to-one relationship. The dashed line depicts a linear regression through the data points ($r^2 = 0.993$), with a slope ($\pm$ 1 SE) of 1.015 ± 0.017 ($P < 0.001$) and intercept of 0.006 ± 0.005 ($P = 0.238$).

for both subsets of the data enabled us to combine them for most analyses, increasing sample sizes and the representation of root profiles from different vegetation types.

On the interpretation of 95% rooting depths

D_{95} values are a measure of the soil depth that holds the bulk of roots, but they are not necessarily closely correlated with maximum rooting depths. Consider the example of temperate grasslands. Semi-arid steppes with $\leq$500 mm annual precipitation had significantly deeper D_{x95} values than prairies with >500 mm precipitation (Fig. 4), but relative root densities below 1.4 m were similar in the two systems (Fig. 5B). Data from Weaver and colleagues show that maximum rooting depths of species in North American grasslands with >500 mm precipitation are on average 2.3 ± 0.2 m ($n = 66$), while species in grasslands with $\leq$500 mm reach only 1.8 ± 0.1 m ($n = 64$) (Weaver 1919, 1920, 1954, 1958, Weaver and Darland 1949). Thus according to the Weaver data set, the absolute depth reached by roots in prairies is greater than in semi-arid grasslands. Our data add additional information to the data of Weaver and colleagues by showing that the bulk of roots in prairie is located much more shallowly than in semi-

arid grasslands (Fig. 5B). These results raise important questions about the functional importance of the deepest 5% of root systems in grasslands and elsewhere. In most systems, the bulk of root activity will be restricted to the zone of 95% rooting depth, but the deepest 5% of roots may contribute an important percentage of ecosystem transpiration in some environments (Stone and Kalisz 1991, Nepstad et al. 1994, Jackson et al. 1999). A possible example is the case where a few deeply rooted plants make water available to more shallowly rooted plants through hydraulic lift (Caldwell et al. 1998).

General patterns in global rooting depths

One interesting finding of this study is that 50% of all roots are within 30 cm (mean 18 ± 1 cm) of the soil surface (or the surface of the organic horizon, where present) in 85% of all profiles examined. In no profile would it have been necessary to dig deeper than 80 cm to sample 50% of all roots. Moreover root densities are highest in the upper 20 cm of the soil profile, including organic horizons, in ~95% of all profiles. Several factors probably contribute to these patterns. Surface layers generally contain the highest concentrations of N, P, and K globally (Sposito 1989, Jobbágy and Jackson 2001). Oxygen deficiencies are also least likely in shallow soil layers. Our data show that ecosystems with thick organic horizons tend to have higher concentrations of roots in these horizons, most likely because they store nutrients and have large water-holding capacities. The high concentrations of roots in these organic layers lead to relatively shallow overall rooting depths.

Only ~6% of all profiles in the database had lower root densities in the upper 20 cm of the profile than in the interval from 20 cm to 40 cm. Of these, more than four-fifths were in deserts, savanna, grasslands, or dry forests with at least one arid month during the growing season (mean 6.1 ± 0.7 mo). These are ecosystems where the upper soil horizons are likely to be too dry for resource uptake during part of the growing season.

Our data suggest that globally 95% of all roots are within 2 m of the soil surface, which was the case in 92% of all profiles. However only 18 studies in the database sampled root profiles to 3 m or more (Table 1), and more importantly only 9% of the 475 root profiles were sampled to a depth at which no further roots were found. This made it necessary to extrapolate profiles in order to estimate the amounts of roots at greater depths. It also highlights the gap in current knowledge for the placement and functioning of relatively deep roots. D_{95} values >2 m are likely more common than suggested by the data in this study. About 30% of the variance in extrapolated D_{x95} for tropical ecosystems is explained by sampling depth, which suggests that many tropical root profiles are sampled too shallowly to allow adequate estimates of D_{95}. Extrapolations of root profiles in seasonally dry tropical environments are often

difficult because they tend to have high root densities close to the soil surface and nearly constant densities from 1 m to $\gg 2$ m depth (Kellman and Roulet 1990, Vandenbeldt 1991, Nepstad et al. 1994, Sternberg et al. 1998). Estimates of D_{95} in such profiles are highly dependent on the cutoff depth chosen for extrapolation. There clearly is an important need for more studies of deep root distributions and functioning in tropical environments.

