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A global analysis of root distributions for terrestrial biomes

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Abstract Understanding and predicting ecosystem functioning (e.g., carbon and water fluxes) and the role of soils in carbon storage requires an accurate assessment of plant rooting distributions. Here, in a comprehensive literature synthesis, we analyze rooting patterns for terrestrial biomes and compare distributions for various plant functional groups. We compiled a database of 250 root studies, subdividing suitable results into 11 biomes, and fitted the depth coefficient β to the data for each biome (Gale and Grigal 1987). β is a simple numerical index of rooting distribution based on the asymptotic equation $Y = 1\text{-}\beta^{d}$, where d = depth and Y = the proportion of roots from the surface to depth d. High values of β correspond to a greater proportion of roots with depth. Tundra, boreal forest, and temperate grasslands showed the shallowest rooting profiles (β = 0.913, 0.943, and 0.943, respectively), with 80–90% of roots in the top 30 cm of soil; deserts and temperate coniferous forests showed the deepest profiles (β = 0.975 and 0.976, respectively) and had only 50% of their roots in the upper 30 cm. Standing root biomass varied by over an order of magnitude across biomes, from approximately 0.2 to 5 kg m^{-2}. Tropical evergreen forests had the highest root biomass (5 kg m^{-2}), but other forest biomes and sclerophyllous shrublands were of similar magnitude. Root biomass for croplands, deserts, tundra and grasslands was below 1.5 kg m^{-2}. Root/shoot (R/S) ratios were highest for tundra, grasslands, and cold deserts (ranging from 4 to 7); forest ecosystems and croplands had the lowest R/S ratios (approximately 0.1 to 0.5). Comparing data across biomes for plant functional groups, grasses had 44% of their roots in the top 10 cm of soil (β = 0.952), while shrubs had only 21% in the same depth increment (β = 0.978). The rooting distribution of all temperate and tropical trees was β = 0.970 with 26% of roots in the top 10 cm and 60% in the top 30 cm. Overall, the globally averaged root distribution for all ecosystems was β = 0.966 (r^2 = 0.89) with approximately 30%, 50%, and 75% of roots in the top 10 cm, 20 cm, and 40 cm, respectively. We discuss the merits and possible shortcomings of our analysis in the context of root biomass and root functioning.

Key words Terrestrial biomes · Cumulative root fraction · Root biomass · Rooting density · Soil depth

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Introduction

The formal study of root distributions is over 250 years old, with its origins in studies of crop species (Hales 1727). Historical improvements in techniques of root excavation and *in situ* root studies included using a hose to wash out crop roots in a profile wall (Schubart 1857), observing roots growing against a glass panel (Sachs 1873), and the formalization of root excavations (Weaver 1926). Beginning in the 1950s, tracer techniques provided a powerful tool for assessing functional rooting zones, including radioisotopes, stable isotopes, and stable tracers (e.g., Hall et al. 1953; Dansgaard 1964). More recently, dramatic improvements in video recording and image processing have led to the widespread use of minirhizotrons for *in situ* studies of root growth and demography (e.g., Taylor 1987). These improvements notwithstanding, the most commonly used technique for biomass assessment remains the coring or excavation of soil and subsequent separation of roots. Böhm (1979) provides an excellent historical overview of methods for root studies.

In spite of this long history of study, our understanding of root distributions, and belowground processes in general, remains inadequate. Gaps in our knowledge include root attributes (e.g., distribution, production, demography), the scaling of soil processes, and the diversity of soil organisms and their role in ecosystem processes (e.g., Burke et al. 1991; Jackson and Caldwell 1993; Hawksworth and Ritchie 1993; Pregitzer et al. 1993; Freckman 1995). Together with litterfall, root production provides the primary input of organic carbon to soils (Raich and Nadelhoffer 1989) and is of obvious importance, since belowground carbon storage is more than twice aboveground storage (Schlesinger 1991). In many non-forest ecosystems, the proportion of plant biomass found in the soil is greater than 80% of total plant biomass (Caldwell and Richards 1986). Even when forests are included, belowground primary production is often 60–80% of total net primary production (Reichle et al. 1973; Coleman 1976; Ågren et al. 1980). Fine roots frequently contribute the majority of belowground production and their life expectancy ranges from weeks to years, depending on the species and environmental conditions (Shaver and Billings 1975; Vogt and Bloomfield 1991; Hendrick and Pregitzer 1993). Coarse, woody roots can be much longer-lived, in some cases effectively as old as the plant itself (Vogt and Bloomfield 1991).

In this review we (1) synthesize data on root distributions, densities, and biomass for major terrestrial biomes, (2) compare root data across biomes for various plant functional groups (grasses, shrubs, and trees), and (3) compute a globally averaged rooting distribution for all biomes. The compiled distributions are based on a comprehensive literature synthesis. Examples of processes where root distributions are important include water fluxes to the atmosphere and groundwater, soil litter decomposition, carbon sequestration, and nutrient cycling. We highlight a number of directions for future research, including incorporating more realistic root distributions into global models for predicting the consequences of global environmental change.

Methods

The database

We first compiled a database of approximately 250 references that were useful for the project (listed and numbered in Appendix 1). These references were found in journals, book chapters, reports, and unpublished manuscripts and include data from all continents except Antarctica. The oldest references date from early this century and several recent publications provided numerous references (e.g., Richards 1986; Rundel and Nobel 1991; Stone and Kalisz 1991). A reference was included in the analysis of root depth distributions if root samples were taken to at least 50 cm in at least three soil increments. Approximately 80 references met these criteria (Appendix 2), and many included multiple sites per study. Additional studies in the database were used for biomass estimates and root/shoot ratios (see below). In some cases a given study supplied data for several species at a given location and these data were combined into one ecosystem estimate. For each study we also noted the location, latitude and longitude, annual precipitation, soil type or texture, type of roots measured (e.g., fine or total, live or dead), sampling method, and depth of sampling (see Appendix 2). Where possible, the data were analyzed as cumulative root biomass (kg m^{-2}, soil surface-area basis), root density (kg m^{-3}), and cumulative root fraction (the proportion of roots from the soil surface to a given depth in the soil). Where root biomass data were not available (e.g., data presented as root length or number of intersections), a study was included only in the analysis of cumulative root distributions. The data from each reference were separated into 11 biomes: boreal forest, crops, deserts, sclerophyllous shrubland/forest, temperate coniferous forest, temperate deciduous forest, temperate grassland, tropical deciduous forest, tropical evergreen forest, tropical grassland/savanna, and tundra. We have attempted a complete review of the literature for root distributions based on the above criteria, with the exception of crop systems where we merely provide some comparative examples (O'Toole and Bland 1987). In addition to root distributions with depth, we also calculated the average root biomass and root/shoot ratios (R/S) for each biome, based on values in our database and in reviews by Caldwell and Richards (1986); Hilbert and Canadell (1996); Kummerow (1981); O'Toole and Bland (1987); Risser et al. (1981); Rodin and Bazilevich (1967); Rundel and Nobel (1991); Santantonio et al. (1977); Viereck et al. (1986); Vogt et al. (1996). Since R/S ratios sometimes change for systems over time (e.g., decreasing with canopy closure in forests), we emphasized data for mature vegetation.

The model

Gale and Grigal (1987) presented a model of vertical root distribution based on the following asymptotic equation:

$$Y = 1 - \beta^{d}$$

where Y is the cumulative root fraction (a proportion between 0 and 1) from the soil surface to depth d (cm), and β is the fitted "extinction coefficient". β is the only parameter estimated in the model and provides a simple numerical index of rooting distribution. High β values (e.g., 0.98) correspond to a greater proportion of roots at depth and low β values (e.g., 0.92) imply a greater proportion of roots near the soil surface (Fig. 1). β values were fitted to the data for each biome for those studies that sampled to a minimum soil depth of 1 m. Approximately 50 studies met these criteria, though coverage for some biomes was relatively weak (e.g., boreal forest with three such studies, temperate coniferous forest with four, and tropical deciduous forest with only one).

In addition to biome analyses, we examined the data by plant functional groups using only studies where roots were sampled to depths of 1 m or more. In comparing grass and shrub life forms, we examined data from temperate grasslands, tropical grasslands and deserts (i.e., systems in which the two growth forms co-occur). Many studies in those biomes compared root biomass near shrubs with similar data near grasses, while in other studies nearby shrub and grass sites were compared. To assess trees as a functional group, we combined data for all temperate and tropical forests. We also calculated a globally averaged rooting distribution by pooling all data from systems sampled to at least 1 m depth in the soil.

