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Maximum rooting depth of vegetation types at the global scale

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Abstract The depth at which plants are able to grow roots has important implications for the whole ecosystem hydrological balance, as well as for carbon and nutrient cycling. Here we summarize what we know about the maximum rooting depth of species belonging to the major terrestrial biomes. We found 290 observations of maximum rooting depth in the literature which covered 253 woody and herbaceous species. Maximum rooting depth ranged from 0.3 m for some tundra species to 68 m for *Boscia albitrunca* in the central Kalahari; 194 species had roots at least 2 m deep, 50 species had roots at a depth of 5 m or more, and 22 species had roots as deep as 10 m or more. The average for the globe was 4.6±0.5 m. Maximum rooting depth by biome was 2.0±0.3 m for boreal forest, 2.1±0.2 m for cropland, 9.5±2.4 m for desert, 5.2±0.8 m for sclerophyllous shrubland and forest, 3.9±0.4 m for temperate coniferous forest, 2.9±0.2 m for temperate deciduous forest, 2.6±0.2 m for temperate grassland, 3.7±0.5 m for tropical deciduous forest, 7.3±2.8 m for tropical evergreen forest, 15.0±5.4 m for tropical grassland/savanna, and 0.5±0.1 m for tundra. Grouping all the species across biomes (except croplands) by three basic functional groups: trees, shrubs, and herbaceous plants, the maximum rooting depth was 7.0±1.2 m for trees, 5.1±0.8 m for shrubs, and 2.6±0.1 m for herbaceous plants. These data show that deep root habits are quite common in woody and herbaceous species across most of the terrestrial biomes, far deeper than the traditional view has held up to now. This finding has important implications for a better understanding of ecosystem function and its application in developing ecosystem models.

Key words Deep roots function · Terrestrial vegetation · Biomes · Plant forms · Root depth

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Introduction

There is good evidence that some plant species are able to send roots very deep in the soil. This pattern is indicated by plants that grow well into the summer drought and by desert plants that grow for years with minimal or no rainfall (Batanouny and Abdel Wahab 1973; Poole and Miller 1975). In fact, survivorship of some species in arid systems has been shown to depend completely on a plant's ability to tap water from permanent water tables, which are sometimes located at depths of 18 m or more (Rawitscher 1948; Lewis and Burghy 1964). In addition, there have been direct observations of roots at depths below 2–3 m in caves, road cuts, mine shafts and trenches, and in some instances, roots of woody species have been seen exceptionally deep in the soil. This is the case of *Boscia albitrunca* and *Acacia erioloba* whose roots have been found at a depth of 68 m and 60 m, respectively, in the central Kalahari, Botswana (Jennings 1974), and the case of mesquite roots (*Prosopis juliflora*) found at 53 m deep in the Sonoran Desert, United States (Phillips 1963). Similarly, Stone and Kalisz (1991) reported 11 tree species rooted below 20 m depth. Hence, we know of the potential of some species to have very deep roots at few sites, yet very little is known about how common the habit of deep rooting is across species and environments.

There are two main reasons why this below-ground aspect of ecosystem structure, with its important functional implications, has been under-emphasized. First of all, there are a number of studies on root biomass distribution that show that most of the root biomass occurs within the first 50 cm of the soil, and that only a minimal fraction reaches depths below that depth (for a recent review see Jackson et al. 1996). Therefore, it has been assumed that a good understanding of the role of the root system regarding structure and function at the ecosystem level can be achieved by studying only the first 0.5 m of soil. Secondly, after a whole century of research on root systems, the means of obtaining data on root distribution and structure has not changed substantially: methods include the manual digging of trenches, the use of various mechanical excavation devices, dynamite, or high pressure water. When it comes to looking at patterns of maximum rooting depth, some of that technology is not even sufficient to provide access to deeper soil layers.

The functional significance of deep roots and their contribution to whole-ecosystem processes is still poorly understood. However, there is an increasing body of research in this field that shows the major role of deep roots, particularly for ecosystem water fluxes, as well as for carbon and nutrient cycling (Nepstad et al. 1994; Fisher et al. 1994; Richter and Markewitz 1985; Trumbore et al. 1995; Dawson 1996; Schulze et al. 1996).

The main objective of this review is to summarize what we know about the maximum rooting depth of the major terrestrial biomes ranging from tundra to tropical forest. The data set presented here provides information on plant structure which is relevant for a better mechanistic understanding of ecosystem function.