There was no significant difference between D_{95} for fine and total roots in forests, which suggests that errors introduced by combining these measurements in our analyses were likely small. But D_{50} values in forests were slightly deeper for total than for fine roots, suggesting that some of the estimates for D_{x50} in woody vegetation (e.g., Fig. 4 and Table 4) may be ~3–6 cm deeper than they would be for fine roots alone.

Effects of climate on rooting depths for vegetation types

Mean and maximum D_{95} values increased with decreasing latitude from arctic regions to the edge of the tropical climatic zone (Fig. 6, Table 6). This increase appears to be primarily driven by warmer temperatures, longer growing seasons, and increased evaporative demand. These climatic factors largely explain the increase in mean rooting depths from boreal to cool- and warm-temperate forests (Fig. 5A).

Differences in rooting depths between and within tropical vegetation types appear to be less pronounced than between and within arctic, boreal, and temperate ones (Fig. 4). However tropical cloud forests and floodplain forests are apparently more shallowly rooted than the drier vegetation types examined in this study, and it is likely that rooting depths in the tropics are as variable as the soil water regimes in this zone. In general, root profiles in the tropics become shallower with increased precipitation and precipitation surplus, and become deeper in systems with a longer dry season (Table 5). Rooting depths in the tropics were more highly correlated with precipitation than with PET, suggesting that they are driven more by water supply than by uniformly high evaporative demand (generally >1000 mm of PET per year, except in cloud forests).

Water supply and demand appear to have a stronger influence on rooting depths in non-forest vegetation than in forests (e.g., Fig. 7), likely because forests tend to grow under conditions where water is less limiting. For example, the degree of aridity (e.g., length of the dry season) was highly correlated with rooting depths in temperate and boreal grasslands, shrublands, and savannas, but not in temperate and boreal forests (Table 5). Precipitation appears to be the driving factor for differences in rooting depths between prairies and semi-arid steppes, which occur at similar latitudes with similar evaporative demands (Sims et al. 1978). The mean depth of infiltration is often smaller in semi-arid grasslands than in more humid ones, but the upper soil

layers are also more likely to be dry during parts of the growing season (Sala et al. 1992). Meadows and pastures in the forest zone tend to be even more humid than prairies and have lower evaporative demands, which may explain their shallower root profiles (Figs. 4 and 5B).

Within a climatic zone (i.e., boreal, temperate, tropical), arid and semi-arid systems tend to have deeper 50% and 95% rooting depths than humid ones (Fig. 4). This probably reflects a tendency in water-limited ecosystems for plants to access water that was stored at depth during occasional or seasonal wet periods. This may also explain why 95% rooting depths in deserts are shallower than in semi-arid systems, such as temperate and tropical dry savanna and mediterranean shrublands and woodlands (Fig. 4). The main limit to rooting depths in arid ecosystems may be the depth of water infiltration, which can be extremely shallow on slopes and can be quite deep in low-lying areas. The profiles in our database were mostly from relatively level sites that are unlikely to receive or contribute much runoff or lateral movement of water (though few studies measure lateral movement directly). Rooting depths can be very deep locally in periodically flooded desert playas (Freckman and Virginia 1989), but we classified such sites as wetlands and did not include them in our analysis. Differences in the depth of infiltration may also partly explain the observation that water-limited ecosystems tended to have deeper roots in coarse-textured than in fine-textured soils (Fig. 8), because coarse-textured soils have lower water-holding capacities and water tends to percolate more deeply. Other factors being equal, rooting depths are predicted to be deeper in coarse textured soils based on the hydraulic properties of plants and the soil (Sperry et al. 1998, Jackson et al. 2000b).