To create a global map of root distributions, we calculated the percentage of root biomass found in the upper 30 cm of soil for each biome, based on their respective β values. These data were then plotted on a 1°× 1° grid scale for the land-cover classifications of Wilson and Henderson-Sellers (1985). Those classifica-

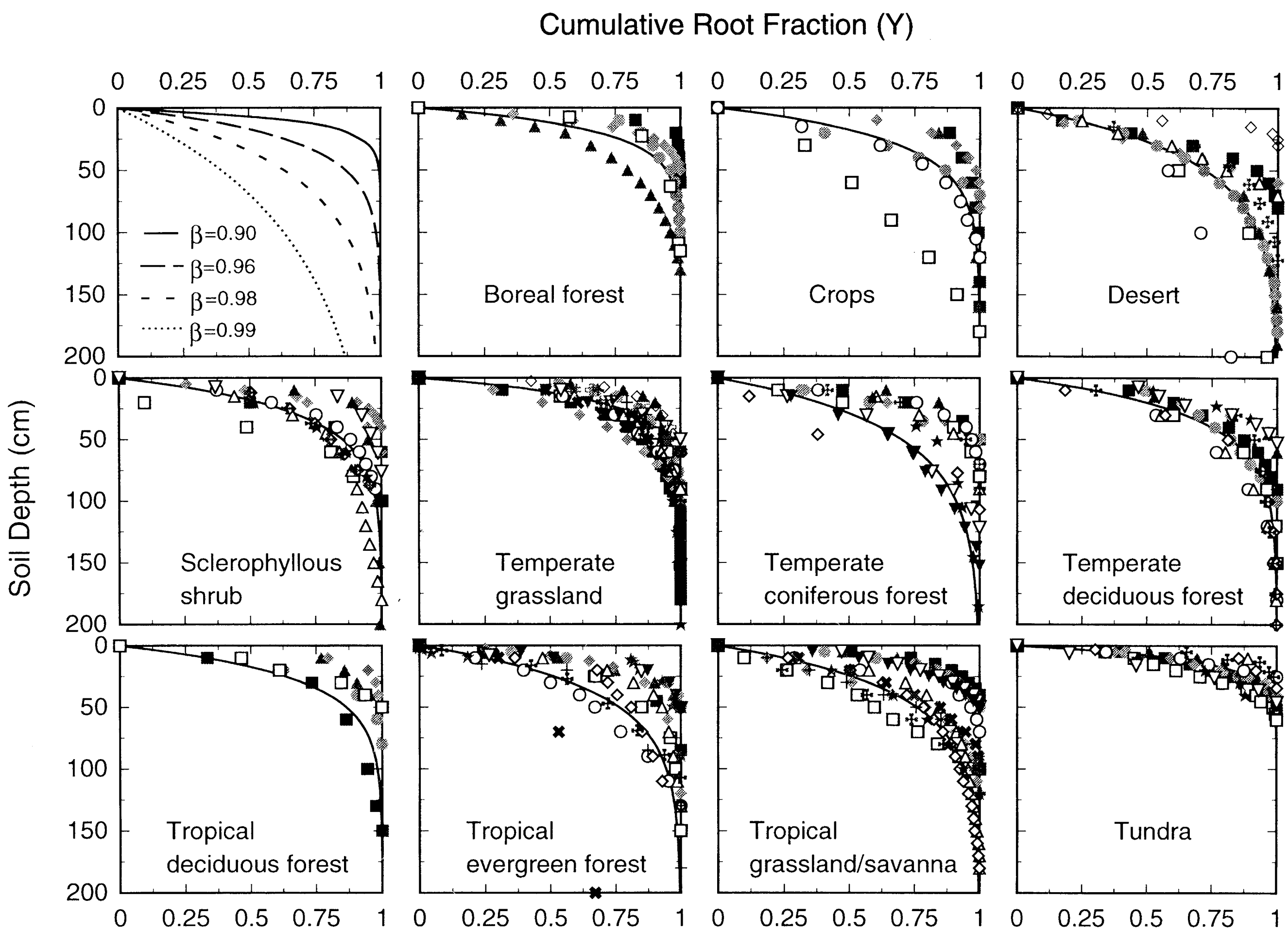

Fig. 1 Cumulative root distribution (cumulative proportion) as a function of soil depth for eleven terrestrial biomes and for the theoretical model of Gale and Grigal (1987). The curve in each biome panel is the least squares fit of β for all studies with data to at least 1 m depth in the soil. The specific β values and the associated r^2 values can be found in Table 1 and the key to the *symbols* in each panel is in Table 2. Gale and Grigal's equation is of the form $y=1-\beta^d$, where Y is the cumulative root fraction with depth (a proportion between 0 and 1), d is soil depth (in cm), and β is the fitted parameter. Larger values of β imply deeper rooting profiles

Table 1 Values of β (and associated r^2 values) for our data and the model of Gale and Grigal (1987), the percentage of roots in the upper 30 cm of soil, average standing root biomass ($kg \cdot m^{-2}$), and root:shoot ratios for each biome. The β values are represented graphically in the panels of Fig. 1. See Methods and Fig. 1 for a description of Gale and Grigal's model; larger values of β imply deeper rooting profiles. The values for root biomass and root:shoot ratios summarize data from our database and the following reviews: Caldwell and Richards (1986), Hilbert and Canadell (1996), Kummerow (1981), O'Toole and Bland (1987), Risser et al. (1981), Rodin and Bazilevich (1967), Rundel and Nobel (1991), Santantonio et al. (1977), Viereck et al. (1986), and Vogt et al. (1996) (listed in Appendix 1). The dual values for desert root biomass and root/shoot ratios are for cold and warm deserts, respectively

Biome	β	r^2	% Root biomass in upper 30 cm	Root biomass ($kg \cdot m^{-2}$)	Root/shoot ratio
Boreal forest	0.943	0.89	83	2.9	0.32
Crops	0.961	0.82	70	0.15	0.10
Desert	0.975	0.95	53	1.2, 0.4	4.5, 0.7
Sclerophyllous shrubs	0.964	0.89	67	4.8	1.2
Temperate coniferous forest	0.976	0.93	52	4.4	0.18
Temperate deciduous forest	0.966	0.97	65	4.2	0.23
Temperate grassland	0.943	0.88	83	1.4	3.7
Tropical deciduous forest	0.961	0.99	70	4.1	0.34
Tropical evergreen forest	0.962	0.89	69	4.9	0.19
Tropical grassland savanna	0.972	0.95	57	1.4	0.7
Tundra	0.914	0.91	93	1.2	6.6

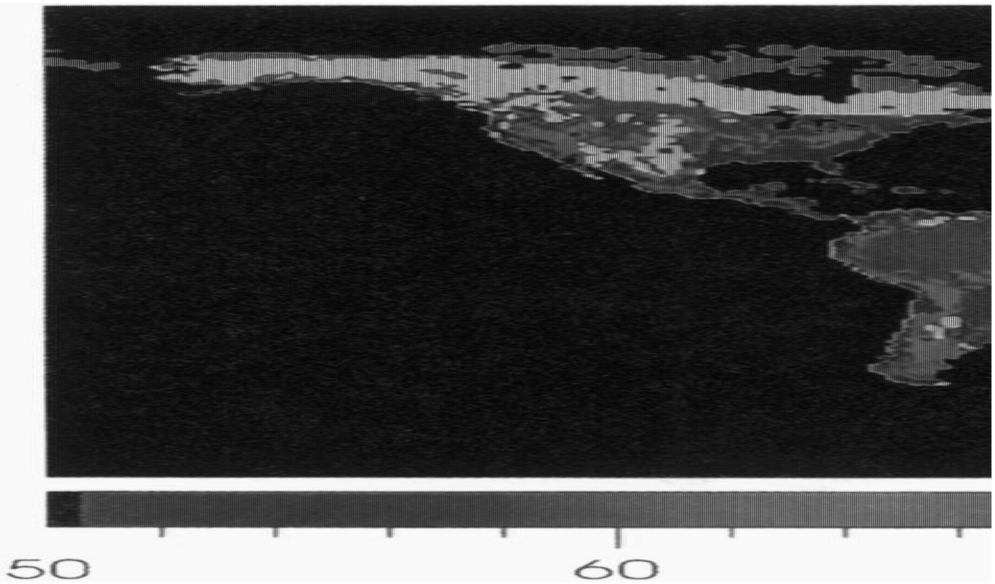

Fig. 2 A global map of the percentage of root biomass found in the upper 30 cm of soil plotted on a 1° × 1° grid scale for the land-cover classifications of Wilson and Henderson-Sellers (1985). *White areas* indicate a lack of information; see Table 1 and Methods for additional information