Methods

We selected references which had species- or community-level information on root depth below 1.0 m, except for the tundra biome for which we considered all depths because permafrost usually limits root growth beyond 30–50 cm. Here we included references from journal papers, books, reports, and unpublished data when relevant, which cover all continents except Antarctica. The major biomes we considered were: boreal forest, croplands, desert, sclerophyllous shrubland and forest, temperate coniferous forest, temperate deciduous forest, temperate grassland, tropical deciduous forest, tropical evergreen forest, tropical grassland/savanna, and tundra. The species were grouped by biome which means that in some instances two different functional groups, such as grasses and shrubs, may be in the same biome category. This was the case of the tropical grasslands and savannas where both herbaceous and woody species occur together. Similarly, in the temperate grassland we also found a few common shrub species along with the bulk of herbaceous plants. Finally, root data for the commonest agricultural crops were collected, including wheat, soybean, alfalfa, barley, and a few other species.

For each rooting depth observation, we recorded the species from which the observation was made, and the community's dominant species when roots were not identified at the species level. For most of the references, the maximum root depth observed corresponded with the depth of the trench, road cut, mine pit, or other excavation, and it is safe to say that roots probably reached much deeper layers than those recorded. Almost all the data presented here came from direct observations of roots in road cuts, mine shafts, open-cut mines and trenches, and only a few values were inferred from the results of isotopic trace studies or plant and soil water potential measurements. Finally, we also recorded the soil type or any soil textural attribute available to characterize the soil environment in which roots were growing.

Results and discussion

Maximum rooting depth across biomes

We compiled a total of 290 observations of rooting depth which covered 253 different plant species from 11 biomes around the world. From this data set, 194 species had roots at least 2 m deep, 50 species had roots at a depth of 5 m or more, and 22 species had roots as deep as 10 m or more (Appendix 1). The average maximum rooting depth for the globe was 4.6±0.5 m, and the individual maximum rooting depth was 68 m for *Boscia albitrunca*, the roots of which were found during well drilling in deep sandy soils in the central Kalahari, Botswana (Jennings 1974). The ten deepest rooting species were in decreasing order: *Boscia albitrunca* (68 m), *Acacia erioloba* (60 m), *Prosopis juliflora* (53 m), *Eucalyptus marginata* (40 m), *Retama raetam* (20 m), *Tamarix aphylla* (20 m), *Andira humilis* (18 m), *Alhagi maurorum* (15 m), *Prosopis farcta* (15 m), and *Prosopis glandulosa* (15 m).

Figure 1 shows the maximum rooting depth for all species across biomes in which only the deepest rooting depth is plotted when a given species has more than one observation. Maximum rooting depth by biome was 2.0±0.3 m ($n = 6$; highest value = 3.3 m) for boreal forest, 2.1±0.2 m (n = 17; highest value = 3.7 m) for cropland, 9.5±2.4 m (n = 22; highest value = 53 m) for desert, 5.2±0.8 m (n = 57; highest value = 40) for sclerophyllous shrubland and forest, 3.9±0.4 m (n = 17; highest value = 7.5 m) for temperate coniferous forest, 2.9±0.2 m (n = 19; highest value = 4.4 m) for temperate deciduous forest, 2.6±0.2 m (n = 82; highest value = 6.3 m) for temperate grassland, 3.7±0.5 m (n = 5; highest value = 4.7 m) for tropical deciduous forest, 7.3±2.8 m (n = 5; highest value = 18 m) for tropical evergreen forest, 15.0±5.4 m (n = 15; highest value = 68 m) for tropical grassland/savanna, and 0.5±0.1 m (n = 8; highest value = 0.9 m) for tundra.

Grouping all the species across biomes (except croplands) by three basic functional groups: trees, shrubs, and herbaceous plants, the maximum rooting depth was 7.0±1.2 m (n = 82) for trees, 5.1±0.8 m (n = 69) for shrubs, and 2.6±0.1 m (n = 85) for herbaceous plants (Fig. 2).

Although differences are large among biomes, there are also important departures from the mean rooting depth pattern within a biome. In the boreal forest, for instance, the water table usually limits the downward growth of roots of *Larix laricina* and *Picea mariana*, whose roots are commonly found no deeper than 0.3 m. Other species, however, do have the capacity to grow below the water table down to a depth of 2 m (Strong and La Roi 1983).

Plants from arid environments or from environments with a long dry season showed the deepest rooting habits of all. The presence of water at deep layers makes it possible for some plants to survive in the rainshadow environments by tapping water from layers as deep as 53 m in the desert of the southwestern United States (Phillips