Vertical root distributions in water-limited systems may be poorly correlated with long-term means of precipitation because of the importance of interannual variation in rainfall (Williams and Ehleringer 2000). Rooting depths in water-limited systems may be substantially deeper than the average depth of infiltration predicted just from annual mean precipitation, in part because plants in such systems are most active in wet years with deep infiltration. Vertical root distributions in such ecosystems may perhaps be better predicted using long-term frequency distributions of precipitation rather than mean annual water infiltration depths.

Effects of plant life-forms on rooting depths

Studies of rooting depths for individual species have clearly shown that woody plants are, on average, more deeply rooted than herbaceous ones (e.g., Shalyt 1952, Baitulin 1979, Kutschera and Lichtenegger 1997, Schenk and Jackson 2002). However this statement may be more valid for comparisons of maximum rooting depths of woody and herbaceous life-forms than for 95% rooting depths of life-forms co-occurring with-

in a given ecosystem. The 14 root profiles in our database that have separate information on roots of woody plants and grasses from the same sites included six that have about equal D_{95} for both, three with deeper D_{95} for woody plants, and five with deeper D_{95} for grasses. Studies comparing water use of co-occurring plant life-forms have shown that woody plants took up water from deeper layers than herbaceous ones in some systems (Sala et al. 1989, Ehleringer et al. 1991), but not in others (Le Roux et al. 1995, Le Roux and Bariac 1998).

For comparisons among different sites, our data support the hypothesis that forests and shrublands are on average more deeply rooted than grasslands, but only for temperate regions (although comparisons of rooting depths among tropical sites may be hampered by insufficient sampling depths). Overall, differences in 95% rooting depths between shrublands and grasslands under similar climatic conditions were less pronounced than the differences in maximum rooting depths commonly observed between shrubs/semi-shrubs and grasses (e.g., Baitulin 1979, Schenk and Jackson 2002). The reasons for this may include that deep roots in woody plants likely constitute only a small percentage of all roots and that ''shrubland'' and ''grassland'' ecosystems, their names notwithstanding, often contain mixed woody and herbaceous plants.

For predictions on a global scale it may be undesirable to assign fixed rooting depths to life-forms or to simple life-form dominance classes, such as grasslands, shrublands, or forests. In our analysis, 95% rooting depths were more strongly related to climatic variables than to life-form dominance classes (Table 7). For example, grasslands were on average more deeply rooted in tropical regions than in temperate ones.

Rooting depths in vegetation and biogeochemistry models

The data for global vegetation types summarized in Fig. 4 and Table 4 are potentially useful in global biogeography and biogeochemistry models and in land surface parameterization schemes for general circulation models (Zeng et al. 1998, Jackson et al. 2000a), but there are some caveats. Current models generally allow for maximum rooting depths of 1 m to 2 m, similar to the 95% rooting depths determined in this study (Jackson et al. 2000a). However the remaining 5% of roots may reach much greater depths in some ecosystems, and our results showing the strong effects of climate on rooting depths suggest that many systems may have at least some species that reach water at depth if it is available and if there is evaporative demand for it. Simulated transpiration rates in global models are often sensitive to estimated rooting depths (Jackson et al. 2000a), and more comparisons of field measurements with modeled data are needed to determine whether it is better to use maximum rooting depths (e.g., Table 6) or mean rooting depths (e.g., Table 4)

in models. Users of our data should bear in mind that rooting depths varied greatly among sites and that our models accounted for at most 50% of the observed variance.

Models that use fixed, mean rooting depths may predict water limitations under scenarios that increase evaporative demands because they do not allow roots to access water stored at greater depth (Jackson et al. 2000a). An unresolved question is how often such water limitations occur in nature due to a lack of deep roots. Equally unresolved for climate change scenarios is how quickly, if at all, existing plants could grow deeper roots if water stress increased in a system (and whether deeply rooted species would increase in abundance). Studies in North American prairie during the great drought of 1933–1940 generally found reduced rooting depths during drought, but deeply rooted species survived better than did shallowly rooted species (Weaver and Albertson 1943). Invasion of deeply rooted species in response to climatic change, such as encroachment of shrubs into grassland, may also depend on whether the conditions allow seedling establishment of the more deeply rooted species (e.g., Neilson 1986, Anderson et al. 2001). Many other related issues remain uncertain, including the global importance of such processes as hydraulic lift that can make deeper soil water available to more shallowly rooted species (Caldwell et al. 1998, Horton and Hart 1998, Jackson et al. 2000b).