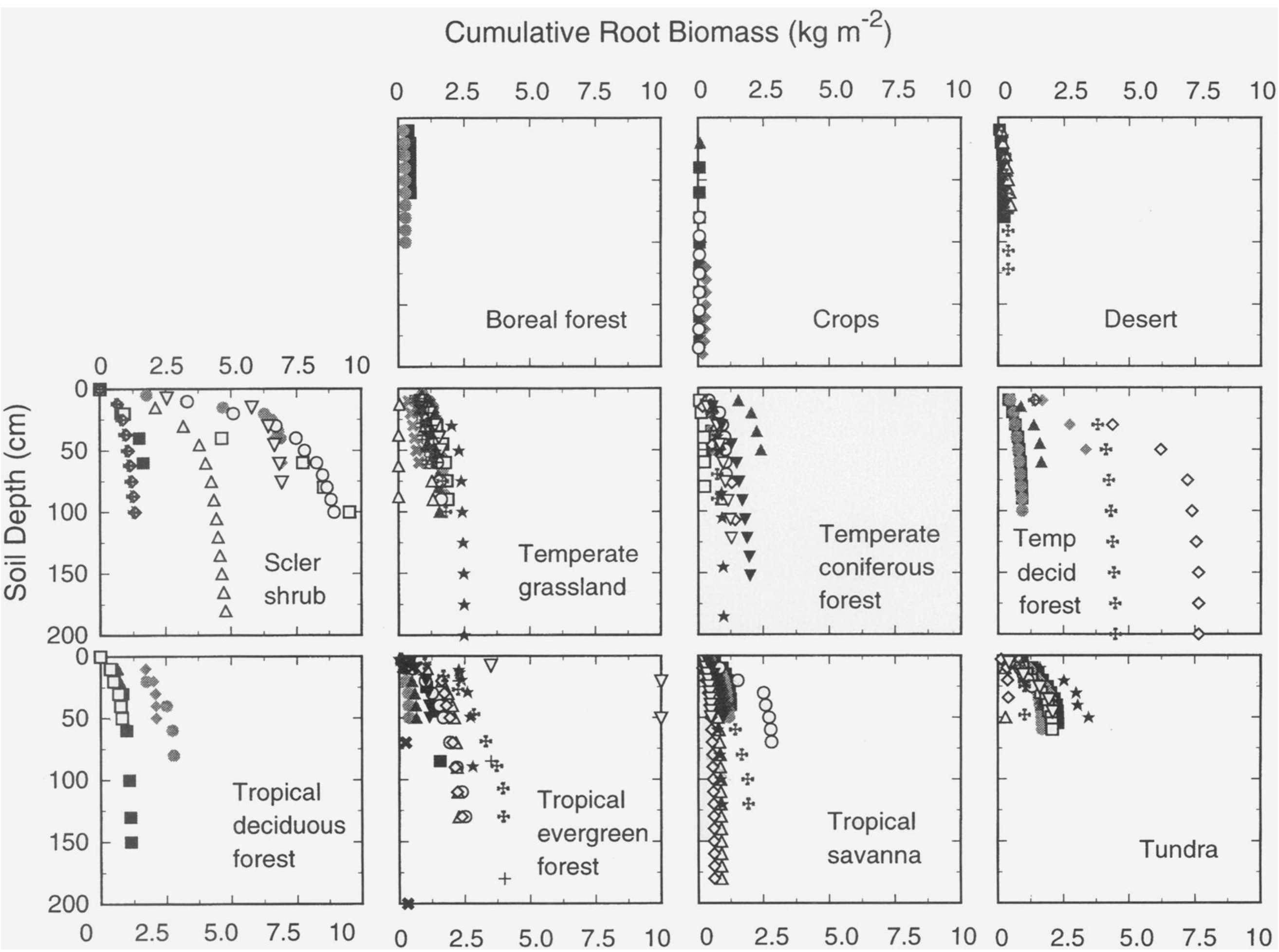

Fig. 3 Cumulative root biomass (kg m^{-2}) for 11 terrestrial biomes. The key to the *symbols* in each panel can be found in Table 2. Actual values for the *two points* shown at the *upper right* corner of tropical evergreen forest are 11.2 and 13.2 kg m^{-2} from Klinge and Herrera (1978)

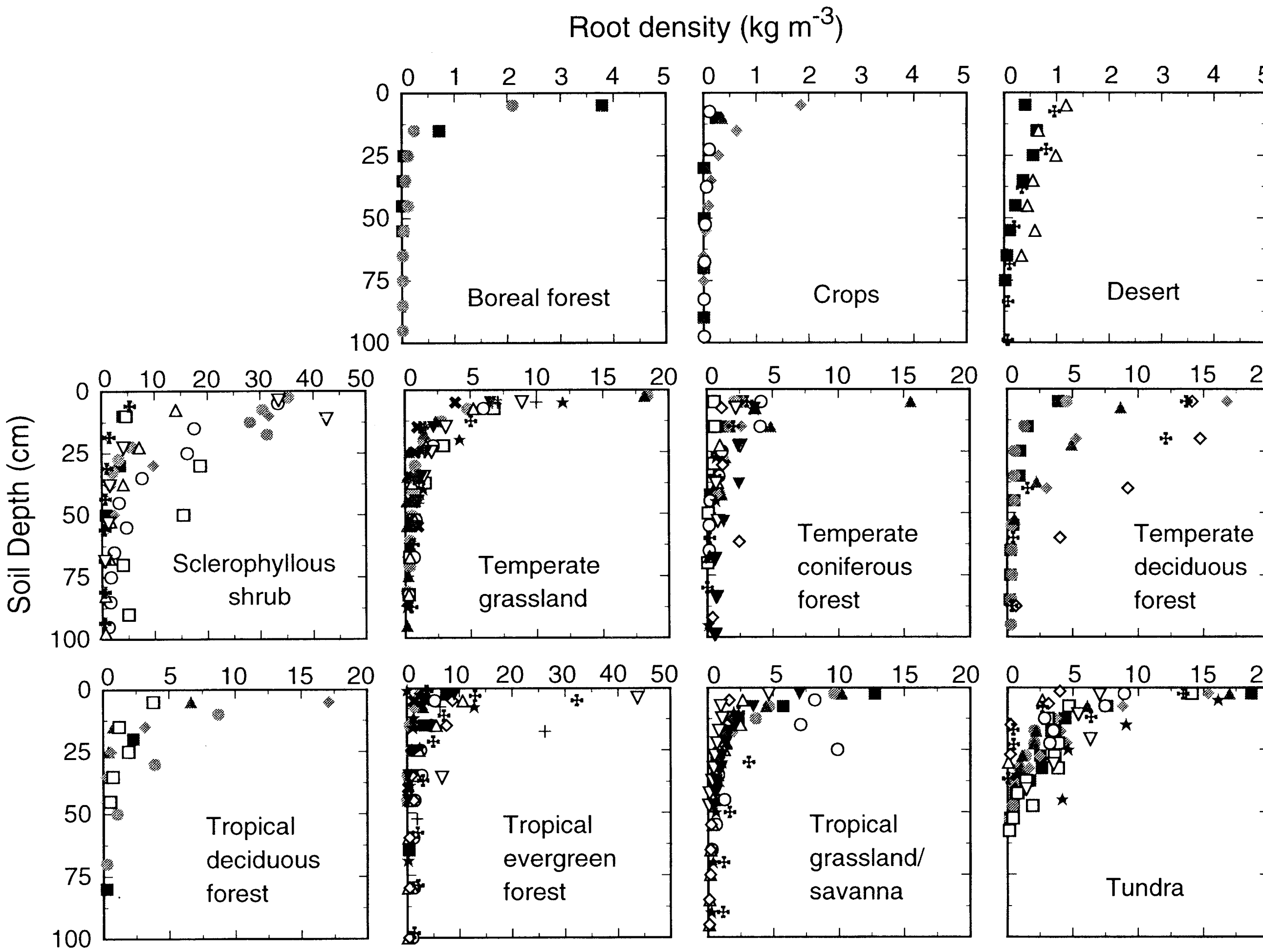

Fig. 4 Root density (kg m^{-3}) for eleven terrestrial biomes. The key to the *symbols* in each panel is in Table 2

tions include tropical broadleaf forest, temperate deciduous forest, mixed coniferous/deciduous forest, boreal coniferous forest, needle-leaf deciduous forest, savanna, temperate grassland, shrubs without ground cover, tundra, desert, and agricultural systems. The data for sclerophyllous shrublands were used for the classification of shrubs without ground cover.

Results

Tundra, boreal forest, and temperate grasslands showed the shallowest rooting profiles (β = 0.913, 0.943, and 0.943, respectively), with 93% of roots occurring in the top 30 cm of soil for tundra and 83% for temperate grasslands and boreal forests (Fig. 1, Table 1). Deserts and temperate coniferous forests showed the deepest rooting profiles (β = 0.975 and 0.976, respectively) with only 50% of the roots in the uppermost 30 cm. To further contrast shallow- and deep-rooted systems, tundra typically had 60% of roots in the upper 10 cm of soil while deserts had only 20% of their roots in the same depth increment. Temperate grasslands had a shallower rooting profile than did tropical grasslands/savannas (β = 0.943 and 0.972, respectively), though this result was due in large part to the occurrence of woody roots in most tropical grassland/savanna studies. A global map of root distributions by depth (Fig. 2) reveals (1) a predominance of shallowly rooted systems at high latitudes associated with permafrost or waterlogging, (2) shallowly rooted grassland regions, and (3) more deeply rooted woody biomes, particularly deserts, temperate coniferous forests, and tropical savannas.