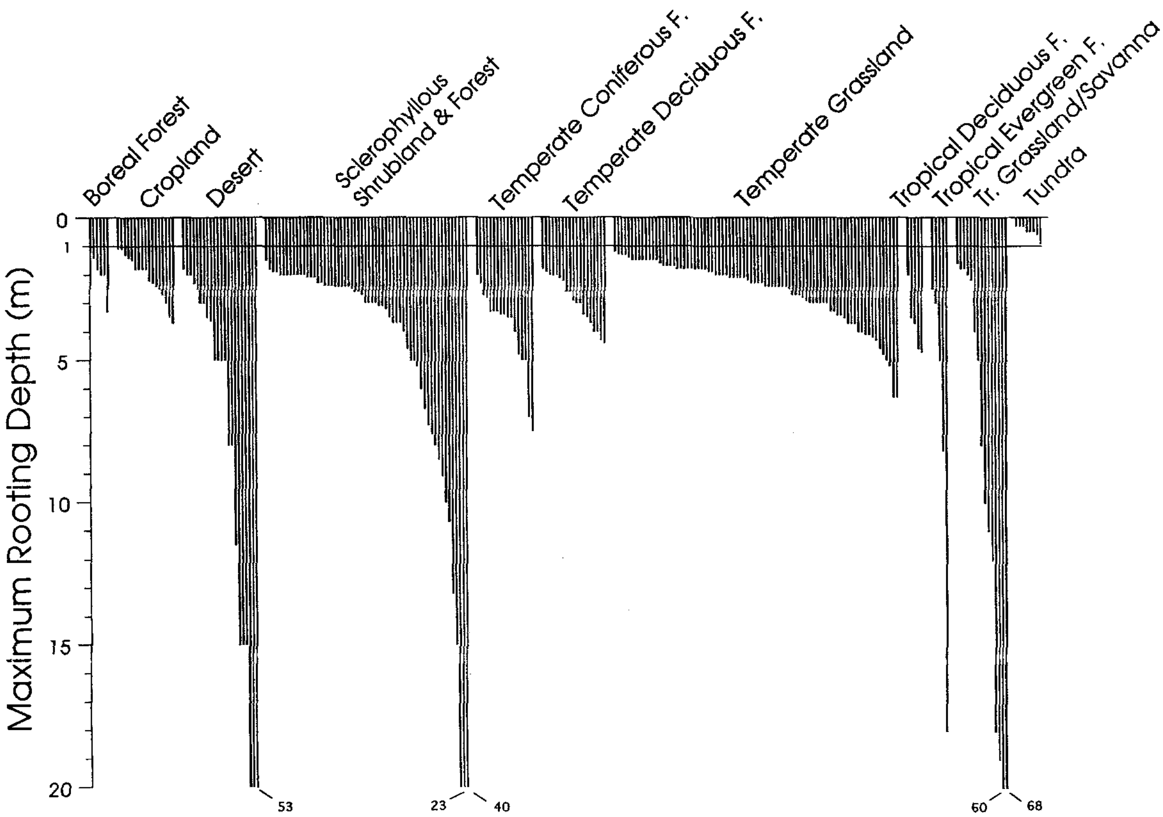

Fig. 1 Reported species maximum rooting depth (m) grouped by terrestrial biome. When there are more than one observations for a given species, only the maximum value is plotted

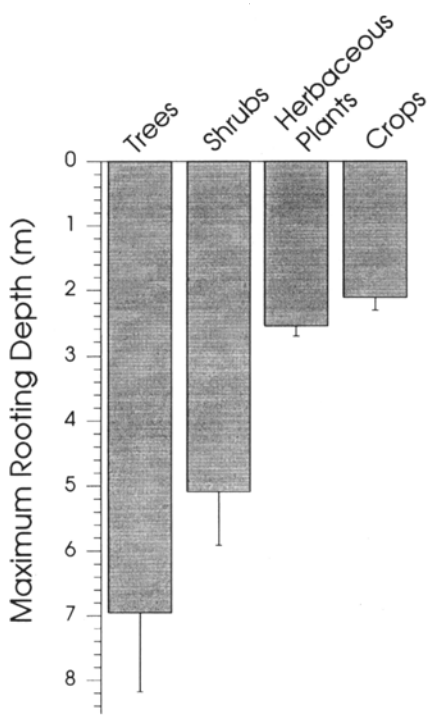

Fig. 2 Mean and SE of reported maximum rooting depth (m) by three major functional groups (trees, shrubs, and herbaceous plants) and crops

1963), and from 68 m deep, possibly even from 140 m deep where the water table was located, in the dry savanna of the central Kalahari (Jennings 1974). Likewise a group of species which also has a consistent pattern of deep rooting is that of the sclerophyllous trees, mostly made up of *Eucalyptus* spp. and *Quercus* spp. from the various Mediterranean regions of the world. The mean maximum rooting depth for sclerophyllous trees is 12.6±3.4 m (n = 11), with *E. marginata* in Australia the deepest of all at about 40 m (Dell et al. 1983). Sclerophyllous shrubs, although with deep rooting habits, has a shallower rooting pattern with a maximum rooting depth of 3.5±0.3 m (n = 48).

It is generally thought that roots in the evergreen tropical forest tend to be very shallow, but in this review the mean maximum rooting depth of 6 observations is 6.5±2.5 m. The only study that presented data from a depth beyond a few meters in the tropical forests of Brazil found roots all the way down to 18 m deep (Nepstad et al. 1994).