Generalizations about ''deep'' and ''shallow'' roots abound in the literature. This study provides a framework in which such generalizations can be tested and new data can be added. Our results also highlight specific systems, such as tropical ones, where deeper root sampling is needed. We also acknowledge the need for a better understanding of root functioning at depth and the integration of root and shoot processes. Such integration will likely improve our predictions and understanding of water use, nutrient uptake, and other plant and ecosystem processes locally, regionally, and globally.

of the Hydrological Cycle (BAHC) Core Projects of the International Geosphere Biosphere Programme (IGBP).

Literature Cited

Anderson, L. J., M. S. Brumbaugh, and R. B. Jackson. 2001. Water and tree–understory interactions: a natural experiment in a savanna with oak wilt. Ecology **82**:33–49.

Bailey, R. G. 1998. Ecoregions: the ecosystem geography of the oceans and continents. Springer-Verlag, New York, New York, USA.

Baitulin, I. O. 1979. Kornevaja sistema rastenij aridnoj zony Kazakhstana. [Root systems of plants of the arid zone of Kazakhstan.] [In Russian.] Nauka, Alma-Ata.

Bille, J. C. 1977. Étude de la production primaire nette d'un écosystème Sahélien. Travaux et Documents de l'O.R.S.T.O.M. 65. O.R.S.T.O.M., Paris, France.

Bormann, B. T., D. Wang, F. H. Bormann, G. Benoit, R. April, and M. C. Snyder. 1998. Rapid, plant-induced weathering in an aggrading experimental ecosystem. Biogeochemistry **43**:129–155.

Box, E. O. 1981. Predicting physiognomic vegetation types with climate variables. Vegetatio **45**:127–139.

Box, E. O. 1996. Plant functional types and climate at the global scale. Journal of Vegetation Science **7**:309–320.

Bruijnzeel, L. A., and J. Proctor. 1995. Hydrology and biogeochemistry of tropical montane cloud forests: What do we really know? Pages 38–78 *in* L. S. Hamilton, J. O. Juvik, and F. N. Scatena, editors. Tropical montane cloud forests. Ecological Studies 110. Springer-Verlag, New York, New York, USA.

Cairns, M. A., S. Brown, E. H. Helmer, and G. A. Baumgardner. 1997. Root biomass allocation in the world's upland forests. Oecologia **111**:1–11.

Caldwell, M. M., T. E. Dawson, and J. H. Richards. 1998. Hydraulic lift: consequences of water efflux from the roots of plants. Oecologia **113**:151–161.

Canadell, J., R. B. Jackson, J. R. Ehleringer, H. A. Mooney, O. E. Sala, and E.-D. Schulze. 1996. Maximum rooting depth of vegetation types at the global scale. Oecologia **108**:583–595.

Carbon, B. A., G. A. Bartle, A. M. Murray, and D. K. MacPherson. 1980. The distribution of root length, and the limits to flow of soil water to roots in a dry sclerophyll forest. Forest Science **26**:656–664.

Cerri, C. C., and B. Volkoff. 1987. Carbon content in a yellow Latosol of central Amazon rain forest. Acta Oecologica. Oecologia Generalis **8**:29–42.

Chen, Z., H. Chang, and B. Wang. 1994. Studies on biomass and production of the lower subtropical evergreen broad-leaved forest in Heishiding nature reserve, China. VI. Distribution, biomass and production of roots. Journal of Tropical Ecology **10**:273–279.

Choudhury, B. J. 1997. Global pattern of potential evaporation calculated from the Penman-Monteith equation using satellite and assimilated data. Remote Sensing of Environment **61**:64–81.