Average root biomass varied by over an order of magnitude across biomes, to a maximum of 5 kg m^{-2} for forests and sclerophyllous shrublands (Table 1, Fig. 3). Ecosystems with the lowest root biomass were croplands, deserts, tundra, and grasslands, all of which had root biomass < 1.5 kg m^{-2}. Deserts and croplands were lowest of all, though cold deserts had three times the root biomass of warm deserts. Root biomass in forest ecosystems ranged from approximately 2 to 5 kg m^{-2} (Table 1, Fig. 3). Individual studies finding the greatest root biomass included those in Venezuelan caatinga rainforest (Klinge and Herrera 1978) and the California chaparral (Kummerow et al. 1977; Kummerow and Mangan 1981). Root/shoot ratios for each ecosystem varied from approximately 0.1 to 7 (Table 1). The ecosystem with the smallest R/S ratio was managed croplands (R/S = 0.1). For more natural systems, forest ecosystems had the

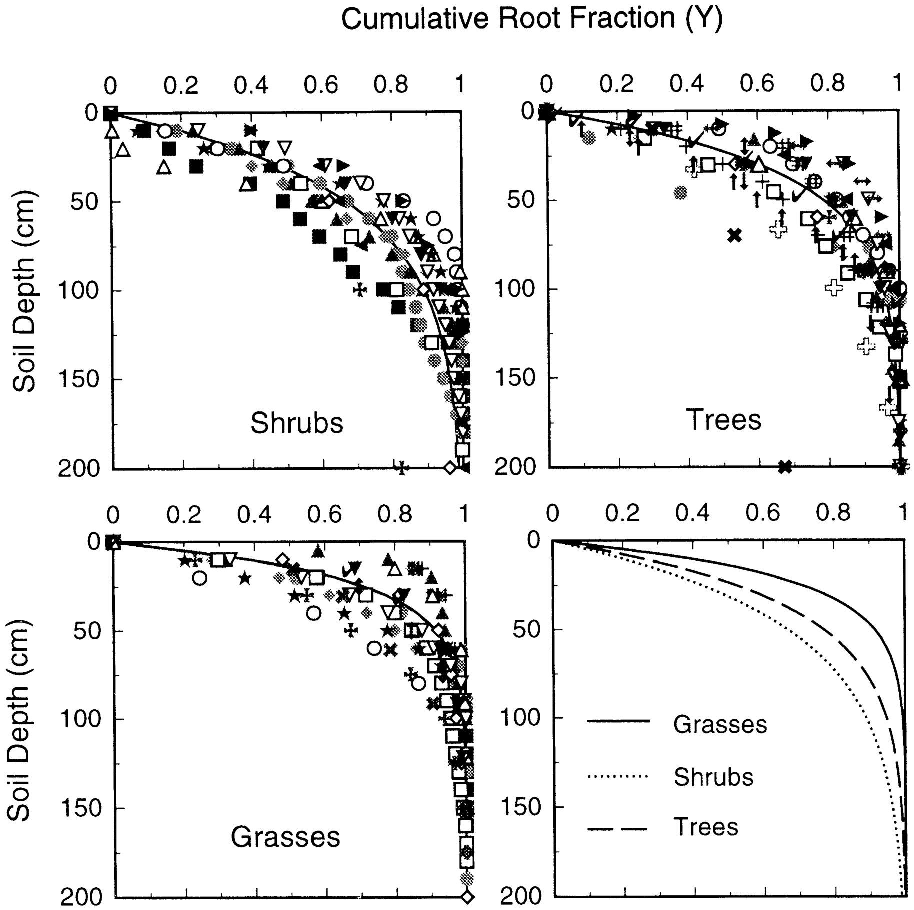

Fig. 5 The distribution of grass, tree, and shrub roots as a function of soil depth across all relevant biomes. The data for trees include temperate deciduous, temperate coniferous, tropical deciduous, tropical evergreen, and tropical savanna trees sampled to at least 1 m depth. The data for grasses and shrubs are from deserts, temperate grasslands, and tropical grasslands sampled to at least 1 m depth where the two life-forms potentially co-occur. The extinction curves derived from these data are $\beta = 0.952$ ($r^2 = 0.88$) for grasses, $\beta = 0.970$ ($r^2 = 0.91$) for trees, and $\beta = 0.978$ ($r^2 = 0.92$) for shrubs (curve fit by least squares minimization; see text for discussion of the model). The key to the grass symbols is as follows (see Appendix 1 for numbered references): ■ *Elymus alinus* (23), ● *Agropyron spicatum* (54), ▲ Belgium grassland (56), ◆ *Bouteloua gracilis* (140), □ Guinea grassland (138), ○ Ghana grassland (175), ↕ Tallgrass prairie (176), ◇ Argentina grassland (203), ✠ *Festuca pallescens* (203), ★ fine-leaved savanna (201), ▽ broad-leaved savanna (201), ▼ *Andropogon furcatus* (243), ▶ *Andropogon scoparious* (243), ◀ *Bouteloua curtipendula* (243), + *Bouteloua gracilis* (243), × *Agropyron smithii* (243), # *Panicum virgatum* (244), △ *Poa pratensis* (244), ✓ *Buchloe dactyloides* (244). Shrub data: ■ *Chrysothamnus nauseosus* (23), ● *Artemisia tridentata* (23), ▲ *Sarcobatus vermiculatus* (23), ◆ *Atriplex confertifolia* (23), □ *Artemisia tridentata* (54), ○ *Senecio filaginoides* (63), △ *Mulinum spinosum* (63), ◇ *Larrea tridentata* (71), ✠ *Prosopis glandulosa* (71), ★ Burkea africana (125), ▽ Guinea shrubs (138), ▼ Ghana shrubs (175), ▶ *Mulinum spinosum* (203), ◀ *Adesmia campestris* (203). Tree data: ● (189), ▲ (230), ◆ (250) 45 years, □ (250) 80 years, ○ (60), △ (126) Virginia, ◇ (126) Cove, ✠ (126) oak-hickory, ★ (203) *Nothofagus pumila*, ▽ (203) *Nothofagus antarctica*, ▼ (6), ▶ (82) Kade, ◀ (82) Yangambi, + (105) Banco, ↔ (105) Thalweg, # (105) Yapo, ✓ (123), × (170), ↕ (231), ✠ (94), ↑ (125), ↓ (240)

smallest R/S ratios, reflecting their large aboveground woody biomass. The highest R/S ratios were observed for tundra, grasslands, and the cold-desert component of deserts (R/S ranging from approximately 4 to 6). Average root densities for each biome followed similar relative patterns as root biomass (Fig. 4). Sclerophyllous shrublands and tropical evergreen forests had the highest root densities, in some cases densities over 40 kg m^{-3} in the shallowest depths. Deserts and croplands had the lowest densities, with values never more than 5 kg m^{-3} even in the most densely rooted cases.

To obtain a globally averaged rooting distribution, we combined all studies in which roots were sampled to at least 1 m depth (which included data from every biome except tundra). The global average for all ecosystems was $\beta = 0.966$ ($r^2 = 0.89$; data not shown). Consequently, in the average global root profile approximately 30% of roots were in the top 10 cm, 50% in the top 20 cm, and 75% in the top 40 cm. In addition, we also compared rooting patterns for various plant functional groups across biomes, including grasses, shrubs, and trees. While grasses had 44% of their root biomass on average in the top 10 cm of soil, shrubs had only 21% of their roots in the same depth increment (Fig. 5). Grasses had 75% of their root biomass in the top 30 cm, compared to 47% for shrubs. The respective extinction coefficients were $\beta = 0.952$ ($r^2 = 0.88$) for grasses and $\beta = 0.978$ ($r^2 = 0.92$) for shrubs (Fig. 5). The average

Table 2 Key to the symbols for Figs. 1, 3, and 4. Each *number* in the table identifies a reference in Appendix 1. Each *column* contains all of the references for a given biome in alphabetical order

Symbol	Boreal forest	Crops	Desert	Sclerophyllous shrubs	Temperate coniferous forest	Temperate deciduous forest	Temperate grassland	Tropical deciduous forest	Tropical evergreen forest	Tropical grassland/ savanna	Tundra
■	184	3	9	33	2	60	23	6	15	65	50
●	186	76	23	39	2	60	45	37	81	65	50
▲	216	102	54	98	2	89	56	137	81	65	50
◆	216	206	62	128	2	118	140	137	82	125	50
□	218	222	71	131	77	126	141	137	82	125	50
○		249	71	133	89	126	141		105	136	52
△			166	142	151	126	141		105	138	99
◇			172	149	189	203	152		105	138	106
✠			220	150	228	203	176		123	175	106
★				160	230	204	203		123	175	121
▽				212	250	252	207		124	178	121
▼					250		207		155	178	
+							207		231	201	
×							207		170	201	
#							207				
⇧							209				
✓							244				

rooting distribution for all temperate and tropical trees was $\beta = 0.970$ ($r^2 = 0.91$), with 26% of roots in the top 10 cm, 60% in the top 30 cm, and 78% in the top 50 cm (Fig. 5). Boreal forest trees were considerably more shallowly rooted ($\beta = 0.943$, see above). Combining data from 25 studies of all woody plants (trees and shrubs), the average rooting distribution was $\beta = 0.975$ ($r^2 = 0.90$), with 40% of roots in the top 20 cm (data not shown).