Another surprising result is the depth to which roots of herbaceous plants can descend, that was 2.4±0.1 m as average in this review. Weaver (1919) has published the most complete study to date, on rooting depth habits of herbaceous plants in a prairie in Nebraska, United StatesA. Of 33 species he studied, 18 species have roots that extend beyond depths of 1.5 m, most of them between 2.1 m and 2.7 m, and few to a maximum depth of from 4 m to 6.1 m.

These results offer plenty of evidence that many plant species have the capacity for deep rooting in the soil, and they provide enough data to challenge the dogma that plants are shallow rooted. Here we have presented, however, data on maximum rooting depth for individuals with the greatest depth. This value represents the observed maximum capacity of a given species to send roots deep into the soil, depths which may be reached by a small number of species and/or individuals within a community. In addition, an average or community weighted maximum rooting depth would also be functionally significant, yet data regarding this are hardly available for any biome. To illustrate the differences between absolute and average maximum rooting depth we shall present data from the root atlas published by Kutschera (1960). A random selection of 69 dicotyledonous species from grasslands in Mid Europe have an average maximum rooting depth of 1.1 m, the average of the 10 deepest species is 4.2 m and the absolute maximum rooting depth is 6.3 m. The average maximum rooting depth, which is the measurement most relevant to ecosystem functioning, will depend on species composition and density, and soil characteristics, all of which are fairly variable in space.

Getting very deep

Plants show a variety of root types through which they have access to deep soil layers. The most common are tap roots, sinker roots and obliquely descending lateral roots, all of them important adaptations for reaching deep soils. The phenotypic expression of these root types is species dependent, but environmental conditions may completely change root structure, architecture, and depth to which roots are able to descend (Feldman 1984). Tap roots are probably the most specialized root type to access and transport water from deep soil horizons. Tap roots are very common across species and they were found in up to 75% of tropical trees (Klinge 1973), in 73 of 100 Mediterranean woody species (Canadell and Zedler 1995), and in 19 of 30 herbaceous species in the Rocky Mountains foothills, United States (Holch et al. 1941).

The downward growth of roots can be limited by a variety of factors, such as soil bulk density or shallow bedrock, but probably the most efficient barriers are horizontally stratified layers of shale or clay, permafrost, and water table (Dennis et al. 1978; Bennie 1991). There is a common notion that deep roots are mainly limited to sandy loose soils where mechanical impedance to root penetration is least. On the contrary, we have reported in this review a number of examples in which plants have found their way down to very deep layers, even in compact clay and rocky soils, and through hard pans (Appendix 1).

Bedrock and heavy clay soils allow varying degrees of deep root penetration through highly weathered material or through a network of cracks, fissures and channels. Channels, or low resistance pathways, are permanent features of the soil profile, and it has been suggested that they result from dissolution of laterite by humic acid produced by the root itself (Plum and Gosting 1973). Gaiser (1952) found more than 10,000 cavities and root channels per hectare in a hardwood forest in Ohio, United States, pathways that can be reused and expanded by each new generation of trees. Hence, the soil volume should be viewed as a complex network of fissures, cracks and channels on which new root growth largely depends. It has even been suggested that soil compaction in forests may not affect the overall forest productivity, provided that sufficient low resistance pathways allow adequate root development (Nambiar and Sands 1992).

Roots have also been observed penetrating through hard pans and caliche layers in a variety of systems (Silva et al. 1989; Dawson 1993; Day 1994), and into rocks through fissures and cracks (Hellmers et al. 1955, Davis and Pase 1977). Pre-existing old tree channels and earthworm tunnels have also been shown to be important in the downward root development in crop systems (Nambiar and Sands 1992; Nicoullaud et al. 1994).

Finally, some plants find their way deep into the soil by penetrating directly through the bedrock. This phenomenon has been reported for several Mediterranean woody species growing on porous calcareous soils in Israel (Oppenheimer 1958; Orshansky 1951).

Ecological significance of deep roots

Although a small fraction of root biomass might be found at depths below 1 m, the functional significance of those roots may nevertheless be most important for ecosystem water and carbon fluxes, and nutrient cycling.

The water extracted by plants during the wet season comes from shallow layers where the root density is highest. However, as those layers dry there is a progressive shift towards using deeper water, which allows plants to keep stomata open and extend growth far into the dry season (for review see Gardner 1983). Although we know of the differential water sources in the soil profile, there are very few studies which have quantified the contribution of deep water to the whole ecosystem fluxes. Gregory et al. (1978) showed for winter wheat that few roots below 1 m (about 3% of the total root weight) were responsible for supplying 20% of the transpired water during dry periods. In an Amazonian tropical forest, Nepstad et al. (1994) found that had not considered roots deeper than 2 meters they would have underestimated evapotranspiration by >60% during the dry season. The water available to plants stored below 2 m in the soil provided >75% of the water extracted from the entire soil profile.