Choudhury, B. J., and N. E. DiGirolamo. 1998. A biophysical process-based estimate of global land surface evaporation using satellite and ancillary data. I. Model description and comparison with observations. Journal of Hydrology **205**:164–185.

Coupland, R. T., and R. E. Johnson. 1965. Rooting characteristics of native grassland species in Saskatchewan. Journal of Ecology **53**:475–507.

Dickinson, R. E., A. Henderson-Sellers, and P. J. Kennedy. 1993. Biosphere Atmosphere Transfer Scheme (BATS) Version 1e as coupled to the NCAR Community Climate Model. NCAR Technical Note TN-387+STR. National Center for Atmospheric Research, Boulder, Colorado, USA.

Ehleringer, J. R., S. L. Phillips, W. S. F. Schuster, and D. R. Sandquist. 1991. Differential utilization of summer rains by desert plants. Oecologia **88**:430–434.

Freckman, D. W., and R. A. Virginia. 1989. Plant-feeding nematodes in deep-rooting desert ecosystems. Ecology **70**:1665–1678.

Gale, M. R., and D. F. Grigal. 1987. Vertical root distribution of northern tree species in relation to successional status. Canadian Journal of Forest Research **17**:829–834.

GCOS/GTOS Terrestrial Observation Panel for Climate. 1997. GCOS/GTOS plan for terrestrial climate-related observations. Version 2. GCOS-32. WMO/TD-No. 796. UNEP/DEIA/TR.97-7. World Meteorological Organization. Global Climate Observing System (GCOS), Geneva, Switzerland.

Haxeltine, A., and I. C. Prentice. 1996. BIOME3: an equilibrium terrestrial biosphere model based on ecophysiological constraints, resource availability, and competition among plant functional types. Global Biogeochemical Cycles **10**:693–709.

Hertel, D. 1999. Das Feinwurzelsystem von Rein- und Mischbeständen der Rotbuche: Struktur, Dynamik und interspezifische Konkurrenz. Dissertationes Botanicae 317. J. Cramer, Berlin, Germany.

Higgins, K. B., A. J. Lamb, and B. W. van Wilgen. 1987. Root systems of selected plant species in mesic mountain fynbos in the Jonkershoek Valley, south-western Cape Province. South African Journal of Botany **53**:249–257.

Horton, J. L., and S. C. Hart. 1998. Hydraulic lift: a potentially important ecosystem process. Trends in Ecology and Evolution **13**:232–235.

Hosegood, P. H. 1963. The root distribution of Kikuyu grass and Wattle trees. East African Agricultural and Forestry Journal **29**:60–61.

Jackson, R. B., J. Canadell, J. R. Ehleringer, H. A. Mooney, O. E. Sala, and E.-D. Schulze. 1996. A global analysis of root distributions for terrestrial biomes. Oecologia **108**:389–411.

Jackson, R. B., H. A. Mooney, and E.-D. Schulze. 1997. A global budget for fine root biomass, surface area, and nutrient contents. Proceedings of the National Academy of Sciences (USA) **94**:7362–7366.

Jackson, R. B., L. A. Moore, W. A. Hoffmann, W. T. Pockman, and C. R. Linder. 1999. Ecosystem rooting depth determined with caves and DNA. Proceedings of the National Academy of Sciences (USA) **96**:11387–11392.

Jackson, R. B., et al. 2000*a*. Belowground consequences of vegetation change and their treatment in models. Ecological Applications **10**:470–483.

Jackson, R. B., J. S. Sperry, and T. E. Dawson. 2000*b*. Root water uptake and transport: using physiological processes in global predictions. Trends in Plant Science **5**:482–488.

Jama, B., R. J. Buresh, J. K. Ndufa, and K. D. Shepherd. 1998. Vertical distribution of roots and soil nitrate: tree species and phosphorus effects. Soil Science Society of America Journal **62**:280–286.

Jobbágy, E. G., and R. B. Jackson. 2000. The vertical distribution of soil organic carbon and its relation to climate and vegetation. Ecological Applications **10**:423–436.