Discussion

One goal of our root analysis was to provide a database for use in assessing soil C distributions and in examining the effect of roots on C, H_2O, and nutrient fluxes between soil, plants, and the atmosphere. One of the only approaches for addressing such questions at regional and global scales, and for predicting the consequences of global change, is modeling. Currently, the most explicit root descriptions in well accepted biome or global models are simple two- or three-layer representations that separate shallow and deep water at arbitrary depth (e.g., Potter et al. 1993; Neilson 1995). For example, MAPSS (Neilson 1995) is an ecosystem-biogeographic model that links vegetation with water balance processes. It has three soil layers (L1 from 0–50 cm, L2 from 50–150 cm, and L3 below 150 cm), with grasses extracting water only from L1, shrubs from L1 and L2, and L3 containing no roots (but consisting of a pool of H_2O for gravity-driven drainage to streams). CASA (Potter et al. 1993) is a process model of terrestrial ecosystem production that uses two sets of rooting depths. For water uptake the soil rooting depth is 1.0 m for grasslands, tundra, and croplands and 2.0 m for forests; the scalar used to estimate C turnover and N mineralization includes a depth of only 0.3 m (Potter et al. 1993). Other models, including TEM (Raich et al. 1991; Melillo et al. 1993), BIOME2 (Prentice et al. 1992) and BIOME-BGC (e.g., Running and Hunt 1993), either do not specifically include soil depth and root distributions, or use only a single biome-specific soil depth parameter. CENTURY (Parton et al. 1988, 1992), an ecosystem model used to simulate patterns of plant primary production, soil organic matter dynamics, and nutrient cycling, is a notable exception with five soil depths: 0–15 cm, 15–30 cm, 30–45 cm, 45–60 cm, and 60–90 cm.

Mechanistic models that examine the feedbacks between vegetation and climate (including atmospheric CO_2) are critical for predicting the consequences of global change and for understanding the cycling of C, H_20, and nutrients (e.g., Vitousek and Matson 1984; Wullschleger et al. 1994; Paruelo and Sala 1995; Field et al. 1995). Given these models as examples, how might information on root distributions improve predictions of ecosystem response to global change? One promising approach would be to incorporate the observed root distributions into biome or global models. One or more of the models might then be linked to a GCM (general circulation or global change model) to quantify feedbacks between vegetation and climate. Such feedbacks are necessary for dynamic models that allow biomes to fluctuate geographically, both affected by and affecting the earth's climate. More specific questions based on plant functional groups or a subset of biomes might also be addressed by combining our root data with models. For example, if the world's grasslands were converted to shrublands, how would H_2O fluxes and C sequestration be altered? How might the conversion of tropical forests to pasture affect C distributions in the soil, and what would be the consequences for recirculation of H_2O? The observed root distributions provide information to help answer many such questions.

By far the majority of ecosystem root biomass resides in the upper 1 m of soil (Fig. 3; Table 1). Despite this predominance of biomass in the upper soil layers, our knowledge of the importance of the deep soil to nutrient and water balances could be much improved, particularly considering how few studies have quantitatively sampled roots below 2 m. We found only nine studies that measured root distributions to at least 2 m depth in the soil. Those studies included one each in cold and warm deserts (Dobrowolski et al. 1990; Freckman and Virginia 1989), one chaparral dataset (the mountain fynbos of Higgins et al. 1987), three forest studies (the pine plantation of Van Rees and Comerford 1986; Kochenderfer 1973 in temperate hardwood forest; and Nepstad et al. 1994 for the Amazon), two savanna studies (*Prosopis glandulosa* data in Heitschmidt et al. 1988; Watts 1993) and data for five sites in Patagonia, Argentina (a transect from *Nothofagus* forest through grassland to desert, Schulze et al. 1996). From a practical perspective it is interesting to ask how much information was gained in these studies by sampling below 1 m depth. In five of the nine studies, 93%–100% of the roots observed in the profile occurred in the uppermost 1 m. Two minor exceptions were Heitschmidt et al. (1988), who found 90% of roots at 133 cm, and Watts (1993), who found 92% of root biomass at 120 cm. The two notable exceptions were Freckman and Virginia (1989) and Nepstad et al. (1994). The Jornada desert data in Freckman and Virginia (1989) included two community types, one dominated by the phreatophyte *Prosopis glandulosa* and one dominated by *Larrea tridentata*. *P. glandulosa*, one of the most deeply rooted species in the world (Canadell et al. 1996), had 30% of its roots below 1 m, while *L. tridentata*, with a shallower rooting profile, had only 11% below 1 m. Nepstad et al. (1994) measured fine-root biomass (< 1 mm) to a depth of approximately 6.5 m in eastern Amazonia, Brazil. Their data show small but consistent fine-root biomass between 1 m and 6.5 m, enough to contribute substantially to total fine-root biomass; 50% of fine roots in that system occurred in the upper 70 cm of soil, but nearly one-third were below 2 m. Based on Table 1 and the data in Nepstad et al. (1994), we estimate fine root biomass in that system to be approximately 10% of total root biomass (assuming 5 kg m^{-2} for the latter). Deep roots are likely to be important for C and H_2O dynamics in a number of ecosystems that experience periodic drought. An examination of deep-rooted species, including *Acacia*, *Prosopis*, and *Eucalyptus* spp., shows that they are most often found in water-limited systems (see recent reviews by Stone and Kalisz 1991; Canadell et al. 1996).

The root distributions presented here (Fig. 1) are based primarily on root biomass in the upper 1–2 m of soil (Appendix 2). What additional factors may be important for belowground resource capture and ecosystem attributes? In addition to biomass, root surface area is important for resource uptake, with important contributions from the relative activity of roots (Newman 1974; Fitter 1982; Jackson et al. 1990) and root symbioses (e.g., Vincent 1974; Allen 1991). Although the uptake of nutrients may be limited primarily to upper soil layers, a relatively small proportion of roots deep in the soil can be quite important for water uptake. To assess functional rooting zones, tracer techniques and other approaches are an important supplement to direct excavation. Relevant tracers include radioisotopes, stable isotopes, and stable tracers (e.g., Fox and Lipps 1964; McKane et al. 1990). Both short term and seasonal fluctuations in deep soil water can indicate root activity (Holmes and Colville 1970). Seasonality of CO_2 concentrations in soil air with depth can also indicate activity of roots. Richter and Markewitz (1995) show substantial soil acidity (pH $\leq$ 4.2) to at least 6 m depth in the soil, considerably more acidity than for the underlying parent material (pH 7.9).

The data for certain systems were quite variable. Sclerophyllous shrublands include such diverse systems as the shallowly rooted mountain fynbos of South Africa, dominated by *Protea* spp. (Higgins et al. 1987), to the potentially deep-rooted chaparral of southern California (Kummerow and Mangan 1981, though we were unable to identify any southern California study that quantitatively sampled roots to > 1 m depth). R/S ratios in sclerophyllous shrublands ranged from approximately 0.3 to 5, while R/S ratios in forest systems were much more consistent. In general, variation in root distributions requires more detailed spatial and temporal integration in some systems if accurate root assessments are to be made. Deserts are comprised of shallow-rooted ephemerals, shallow-rooted perennials, and deep-rooted perennials (Rundel and Nobel 1991). Where desert root distributions have been examined, studies have typically focused on individual species. Shallow-rooted ephemerals typically avoid drought, with root depths less than 20 cm (Evenari et al. 1971; Golluscio and Sala 1993). Shallow-rooted perennials include cacti, which rarely grow roots below 50 cm (Cannon 1911; Nobel 1989). In contrast, roots of phreatophytes such as *Prosopis glandulosa* or *Zizyphus lotus* can reach depths of 50 m or more in the soil (Phillips 1963; Zohary 1961; Canadell et al. 1996). Accurately assessing desert rooting patterns requires spatial integration (either by examining a number of species or by random sampling) and temporal integration (to capture the changing phenologies of root abundance). Forest studies face similar difficulties, and should address sampling distance from the tree and tree density. A few examples of attempts to integrate such spatial or temporal dynamics in woody systems are Reich et al. (1980), Farrish (1991), and Le Roux et al. (1995).

Relative root distributions among and within biomes differ in part because of physical barriers to growth. For example, permafrost restricts rooting depth in tundra and in some boreal forests (e.g., Bonan 1992), though less commonly in the boreal forests of North America (Solomon 1992). In addition, waterlogging can also inhibit root growth (Kane et al. 1992). These and other factors make tundra ecosystems the most shallowly rooted of all biomes examined, and lead to a shallower rooting profile for boreal forests than for other forest types (Fig. 1, Table 1). Poor soil aeration from waterlogging can decrease rooting depth in all ecosystems (Klinge and Herrera 1978; Drew 1990; Rundel and Nobel 1991). Strong mechanical resistance to root penetration can be found in arid and semi-arid ecosystems with a substantial caliche layer (Gile et al. 1966), or in tropical savannas and tropical forests with a prevalent ironpan (Richards 1986). Not surprisingly, shallow bedrock also inhibits root growth, but channels and cracks can sometimes increase functional rooting depth. Though all of these factors can limit rooting depth, high temperatures can result in decreased root abundance near the soil surface. In unshaded desert soils the surface temperature can reach 70°C (Buxton 1925), reducing or eliminating roots in the upper soil layer (e.g., Nobel 1988).