There is also plenty of evidence that plants with different rooting habits show different seasonal courses of water potential, and that the duration of water stress and the distribution of soil moisture with depth will determine whether a species can succeed in a particular environment (Davis and Mooney 1986; Crombie et al. 1988; Sala et al. 1989; Hodgkinson 1992).

For some species (e.g., phreatophytes), survival in arid systems depends exclusively on the capacity to send roots to permanent water tables, as in the case of *Prosopis tamarugo* in the virtually rainless Atacama Desert in Chile (Mooney et al. 1980). Stone and Kalisz (1991) gathered thirty references of plants having contact with water tables at depths from 1.5 to 35 m. In these cases, even if a very small fraction of the roots are tapping water from the water table, the amount of water transferred into the plant may be large. Reicosky et al. (1964) showed that roots tapping water from the water table are hundreds of times more efficient in absorbing it than roots in drier soil. Furthermore, tap roots often show cross sections with a high number of vessels per unit area, indicating a major water transport function (Higgins et al. 1987; see also Pate et al. 1995).

The functional significance of deep roots for water flux in ecosystems under high evaporative conditions has been shown regarding the "hydraulic lift" mechanism which has been reported for several species (Richards and Caldwell 1987; Caldwell and Richards 1989; Dawson 1993). During the night roots take up water from deep soil layers which is released from shallow roots back to the soil in the upper layers. The water is reabsorbed during the next day by the same plants and by shallow-rooted neighbors with no access to deep water. This mechanism has important ecological significance, allowing plants to maintain high transpiration rates during dry periods. Caldwell and Richards (1989) showed that hydraulic lift was responsible for a 30–50% increase of the daytime canopy water flux in artificial mixtures of *Artemisia tridentata* and *Agropyron desertorum* (see also Dawson 1996).

Unlike water relations, much less is known about the contribution of deep soil nutrients to the overall plant nutritional demands. Richter and Markewitz (1995) showed the importance of biological processes in weathering materials in a 8 m-soil profile of a *Pinus taeda* forest in South Carolina, United States; the biological processes were tightly associated with soil influenced by root activity (rhizosphere) all along the soil profile. The importance of deep roots for ecosystem nutrient cycling has also been shown for tropical soils with seasonal drought, Cerrado (Schachtschabel et al. 1992). Nitrate salts from mineralization of organic matter cannot be fully utilized by the vegetation early in the rainy season, and so, are washed out of the top soil down to deep soil horizons. There, nitrate is immobilized by the positive charge balance of Fe^{3+} and Al^{3+} found at depths of 1.6 m or more; deep roots will then have access to this nitrate store later in the growing season.

In the deep rhizosphere of *Prosopis glandulosa* in the Chihuahuan desert, United States, a variety of microarthropod taxa has been found down to a depth of 13 m (Silva et al. 1989). The abundance of microarthropods was positively correlated with root biomass, which suggests that deep rhizosphere processes such as decomposition and mineralization operate in a similar way to those processes in shallow layers. It is also known that plant-feeding nematodes, which are found deep in the rhizosphere, increase nodulation and nitrogen fixation (Huang 1987), and provide infection sites for vesicular-arbuscular mycorrhizal fungi (Freckman and Virginia 1989). In fact, Jenkins et al. (1988) found N_2-fixing root nodules at a depth of 7 m in the Chihuahuan desert.

Deep roots, in addition to extract water and contribute to the cycling of nutrients, also provide carbon to the soil. In an Amazonian tropical forest Nepstad et al. (1994) found that deep soil layers below 1 m contain large active carbon stocks, 15% of which turns over on annual to decadal timescale. The possession of an active carbon cycle at depth seems to be fairly common in the highly wheathered soils in terra firme tropical forest of Amazonia (Trumbore et al. 1995), but almost nothing is known about how common it might be in other biome types.

Ecosystem models which predict carbon sequestration have conventionally used root functional depths between 0.3 m and 2.0 m, which are usually used as fixed factors that do not change or only change for different ecosystem types. The depth at which roots will decay and decompose is essential for determining the ultimate fate of that carbon, and therefore, the capacity of carbon sequestration by different ecosystems. Fisher et al. (1994) showed that increased abundance of introduced deep-rooted grasses in the tropical South American savannas account for an increased sequestration of 100–507 Mt carbon per year, which could explain a substantial part of the missing carbon-sink (Siegenthaler and Sarmiento 1993).

In this review we have shown that deep root habits are quite common in woody and herbaceous species across most of the terrestrial biomes. Roots commonly reach far deeper into the soil than the traditional view has held up to now. This structural trait has important implications for ecosystem water fluxes, as well as for carbon and nutrient cycling, and hence should be appropriately taken into account in the development of ecosystem models.