Jobbágy, E. G., and R. B. Jackson. 2001. The distribution of soil nutrients with depth: global patterns and the imprint of plants. Biogeochemistry **53**:51–77.

Johnston, C. D., D. H. Hurle, D. R. Hudson, and M. I. Height. 1983. Water movement through preferred paths in lateritic profiles of the Darling Plateau, Western Australia. CSIRO Groundwater Research Technical Paper **1**:1–34.

Kellman, M., and N. Roulet. 1990. Nutrient flux and retention in a tropical sand-dune succession. Journal of Ecology **78**:664–676.

Kutschera, L., and E. Lichtenegger. 1982. Wurzelatlas mit-

teleuropäischer Grünlandpflanzen. Band 1: Monocotyle-donae. Gustav Fischer, Stuttgart, Germany.

Kutschera, L., and E. Lichtenegger. 1997. Bewurzelung von Pflanzen in verschiedenen Lebensräumen. 5. Band der Wurzelatlas-Reihe. Stapfia 49. Land Oberösterreich, OÖ. Landesmuseum, Linz, Austria.

Leishman, M. R., and M. Westoby. 1992. Classifying plants into groups on the basis of associations of individual traits–evidence from Australian semi-arid woodlands. Journal of Ecology **417**:417–424.

Le Roux, X., and T. Bariac. 1998. Seasonal variations in soil, grass and shrub water status in a West African humid savanna. Oecologia **113**:456–466.

Le Roux, X., T. Bariac, and A. Mariotti. 1995. Spatial partitioning of the soil water resource between grass and shrub components in a West African humid savanna. Oecologia **104**:147–155.

Lichtenegger, E. 1996. Root distribution in some alpine plants. Acta Phytogeographica Suecica **81**:76–82.

Lucot, E., and S. Bruckert. 1992. Organisation du système racinaire du chêne pédonculé (*Quercus robur*) développé en conditions édaphiques non contraignantes (sol brun lessivé colluvial). Annales des Sciences Forestieres **49**:465–479.

Mahfouf, J.-F., C. Ciret, A. Ducharne, P. Irannejad, J. Noilhan, Y. Shao, P. Thornton, Y. Xue, and Z.-L. Yang. 1996. Analysis of transpiration results from the RICE and PILPS workshop. Global and Planetary Change **13**:73–88.

Meek, B. D., E. R. Rechel, L. M. Carter, W. R. DeTar, and A. L. Urie. 1992. Infiltration rate of sandy loam soil: effects of traffic, tillage, and plant roots. Soil Science Society of America Journal **56**:908–913.

Miroshnichenko, Y. M. 1975. Kornevye sistemy drevesnych i kustarnikovych rastenij i ich zkologija v vostocnych karakumach. [Root systems of trees and bushes and their ecology in eastern Karakum.] [In Russian.] Botanicheskii Zhurnal **60**:1776–1795.

Nechaeva, N. T. 1985. Description of plants used for vegetative range improvement. Pages 55–120 *in* N. T. Nechaeva, editor. Improvement of desert ranges in Soviet Central Asia. Advances in desert and arid land technology and development 4. Harwood Academic Publishers, Chur, Switzerland.

Neilson, R. P. 1986. High-resolution climatic analysis and Southwest biogeography. Science **232**:27–34.

Neilson, R. P. 1995. A model for predicting continental-scale vegetation distribution and water balance. Ecological Applications **5**:362–385.

Nepstad, D. C., C. R. de Carvalho, E. A. Davidson, P. H. Jipp, P. A. Lefebvre, G. H. Negreiros, E. D. da Silva, T. A. Stone, S. E. Trumbore, and S. Vieira. 1994. The role of deep roots in the hydrological and carbon cycles of Amazonian forests and pastures. Nature **372**:666–669.

Popov, K. P. 1979. Fistashka v srednei Azii. [The pistachio in central Asia.] [In Russian.] Ylym, Ashkhabad.

Prentice, I. C., W. Cramer, S. P. Harrison, R. Leemans, R. A. Monserud, and A. M. Solomon. 1992. A global biome model based on plant physiology and dominance, soil properties and climate. Journal of Biogeography **19**:117–134.