The ideal root study provides data to compare not just total root biomass, but fine roots alone, coarse roots, the distribution of root length and surface area with depth, the proportion of live and dead roots, and root distributions for ecosystems and individual species. Not surprisingly, few studies include all of this information. Although it is unrealistic to expect every study to do so, there are simple improvements that could be made to increase the benefit of many future studies. One such improvement would be to document the sampling methods more clearly. Spelling out the core diameter or area over which sampling occurred, and accompanying depth increments, enables data to be converted easily between a soil-density and soil surface-area basis (e.g., kg m^{-3} or kg m^{-2}). This conversion is important when, for example, the same data are used to compare total ecosystem biomass (where a soil surface-area basis is appropriate) and soil organic matter concentrations (where density is appropriate). Studies should be specific about whether root mass included dead roots, a subset of root size classes, or total root biomass. One chronic problem is the underestimation of fine root biomass. Grier et al. (1981) estimated that two-thirds of net primary production in a 180-year-old stand of *Abies amabilis* went to fine root production, but such roots are often overlooked in biomass estimates for woody vegetation. In some forests, the majority of fine roots are < 1.0 mm in diameter and may be difficult to recover from the soil (Hendrick and Pregitzer 1993). Certain techniques, such as separating roots from soil with pressurized water, almost certainly underestimate fine roots.

This review provides a current synthesis of the literature, to be improved with the addition of new studies and the inclusion of older studies that were unintentionally omitted. There are a number of important questions on the controls of plant rooting distributions that we hope to use the database to address, with an emphasis on global environmental change. Global change may induce strong feedbacks between plant rooting distributions and climate. The relatively large global warming predicted for polar regions could have a profound effect on permafrost depth and, consequently, tundra rooting patterns and net C efflux (Chapin et al. 1992; Oechel et al. 1994). Deforestation in the Amazon and other regions could alter recirculation of water between terrestrial ecosystems and the atmosphere, regional hydrology in general, and C storage (e.g., Dickinson and Henderson-Sellers 1988; Lean and Warrilow 1989; Nepstad et al. 1994), though net C loss can be mitigated to some extent by intercropping and by selecting relatively deep-rooted pasture species (Fisher et al. 1994). Increased atmospheric CO_2 and land-use change may alter the proportion of shrubs and grasses across the globe (e.g., Archer 1995; Polley et al. 1996), changing C distributions in the soil and the recirculation of water. We plan to incorporate root distributions into existing biome and global models for more realistic representations of belowground processes. With model developers, we could then address the effects of changes in land use or climate for the cycling of C, H_2O, and nutrients. Our long-term goal is to link one or more of these global terrestrial models with a GCM to examine the feedbacks between vegetation and climate. Such global models, together with paleo-analyses, provide the only integrative method for predicting the potential consequences of global environmental change.

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Appendix 1

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Appendix 2

References meeting criteria for inclusion in analysis of root depth distributions (listed in Appendix 1)

Vegetation type	Reference	Specifics	Location	Coordinates	Annual precip.	Soil type texture	Root type	Method	Measurement	Other
Boreal coniferous forest	Persson 1982	Table 2	Central Sweden	60:49 N 16:30 E	607 mm		Fine and coarse	Monolith	$g \cdot m^{-2}$ to 60 cm	*Pinus sylvestris* stand
	Persson et al. 1995	Table 1	SW-Sweden	56:33 N 13:13 E		Haplic podzol	Live and dead fine roots	Monolith	$g \cdot m^{-2}$ to 100 cm	*Picea abies* stand
	Strong & La Roi 1983	Figs. 2 & 3	Alberta, Canada		475 mm	Sandy and Eutric Brunisols	Total	Excavated soil pits	# roots dm^{-2} to 140 cm	Four boreal forest forest stands (*Larix, Picea, Pinus,* and *Populus*)
	Strong & La Roi 1985	Table 1	Alberta, Canada			Eutric Brunisolic or Gray Luvisolic	Total (5 diam classes)	Profile face	# roots to 115 cm	*Populus, Pinus,* and *Picea*
Crops	Armstrong et al. 1994	Fig. 5	Wongan Hills, Western Australia	30:51 S 116:43 E			Nodulated roots	10 cm soil cores	$g \cdot m^{-2}$ to 160 cm	6 field pea genotypes *Pisum sativum*
	Gäth et al. 1989	Fig. 1	25 sites in Germany			Silty-loam and sandy	Total	Soil core and profile methods	Length density ($cm\ cm^{-3}$) to 70 cm	Cereal crops
	Huck et al. 1986	Table 1	Alabama, USA			Marvyn loamy sand	Total	Excavation	$g \cdot m^{-2}$ to 180 cm	Soybeans (*Glycine max*)
	Siddique et al. 1990	Fig. 2	Merredin, W-Australia	31:29 S 118 E		Duplex profile of grey sand over sandy clay	Total	10 cm soil cores	$g \cdot m^{-3}$ and $cm \cdot cm^{-3}$ to 80 cm	Wheat (*Hordeum vulgare*)
	Taylor & Klepper 1973	Table 2	Alabama, USA			Cahaba loamy fine sand	Total	Glass wall	Root density to 180 cm	Corn (*Zea mays*)
	Wilhelm et al. 1982	Fig. 1	Nebraska, USA			Alliance silt loam	Total	Hydraulic probe 7.6-cm-diam. core	$mg \cdot dm^{-3}$ to 120 cm	Wheat (*Hordeum vulgare*)
Desert	Barbour et al. 1977	Fig. 9-6	Arizona, USA				Total	Unknown	kg/ha to 100 cm	Data for three shrub species and in the open
	Branson et al. 1976	Fig. 19	Colorado, USA		<230 cm	Shallow weathered mantle over bedrock	Total	50 cm^2 soil samples	$g \cdot dm^{-3}$ to 180 cm	Data for 12 communities
	Dobrowolski et al. 1990	Fig. 7.8	Utah, USA	41:45 N 111:48 W	468 mm	Rocky Mollisols formed on alluvial fan material	Total	Profile wall mapping	Intersections m^{-2} to 2.5 m	Data for big sage-brush and crested wheatgrass
	Fernandez & Caldwell 1975	Table 1	Utah, USA	41:05 N 113:05 W	230 mm	Lacustrine, silty loams with high salinity	Total	Root observation chambers	Intersections m^{-2} to 60 cm	Three shrub species in two size classes

Appendix 2 (continued)

Vegetation type	Reference	Specifics	Location	Coordinates	Annual precip.	Soil type texture	Root type	Method	Measurement	Other
Desert	Freckman & Virginia 1989	Fig. 1	New Mexico, USA	32:30 N 106:45 W	211 mm	Haplargid, Torrifluvent, or Torrispsamment	Total	Drilling system, 6.5 cm core	Root fresh mass, mg · kg^{-1}	Five Jornada sites, *Larrea* and *Prosopis*
	Jordan & Nobel 1984	Fig. 1	California, USA	33:38 N 116:24 W			Total	Monoliths	Length per soil volume (micro-m · mm^{-3}) to 150 cm	Data for 2 succulent species
	Montana et al. 1995	Fig. 2	Durango, Mexico	26:40 N 103:40 W	264 mm	Haplic Yermosol	Total	Trench wall	# of roots to 70 cm	Three shrubs, one grass
	Moorhead et al. 1989	Fig. 1	New Mexico, USA			Calciorthid and Typic Haplargids	Fine	Soil pit	g · m^{-2} to 70 cm	Creosote community
	Nobel 1989	Fig. 1	California, USA	33:38 N 116:24 W			Total	Unknown	Length (% of total) to 30 cm	Data for 3 succulent species
	Rundel & Nobel 1991	Fig. 13	New Mexico, USA				Total	Unknown to 12 m	mg fw · kg^{-1}	*Prosopis glandulosa*
	Sturges 1980	Fig. 4	Wyoming, USA		500 mm	Developed from sandstone, Argic Cryoboroll subgroup	Total	7.6 cm soil cores	Water depletion and root weight to 122 cm	*Artemisia tridentata*
Miscel-laneous	Beese 1986	Table 2.32	Germany	57:13 N 5:65 E	600 mm	Parabrownearth		Harvest		*Avena sativa*
	Bernard & Fiala 1986	Table 1	New York, USA			Mineral and peat soils	Total, live/dead	Monoliths	g · m^{-2} to 20 cm	3 *Carex* species, wet meadow
	Håland & Brække 1989	Table 2	Ekebergmosen, Trøgstad, Norway	59:38 N 11:14 E		Peat layer over sandy marine shore deposits	Fine/small (<10 mm)	56 mm soil cores	g · m^{-2} to 40 cm	pine bog
	Richards 1986	Fig. 5-3	Various	Varied	Varied	Varied	Total	Varied	g · m^{-2} to various depths	All but Wallace et al. 1980 recorded elsewhere
	Weaver 1977	Table 4	Montana, USA	Varied (all within 30 km of Bozeman)	338–909 mm	Varied	Live feeder root (<5 mm)	2 cm soil cores to 70 cm	g · m^{-2}	Various grass and shrub spp.
	Webber & May 1977	Fig. 3	Colorado, USA	40:03 N 105:36 W		Coarse with thin organic-rich surface horizons, often with loess fraction	Live/dead	5 × 5 cm soil monoliths	g · m^{-2} to 100 cm	Alpine tundra