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Appendix 1 Reported maximum rooting depth (m) by species with soil type, country and reference grouped by biome

Species/ dominant species[a]	Maximum rooting depth (m)	Soil type	Country	Reference
BOREAL FOREST				
Latrix laricina	1.2	medium-coarse sand/podzol	S-Canada	Bannan 1940
Latrix sibirica	1.8	medium-loamy	Russia	Verzunov 1980
Picea glauca	1.8	medium-loamy	Russia	Verzunov 1980
Pinus banksia	1.2	medium-coarse sand/podzol	S-Canada	Bannan 1940
Pinus banksiana	2.0	aeolian sands/Eutric brunisol	S-Canada	Strong and La Roi 1983
Pinus contorta	3.3	–	S-Canada	Horton 1958
Populus tremuloides	2.0	sandy substrate	S-Canada	Strong and La Roi 1983
CROPS				
Andropogon sorghum	1.1	lowland silt loam	Nebraska, USA	Weaver 1926
Avena sativa	1.8	–	Kansas, USA	Weaver 1926
Beta vulgaris	1.8	sandy loam	Nebraska, USA	Weaver 1926
Bromus inermis	1.1	silty-clay to clay-loam alluvial	Canada	Leyshon 1991
Elymus angustus	3.5	–	S-Canada	Lawrence 1975
Elymus junceus	1.8	–	S-Canada	Lawrence 1975
Glycine max	1.8	Muir silt loam	Kansas, USA	Mayaki et al. 1976
Helianthus annuus	2.7	lowland silt loam	Nebraska, USA	Weaver 1926
Helianthus annuus	2.7	Muir silt loam from alluvium	Kansas, USA	Jaafar et al. 1993
Hordeum vulgare	1.3	Lowland silt loam	Nebraska, USA	Weaver 1926
Hordeum sp.	2.2	loamy sand/Xeric Psamment	W-Australia	Hamblin and Tennant 1987
Lupinus angustifolius	2.5	loamy sand/Xeric Psamment	W-Australia	Hamblin and Tennant 1987
Medicago sativa	3.7	–	Nebraska, USA	Weaver 1926
Secale cereale	1.5	silt loam/hard clayey subsoil	Nebraska, USA	Weaver 1926
Solanum tuberosum	1.4	mellow loess soil	Nebraska, USA	Weaver 1926
Triticum aestivum	1.0	–	England	Welbank et al. 1974
Triticum aestivum	1.4	Muir silt loam	Kansas, USA	Chaudhuri et al. 1990
Triticum aestivum	1.5	lowland silt loam	Nebraska, USA	Weaver 1926
Triticum aestivum	1.8	–	Mid Europe	Kutschera 1960
Triticum aestivum	3.0	loamy sand/Xeric Psamment	W-Australia	Hamblin and Tennant 1987
Triticum durum	2.3	loess soil	Nebraska, USA	Weaver 1926
Zea mays	1.3	deep clay loam	E-France	Pages and Pellerin 1994
Zea mays	2.4	–	Nebraska, USA	Weaver 1926
DESERT				
Alhagi maurorum	15.0	river banks	Israel	Shmueli 1948
Artemisia monosperma	5.0	sand dunes	Israel	Zohary and Fahn 1952
Artemisia tridentata	1.8	shale/sandstone bedrock	Colorado, USA	Branson et al. 1976
Artemisia tridentata	2.2	loamy-skeletal/Haploxerolls	Utah, USA	Richards and Caldwell 1987
Artemisia tridentata	2.3	aeolian sandy loam	Idaho, USA	Reynolds and Fraley 1989
Atriplex halimus	8.0	alluvia soils/run-on habitats	Israel	Zohary 1961
Chrysothamnus vicidiflorus	2.0	aeolian sandy loam	Idaho, USA	Reynolds and Fraley 1989
Franseria deltoidea	1.8	wash with hardpan (caliche)	Arizona, USA	Cannon 1911
Hammada salicornica	2.5	sand dunes	Israel	Zohary and Orshan 1949
Leptadenia pyrotechnica	11.5	sandy and silty/clay at depth	Egytp	Batanouny and Wahab 1973
Leymus cinereus	2.0	aeolian sandy loam	Idaho, USA	Reynolds and Fraley 1989
Mulinum spinosum[a]	3.0	fine sand/caliche layer at 0.6 m	S-Argentina	Schulze et al. 1996
Nassauvia glomerulosa[a]	3.0	sandy loam/caliche at 0.7 m	S-Argentina	Schulze et al. 1996
Nitraria retusa	5.0	sandy	Israel	Ginzburg 1966
Ochradenus baccatus	5.0	sandy	Israel	Ginzburg 1966
Prosopis farcta	15.0	river banks	Israel	Zohary and Orshan 1949
Prosopis glandulosa	2.0	Nuvalde clay loam	Texas, USA	Heitschmidt et al. 1988
Prosopis glandulosa	6.0	clay loam/sand, clay at depth	California, USA	Nilsen et al. 1983
Prosopis glandulosa	12.0	sandy/Torrifluvent	New Mexico, USA	Freckman and Virginia 1989
Prosopis glandulosa	15.0	clay loam	New Mexico, USA	Silva et al. 1989
Prosopis juliflora	53.0	–	Arizona, USA	Phillips 1963
Prosopis tamarugo	3.5	–	N-Chile	Mooney et al. 1980
Prosopis velutine	8.0	–	Arizona, USA	Cannon 1911
Retama raetam	20.0	sand dunes	Israel	Zohary and Fahn 1952
Tamarix aphylla	20.0	alluvial soils/run-on habitats	Israel	Zohary 1961
Tamarix pentantra	3.6	alluvial banks	Arizona, USA	Gary 1963
Zilla spinosa	5.0	–	Israel	Ginzburg 1966