Roupsard, O., A. Ferhi, A. Granier, F. Pallo, D. Depommier, B. Mallet, H. I. Joly, and E. Dreyer. 1999. Reverse phenology and dry-season water uptake by *Faidherbia albida* (Del.) A. Chev. in an agroforestry parkland of Sudanese West Africa. Functional Ecology **13**:460–472.

Sala, O. E., R. A. Golluscio, W. K. Lauenroth, and A. Soriano. 1989. Resource partitioning between shrubs and grasses in the Patagonian steppe. Oecologia **81**:501–505.

Sala, O. E., W. K. Lauenroth, and R. A. Golluscio. 1997. Plant functional types in temperate semi-arid regions. Pages 217–233 *in* T. M. Smith, H. H. Shugart, and F. I. Woodward,

editors. Plant functional types. Cambridge University Press, Cambridge, UK.

Sala, O. E., W. K. Lauenroth, and W. J. Parton. 1992. Long-term soil water dynamics in the shortgrass steppe. Ecology **73**:1175–1181.

Schenk, H. J., and R. B. Jackson. 2002. Rooting depths, lateral root spreads, and belowground/aboveground allometries of plants in water-limited ecosystems. Journal of Ecology, *in press*.

Schimper, A. F. W. 1898. Pflanzen-Geographie auf physiologischer Grundlage. Gustav Fischer, Jena, Germany.

Schulze, E.-D., H. A. Mooney, O. E. Sala, E. Jobbágy, N. Buchmann, G. Bauer, J. Canadell, R. B. Jackson, J. Loreti, M. Oesterheld, and J. R. Ehleringer. 1996. Rooting depth, water availability, and vegetation cover along an aridity gradient in Patagonia. Oecologia **108**:503–511.

Shalyt, M. S. 1950. Podzemnaja cast' nekotorykh lugovykh, stepnykh i pustynnykh rastenyi i fitocenozov. C. I. Travjanistye i polukustarnigkovye rastenija i fitocenozy lesnoj (luga) i stepnoj zon. [Belowground parts of some meadow, steppe, and desert plants and plant communities. Part I: Herbaceous plants and subshrubs and plant communities of forest and steppe zones.] [In Russian.] Trudy Botanicheskogo Instituta im. V. L. Komarova. Akademii nauk SSSR. Seriia III, Geobotanika **6**:205–442.

Shalyt, M. S. 1952. Podzemnaja cast' nekotorykh lugovykh, stepnykh i pustynnykh rastenyi i fitocenozov. C. 2. Travjanistye, polukustarnigkovye i kustarnigkovye rastenija i fitocenozy pustynnoj zony. [Belowground parts of some meadow, steppe, and desert plants and plant communities. Part 2: Herbaceous plants, subshrubs, and shrubs, and plant communities of the desert zone.] [In Russian.] Trudy Botanicheskogo Instituta im. V. L. Komarova. Akademii nauk SSSR. Seriia III, Geobotanika **8**:71–139.

Sims, P. L., J. S. Singh, and W. K. Lauenroth. 1978. The structure and function of ten western North American grasslands. I. Abiotic and vegetational characteristics. Journal of Ecology **66**:251–285.

Smith, D. M., N. A. Jackson, J. M. Roberts, and C. K. Ong. 1999. Reverse flow of sap in tree roots and downward siphoning of water by *Grevillea robusta*. Functional Ecology **13**:256–264.

Sperry, J. S., F. R. Adler, G. S. Campbell, and J. P. Comstock. 1998. Limitation of plant water use by rhizosphere and xylem conductance: results from a model. Plant, Cell and Environment **21**:347–359.

Sposito, G. 1989. The chemistry of soils. Oxford University Press, New York, New York, USA.

Sternberg, L. d. S. L., L. V. Green, M. Z. Moreira, D. Nepstad, L. A. Martinelli, and R. Victória. 1998. Root distribution in an Amazonian seasonal forest as derived from d^{13}C profiles. Plant and Soil **205**:45–50.