Appendix 2 (continued)

Vegetation type	Reference	Specifics	Location	Coordinates	Annual precip.	Soil type texture	Root type	Method	Measurement	Other
Sclero-phyllous shrubland	Canadell & Roda 1991	Table 5	NE-Spain		870 mm	Dystric Xerochrepts sandy-loams	Fine	4 cm diam. cores	tons/ha to 60 cm	*Quercus ilex*
	Chapman 1970	Fig. 1	Dorset, England			Well-developed humus iron podsols	Total	9 cm soil cores	kg/ha to 40 cm	Dry heath
	Higgins et al. 1987	Table 5	Cape Province, South Africa	33:57 S 18:55 S	1700 mm	See Table 1 of article	Total	Water jets	% root mass by depth	Fynbos
	Kummerow et al. 1977	Table 3	California, USA	32:54 N 116:39 W	550 mm	Sandy loam, clay, and decomposing granite	Total	Plant excavations	g · 70 m^{-2} to 60 cm	Data for 5 species
	Kummerow & Mangan 1981	Table IV	California, USA		460 mm	Sandy and clay loam	Total, fine for 1 species	Plant excavations and soil cores	g · m^{-2} to 80 cm; fine roots (g · dm^{-3}) to 40 cm	Data for 5 species
	Kummerow et al. 1990	Fig. 2	Montpelier, France		900 mm	Rich, loamy soil 30–50 cm deep, underlain by cracks with sandy loam	Total	Trenches	% roots to 1 m	*Quercus coccifera*
	Low & Lamont 1990	Table 3	Enaebba, SW Australia	29:52 S 115:15 E	530 mm	Podsolized Sand, acidic	Total	Excavation	g · m^{-2} to 180 cm	*Banksia* scrub heath
	Martinez et al., unpublished work	Table 1	SW Spain		620 mm	Dystric Quaertzipsamment	Total	20-cm-diam. cores	g · m^{-2} to 100 cm	Mediterranean shrub
	Martinez Garcia & Rodriguez 1988	Table 1	SW Spain		620 mm	Dystric Quaertzipsamment	Total	20-cm-diam. cores	g · m^{-2} to 100 cm	Matorral
	Miller & Ng 1977	Table 3	California, USA	32:54 N 116:39 W	550 mm	Sandy loam, underlain	Total	Plant excavations	g · m^{-3} to 1 m	Chaparral shrubs
			Fundo Santa Laura, Chile	33:04 S 71:00 W	550 mm	by decomposed granite at CA site				
	Specht & Rayson 1957	Fig. 10	Ninety-Mile Plain, South Australia		457 mm	Deep, acid sand	Total	Excavations	1000 kg/3 in. depth/acre to 6 feet	25-year-old heath stands
Temperate conifer	Ares & Peinemann 1992	Table 7	Buenos Aires, Argentina			Primarily Mollisols	Fine (<2 mm)	7 cm soil cores and monoliths	kg/ha to 50 cm	Plantations (*Pinus*, *Cedrus* & *Cupressus*)
	Gehrmann et al. 1984	Fig. 6	Germany	57:52 N 5:50 E		Podsol	Fine (<2 mm)	Root cores		*Picea abies* plantation
	Harris et al. 1977	Table 3	Tennesseee, USA		1390 mm	Typic Paleudoults	Total	Excavation and soil cores	kg/ha to 60 and 70 cm	*Pinus taeda*
			North Carolina, USA		1160 mm	Typic Hapludults				

Appendix 2 (continued)

Vegetation type	Reference	Specifics	Location	Coordinates	Annual precip.	Soil type texture	Root type	Method	Measurement	Other
	McClaugherty et al. 1982	Table 1	Harvard Forest, USA			Entic Haplorthods (Spodosol), very stony	Fine: live/dead	19 mm and 50 mm	Mg/ha to depth of soil cores rooting zone (0.6–1.2 m)	*Pinus resinosa* (53-yrs old)
	Reynolds 1970	Table 4	Oxford, England			coarse sand or sandy loan	Total	6 cm diam cores	$kg \cdot m^{-2}$ to 107 cm	36-yr old Douglas Fir *Pseudotsuga taxifolia*
	Ulrich 1986	Abb. 23	Germany	57:52 N 5:50 E		Podsol	Fine (<2 mm)	Root cores		*Picea abies*
	Van Rees & Comerford 1986	Table 2	Florida, USA		1330 cm	Sandy, Ultic Haplaquads	Total	10 cm soil cores	$g \cdot m^{-2}$ for all species	*Pinus elliottii* to 245 cm
	Wright 1955	Fig. 1	Morayshire, Scotland		607 mm	Coarse and fine sand	Total	6-inch cubes (216 in^3)	g in^{-3} to approx. 5 feet	Dune, Corsican pine, Scots pine, and birch
Temperate deciduous forest	Farrish 1991	Tables 2, 4	Louisiana, USA	32 N 92 W		Upland: Fine loamy, siliceous, thermic Typic Paleudults; Bottomland: fine-silty, thermic Typic Glossaqualfs	Live, fine	8 cm soil cores	Mass ($mg \cdot cm^{-3}$) and surface area ($cm^2\,cm^{-3}$) to 90 cm (upland) and 100 cm (bottomland)	Bottomland hardwood forest
	Harris et al. 1977	Table 3	Tennessee, USA North Carolina, USA		1390 mm 1160 mm	Fullerton and Bodine (typic paleudults); Granville series (typic hapludults)	Total	Excavation and soil cores	kg/ha to 60 and 70 cm	Mixed deciduous forest
	Kelly & Joslin 1989	Table 2	Tennessee, USA			Hapludults (derived from weathered sandstone and siltstone)	Total	10 cm soil cores	ton/ha to 50 cm	*Quercus coccinea*
	Kochenderfer 1973	Table 1	West Virginia, USA		1300 mm	Various silt loams	Total	Strip-mine high walls and road cuts	% total root endings to 2.1 m	3 forest types: northern hardwood, cove hardwood, and oak-hickory
	McClaugherty et al. 1982	Table 1	Harvard Forest, USA			Entic Haplorthords (Spodosol), very stony	Fine: live/dead	19 mm and 50 mm	Mg/ha to depth of soil cores rooting zone (0.6–1.2 m)	Mixed hardwood stand
	Schulze et al. 1996		Patagonia, Argentina		770 mm		Total	Monoliths	$g \cdot m^{-2}$ to 200 cm	*Nothofagus pumila*
					522 mm		Total	Monoliths	$g \cdot m^{-2}$ to 225 cm	*Nothofagus antarctica*
	Scully 1942	Table 2	Wisconsin, USA		800 mm	Bellefontaine silt loam	Total	Trenches	# of roots ft^{-2}; % root area ft^{-2} to 3 ft. (1 ft. increments)	Maple-Oak forest

Appendix 2 (continued)

Vegetation type	Reference	Specifics	Location	Coordinates	Annual precip.	Soil type texture	Root type	Method	Measurement	Other
	Yin et al. 1989	Fig. 1	Wisconsin, USA	44:06 N 91:12 W	792 mm	Typic Hapludalf, loam and silt loam	Fine	10 cm soil cores	% biomass to 60 cm	*Quercus* ecosystem
Temperate grassland	Dahlman & Kucera 1965	Table 1	Missouri, USA		1016	Fine loess with claypan subsoil	Total	1.65 inch soil cores	$g \cdot m^{-2}$ to 34 inches	Central Missouri Prairie
	Dumortier 1991	Fig. 1	Bourgoyen Ossemeersen, Belgium	51:06 N 3:40 E		Humuficious upper layer and clay	Total	8.2 cm soil cores	$g \cdot m^{-2}$ to 100 cm for two plots	Two hayfields
	Fernández & Paruelo 1988	Fig. 5	Chubut, Argentina	45:25 S 70:20 W	142 mm	Calciorthid with high gravel content	Total	Excavation	Root length (cm per plant) to 120 cm	*Mulinum* and *Senecio* Two shrub species
	Lee & Lauenroth 1994	Fig. 2	Colorado, USA	40:49 N 104:47 W	321 mm	Sandy clay loam	Total	Monolith	to 110 cm	Shortgrass steppe
	Liang et al. 1989	Fig. 2	Colorado, USA	40:49 N 104:46 W	311 mm	Sandy loam or clay loam	Fine	5 cm soil cores	$g \cdot m^{-2}$ to 90 cm	Shortgrass steppe
	McKell et al. 1962	Fig. 2	California, USA		889 mm	Sutherlin fine gravelly clay loam	Macro organic matter	2.37 inch soil cores	$g \cdot ft^{-2}$ to 24 inches	Unimproved annual grassland
	Old 1969	Table 8	Illinois, USA		910 mm	Mollisol or Alfisol	Total	8 cm soil cores	$g \cdot m^{-2}$ to 100 cm	Tall grass prairie, *Andropogon* spp.
	Schulze et al. 1996		Patagonia, Argentina		290 mm		Total	Monolith	$g \cdot m^{-2}$ to 200 cm	Patagonia grassland
	Sims & Singh 1978	Table 2	Bridger (Montana)	45:57 N 110:47 W	900 mm	Silt loam, stony	Total	See Sims et al. 1978	$g \cdot m^{-2}$ to up to 60 cm	Montana grassland
			Cottonwood (South Dakota)	43:57 N 101:52 W	400 mm	Silty clay loam				South Dakota grassland
			Dickinson (North Dakota)	46:54 N 102:49 W	400 mm	Loamy fine sand				North Dakota grassland
			Hays (Kansas)	38:52 N 99:23 W	600 mm	Loam, shallow bedrock				Kansas grassland
			Jornada (New Mexico)	32:36 N 106:51 W	250 mm	Loamy fine sand, caliche				New Mexico grassland
			Osage (Oklahoma)	36:57 N 96:33 W	900 mm	Silty clay				Oklahoma grassland
			Pantex (Texas)	35:18 N 101:32 N	500 mm	Silty clay loam				Texas grassland
			Pawnee (Colorado)	40:49 N 104:46 W	300 mm	Fine sandy loam				Colorado grassland
	Singh & Coleman 1977	Table 2	Colorado, USA	40:49 N 104:46 W	300 mm	Fine sandy loam	Live/dead	4.5 cm soil cores	$g \cdot m^{-2}$ to 60 cm	Shortgrass prairie
	Weaver 1954	p. 163	Nebraska, USA		580–840 mm	Silty clay-loam and silt-loam	Total	Soil monoliths	% biomass to 5 feet (see Weaver and Darland 1949)	*Andropogon, Boutelouoa, Smittii*