Appendix 1 (continued)

Species/ dominant species[a]	Maximum rooting depth (m)	Soil type	Country	Reference
SCLEROPHYLLOUS SHRUBLAND AND FOREST				
Shrubs				
Adenostoma fasciculatum	2.4	silt sandy	California, USA	Hanes 1965
Adenostoma fasciculatum	7.6	sandy loam on anorthosiste	California, USA	Hellmers et al. 1955
Adenostoma sparsifolium	2.4	silt sandy	California, USA	Hanes 1965
Arbutus unedo	3.5	sandy loam	NE Spain	J Canadell, unpublished work
Arctostaphylos glandulosa	5.2	sandy loam on granodiorite	California, USA	Hellmers et al. 1955
Arctostaphylos glauca	2.6	sandy loam on granodiorite	California, USA	Hellmers et al. 1955
Arctostaphylos glutinosa	2.5	shallow on fractured shales	California, USA	Davis 1972
Arctostaphylos pallida	4.0	shallow on fractured shales	California, USA	Davis 1972
Banksia marginata	2.4	sandy	SE-Australia	Specht and Rayson 1957
Banksia ornata	2.4	sandy	SE-Australia	Specht and Rayson 1957
Baccharis pilularis	3.2	packed sand like a rock	California, USA	Wright 1928
Banksia spp.	5.0	podsolized sand	SW-Australia	Low and Lamont 1990
Calytrix flavescens	2.0	grey sands with hardpan	SW-Australia	Dodd et al. 1984
Casuarina muelleriana	2.0	sandy	SE-Australia	Specht and Rayson 1957
Casuarina pusilla	2.4	sandy	SE-Australia	Specht and Rayson 1957
Ceanothus leucodermis	3.7	sandy loam on granodiorite	California, USA	Hellmers et al. 1955
Ceanothus megacarpus	2.4	sandstone with fissures	California, USA	Thomas and Davis 1989
Ceanothus oliganthus	1.8	clay loam on diorite	California, USA	Hellmers et al. 1955
Ceanothus spinosus	3.1	sandstone with fissures	California, USA	Thomas and Davis 1989
Daviesia brevifolia	2.0	sandy	SE-Australia	Specht and Rayson 1957
Eremaea beaufortioides	6.0	alluvial sand with colluvium	SW-Australia	Hnatiuk and Hopkins 1980
Eremaea pauciflora	2.4	grey sands with hardpan	SE-Australia	Dodd et al. 1984
Erica arborea	2.0	sandy loam	NE-Spain	J. Canadell, unpublished work
Hibbertia hypericoides	2.1	grey sands with hardpan	SW-Australia	Dodd et al. 1984
Jacksonia floribunda	3.1	grey sands with hardpan	SW Australia	Dodd et al. 1984
Jacksonia furcellata	2.0	grey sands with hardpan	SW Australia	Dodd et al. 1984
Laudonia behrii	2.0	sandy	SE-Australia	Specht and Rayson 1957
Leptospermum myrsinoides	2.3	sandy	SE-Australia	Specht and Rayson 1957
Leucadendron salignum	3.0	loamy medium sand	South Africa	Higgins et al. 1987
Lithraea caustica	5.0	–	Central Chile	Giliberto and Estay 1978
Melaleuca scabra	2.0	grey sands with hardpan	SW-Australia	Dodd et al. 1984
Melaleuca seriata	2.1	grey sands with hardpan	SW-Australia	Dodd et al. 1984
Petrophile linearis	2.0	grey sands with hardpan	SW-Australia	Dodd et al. 1984
Photinia arbutifolia	2.1	clay loam on diorite	California, USA	Hellmers et al. 1955
Phyllota pleurandroides	2.3	sandy	SE-Australia	Specht and Rayson 1957
Phyllota remota	2.4	sandy	SE-Australia	Specht and Rayson 1957
Protea neriifolia	3.0	loamy medium sand	South Africa	Higgins et al. 1987
Protea repens	3.0	loamy medium sand	South Africa	Higgins et al. 1987
Quercus calliprinos[a]	4.6	terra-rossa on limestone	Israel	Shachori et al. 1967
Quercus dumosa	8.5	clay loam on diorite	California, USA	Hellmers et al. 1955
Quercus turbinella	6.4	fracturated granite	Arizona, USA	Davis and Pase 1977
Quercus turbinella	9.1	alluvial and redish brown	Arizona, USA	Saunier and Wagle 1967
Quillaja saponaria	8.0	–	Central Chile	Giliberto and Estay 1978
Rhus glabra	6.7	loess hills	Nebraska, USA	Weaver 1919
Rhus laurina	5.4	sandstone with fissures	California, USA	Thomas and Davis 1989
Rhus laurina	13.2	–	California, USA	DeSouza et al. 1986
Salvia apiana	1.5	coarse, loose gravel	California, USA	Hellmers et al. 1955
Scholtzia involucrata	1.9	grey sands with hardpan	SW-Australia	Dodd et al. 1984
Spyridium subochreatum	1.9	sandy	SE-Australia	Specht and Rayson 1957
Stirlingia latifolia	2.6	grey sands with hardpan	SW-Australia	Dodd et al. 1984
Xanthorrhoea australis	2.4	sandy	SE-Australia	Specht and Rayson 1957
Trees				
Eucalyptus marginata	15.0	lateritic, sandy-clay at depth	SW-Australia	Kimber 1974
Eucalyptus marginata	20.0	–	SW-Australia	Carbon et al. 1980
Eucalyptus marginata	40.0	fissured granite, clay subsoil	SW-Australia	Dell et al. 1983
Eucalyptus regnans	2.7	–	SW-Australia	Incoll 1969
Eucalyptus signata	3.0	sandy	NE-Australia	Westman and Rogers 1977
Eucalyptus sp.	10.0	sand dunes	NE-Australia	Westman and Rogers 1977
Quercus agrifolia	10.7	–	California, USA	Cannon 1914
Quercus chrysolepis	7.3	sandy loam on granodiorite	California, USA	Hellmers et al. 1955
Quercus douglasii	3.7	alluvial loam	California, USA	Cannon 1914
Quercus ilex	3.7	sandstone	NE-Spain	J. Canadell, unpublished work
Quercus wislizenii[a]	22.9	fractured rock	California, USA	Lewis and Burgy 1964