Stone, E. L., and P. J. Kalisz. 1991. On the maximum extent of tree roots. Forest Ecology Management **46**:59–102.

Troll, C., and K. Paffen. 1980. Seasonal climates of the earth (map). Second edition. *In* J. Blüthgen and W. Weischet, editors. Allgemeine Klimageographie. Walter de Gruyter, Berlin, Germany.

Vandenbeldt, R. J. 1991. Rooting systems of western and southern African *Faidherbia albida* (Del.) A. Chev. (syn. *Acacia albida* Del.)—a comparative analysis with biogeographic implications. Agroforestry Systems **14**:233–244.

Vogt, K. A., D. J. Vogt, P. A. Palmiotto, P. Boon, J. O'Hara, and H. Asbjornsen. 1996. Review of root dynamics in forest ecosystems grouped by climate, climatic forest type and species. Plant and Soil **187**:159–219.

Walter, H. 1971. Ecology of tropical and subtropical vegetation. Oliver and Boyd, Edinburgh, UK.

Walter, H., E. Harnickell, and D. Mueller-Dombois. 1975.

Klimadiagramm-Karten. Gustav Fischer Verlag, Stuttgart, Germany.

Weaver, J. E. 1919. The ecological relations of roots. Publication No. 286. Carnegie Institution of Washington, Washington, D.C., USA.

Weaver, J. E. 1920. Root development in the grassland formation. Publication No. 292. Carnegie Institution of Washington, Washington, D.C., USA.

Weaver, J. E. 1954. North American prairie. Johnsen, Lincoln, Nebraska, USA.

Weaver, J. E. 1958. Summary and interpretation of underground development in natural grassland communities. Ecological Monographs **28**:55–78.

Weaver, J. E., and F. W. Albertson. 1943. Resurvey of grasses, forbs, and underground plant parts at the end of the great drought. Ecological Monographs **13**:63–177.

Weaver, J. E., and R. W. Darland. 1949. Soil-root relationships of certain native grasses in various soil types. Ecological Monographs **19**:303–338.

Weaver, T. 1977. Root distribution and soil water regimes in nine habitat types of the northern Rocky Mountains. Pages 239–244 *in* J. K. Marshall, editor. The belowground ecosystem: a synthesis of plant-associated processes. Range Science Department Science Series 26. Colorado State University, Fort Collins, Colorado, USA.

Wilkinson, L., L. Engelman, and R. Marcantonio. 1998. Correlations, similarities, and distance measures. Pages 115–148 *in* L. Wilkinson, editor. SYSTAT 8.0: Statistics. SPSS, Chicago, Illinois, USA.

Williams, D. G., and J. R. Ehleringer. 2000. Intra- and interspecific variation for summer precipitation use in pinyon–juniper woodlands. Ecological Monographs **70**:517–537.

Woodward, F. I. 1987. Climate and plant distribution. Cambridge University Press, Cambridge, UK.

Yanagisawa, N., and N. Fujita. 1999. Different distribution patterns of woody species on a slope in relation to vertical root distribution and dynamics of soil moisture profiles. Ecological Research **14**:165–177.

Zar, J. H. 1996. Biostatistical analysis. Third edition. Prentice Hall, Upper Saddle River, New Jersey, USA.

Zeng, X., Y.-J. Dai, R. E. Dickinson, and M. Shaikh. 1998. The role of root distribution for climate simulation over land. Geophysical Research Letters **25**:4533–4536.

Zverev, N. E., and R. D. Seiidova. 1990. Underground mass of shrub and subshrub plants of the Karakum. Problems of Desert Development 1990(1):49–54.

APPENDIX A

A List of studies compiled in the global database of vertical root profiles is available in ESA's Electronic Data Archive: *Ecological Archives* M072-004-A1.

APPENDIX B

A description of the methods used for interpolation and extrapolation of root profiles is available in ESA's Electronic Data Archive: *Ecological Archives* M072-004-A2.

APPENDIX C

Additional statistical tables are available in ESA's Electronic Data Archive: *Ecological Archives* M072-004-A3.