Appendix 2 (continued)

Vegetation type	Reference	Specifics	Location	Coordinates	Annual precip.	Soil type texture	Root type	Method	Measurement	Other
Tropical deciduous	Bang-xing 1991	Table 4	Yunnan, China	21:44 N 100:40 E	1515–1606 mm		Fine	Unknown	$g \cdot cm^{-2}$ to 150 cm	Seasonal rainforest
	Castellanos et al. 1991	Fig. 1	Chamela, Mexico	19:30 N, 2 km east of Pacific coast	707 mm	Deep sandy loam	Total/coarse	0.5 m×2 m excavated trenches	$kg \cdot m^{-2}$ to 80 cm	Chamela deciduous forest
	Lawson et al. 1970	Fig. 14	Kade, Ghana	06:09 N 0:55 W	1650 mm	Reddish yellow latosols consisting of silty clay over sandy clay	Total (by size), fine	25 ×25×10 cm soil monoliths	$g \cdot 10000\ cm^{-3}$	*Celtis, Triplochiton*
Tropical evergreen	Berish 1982	Table 1	Florencia Norte Forest, Costa Rica	9:53 N 83:40 W	2700 mm	Typic Dystrandept	Total (minus large dead roots >2 mm)	4.2 cm soil cores, 25×25 cm soil blocks	$g \cdot m^{-2}$ to 85 cm, fine root surface area to 85 cm	Successional forest
	Gower 1987	Table 1	La Selva, Costa Rica	10:26 N 83:59 W	3800 mm	Fluvaquentic Hapludoll (River site) and Oxic Dystrandept (Arboleda site)	Fine: live/total (up to 5 mm)	7 cm soil cores	$g \cdot m^{-2}$ to 50 cm	La Selva forest
	Greenland & Kowal 1960	Table 8	Ghana		1650 mm	Oxysols or ochrosols	Total	4-cm-diam. cores	to 150 cm	*Diospyros, Strombosia*
	Huttel 1975	Fig. 10-3	Ivory Coast		Banco: 2100 mm Yapo: 1800 mm	Sandy with high clay and silt content	Total	Soil cores, unearthing roots	$g \cdot dm^{-3}$ to 130 cm	*Diospyros, Mapania*
	Klinge 1973	Tables 1, 4	Central Amazonia, Brazil			Pale yellow latosol (loamy), humus podzol (sandy)	Fine	1 m soil pits	kg/ha and length to 18 and 40 cm	Lowland forest
	Klinge & Herrera 1978	Table 3	Southern Venezuela			Spodosols		Excavation	kg/ha to approximately 60 cm	Amazon Caatinga, *Micrandra*
	Mensah & Jenik 1968	Figs. 4, 5, 6	Kade, Ghana	06:0:20 N 0:45 W 06:09 N 0:55 W			Total, fine	Soil monoliths	$g \cdot 6250\ cm^{-3}$	*Chlorophora excelsa*
	Nepstad et al. 1994	Fig. 2	Para, Brazil		1750 mm	deeply weathered clay soils	Fine	Auger borings	$mg \cdot cm^{-3}$ to 6 m	forest and adjacent pasture
	Vance & Nadkarni 1992	Table 3	Monteverde, Costa Rica	10:18 NN 84:48 W	2000 mm	Typic Dystrandept	Live: total/fine	10 cm soil cores, 1 m^2 excavated pits	$g \cdot m^{-2}$ to 180 cm	Monteverde cloud forest

Appendix 2 (continued)

Vegetation type	Reference	Specifics	Location	Coordinates	Annual precip.	Soil type texture	Root type	Method	Measurement	Other
Tropical Grassland/ Savanna	Fiala & Herrera 1988	Tables 1, 4	Cuba	22:15 N 80:41 W 21:38 N 82:59 W 22:53 N 82:53 W 22:59 N 82:23 W	1000–1500 mm 1165–1795 mm 2013 mm 1600–1800 mm	fine deep siliceous gleyed coarse sands fine sandy loam ferralitic red clay	Total, Live/dead	10×10 cm soil monoliths	% biomass to 50 cm	*Byrsonimo-Andropogonetum* *Phyllantho-Aristidetum* *Axonopus compressus* *Panicum maximum*
	Heitschmidt et al. 1988	Fig. 5	Texas, USA		650 mm	Typic Paleustoll	Total	4 m-wide by 2 m-deep profile face	# roots	Texas savanna *Prosopis glandulosa*
	Knoop & Walker 1985	Fig. 1	South Africa	25 S 29 E	630 mm	Sandy	Woody/ Herbaceous	Trenches	Density of 5 mm root lengths m^{-2}	Burkea site: broad-leaf Acacia site: fine-leaf
	Lawson et al. 1968	Fig. 17	Mole Game Reserve, Ghana			Colluvial, with deep sandy loam	Total	26×25×70 cm soil monolith	$g \cdot 10000\ cm^{-3}$ to 70 cm	Guinea savanna
	Le Roux et al. 1995	Fig. 1	Cote D'Ivoire, Africa	6:13 N 5:02 W	1210 mm		Fine	4.4-cm diam. cores	$g \cdot m^{-3}$ to 180 cm	Humid savanna
	Okali et al. 1973	Fig. 5	Accra Plains, Ghana	5:42 N 0:07 W	750 mm	Black loamy soil surrounded by pale sand over mottled sandy clay		25×25 cm soil monoliths	g/monolith for 3 samples and 3 sizes to 120 cm	Grassland and thicket clump
	Pandey & Singh 1992	Fig. 5, Table 1	Vindhyan plateau, India	24:19 N 82:78 E	926–1145 mm	Residual ultisols with sandy loam texture	Total	15×15 cm soil monoliths	% biomass to 50 cm	Northern India plateau
	Scholes & Walker 1993	Fig. 14.3	South Africa	25 S 29 E	630 mm		Fine; woody/grass	0.5 m^2 soil profiles	Length density $(m \cdot m^{-3})$ to 1 m	*Eragrostis, Burkea, Terminalia*
	Watts 1993	Fig. 2	Texas, USA	27:39 N 98:13 W	716 mm	Sandy loam	Total, live	20×20 cm soil monoliths	$g \cdot m^{-2}$ to 200 cm	*Prosopis glandulosa*
Tundra	Dennis & Johnson 1970	Fig. 2	Alaska, USA	71:20 N 156:39 W	104 mm	Marine and lacustrine sediments; loamy texture	Total, live	Soil cores	$g \cdot m^{-2}$ to 30–60 cm	5 sites with data from 5 sampling dates, many spp.
	Dennis et al. 1978	Table 5	Alaska, USA	71:20 N 156:39 W	104 mm	Marine and lacustrine sediments; loamy texture	Live/dead	Soil cores	$g \cdot m^{-2}$ to 25 cm	Barrow tundra, many spp.
	Hobbie 1995	Appendix	Alaska, USA	68:38 N 149:34 W	400 mm	Histosols	Live	Soil monolith	$g \cdot m^{-2}$ to 25 cm	Toolik Lake tundra Permafrost at 50 cm
	Ignatenko & Khakimzyanova 1971	Table 3	Pribaidaratskii region		340 mm		Total	Unknown	$g \cdot m^{-2}$ to 48 cm	Dwarf Birch, Dryas, Willow
	Khodachek 1969	Tabelle III	Taimyr Peninsula				Total	Monolith	$g \cdot m^{-2}$ to 50 cm	*Dryas, Carex*

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