Appendix 1 (continued)

Species/ dominant species[a]	Maximum rooting depth (m)	Soil type	Country	Reference
TEMPERATE CONIFEROUS FOREST				
Abies firma	3.3	sandy soil	Japan	Karizumi 1979
Picea excelsa	2.3	silt loam	Japan	Karizumi 1979
Pinus densiflora	3.4	silt loam	Japan	Karizumi 1979
Pinus echinata	3.3	sandy soil	New Jersey, USA	Lull and Axley 1958
Pinus elliottii	3.3	–	Florida, USA	van Rees and Comerford 1986
Pinus halepensis[a]	7.3	terra-rossa on limestone	Israel	Shachori et al. 1967
Pinus halepensis	7.5	weathered granite	NE-Spain	J. Canadell, unpublished work
Pinus luchuensis	3.5	sandy loam	Japan	Karizumi 1979
Pinus palustris	4.8	Norfold sand deep phase	Florida, USA	Heyward 1933
Pinus pinaster	7.0	–	Australia	Butcher and Havel 1976
Pinus pinea	5.0	weathered granite	NE-Spain	J. Canadell, unpublished work
Pinus ponderosa	3.5	clay loam soil	Oregon, USA	Zwieniecki and Newton 1994
Pinus radiata	2.0	sandy soil	S-Australia	Nambiar and Sands 1992
Pinus resinosa	2.7	Hinckley coarse sand	New York, USA	White and Wood 1958
Pinus resinosa	5.0	sandy outwash	New York, USA	Leaf et al. 1955
Pinus rigida	2.7	sandy soil	New Jersey, USA	McQuilkin 1935
Pinus rigida	3.4	sandy soil	Japan	Karizumi 1979
Pinus strobus	2.8	sandy soil	Japan	Karizumi 1979
Pinus sylvestris	2.7	sand overlying chalky drift	United Kingdom	Roberts 1976
Pinus taeda	2.0	fullerton and bodine	Tennessee, USA	Harris et al. 1977
Pinus taeda	4.0	granite wheathered/Ultisol	S-Carolina, USA	Richter and Markewitz 1995
TEMPERATE DECIDUOUS FOREST				
Acer negundo	4.0	upland clay	Missouri, USA	Biswell 1935
Acer saccharum	3.7	silty loams with hardpan	New York, USA	Dawson 1993
Carya spp.	1.8	sandstone	Ohio, USA	Gaiser 1952
Corylus americana	3.5	loess hills	Nebraska, USA	Weaver 1919
Fraxinus japonica	2.0	fine texture clay	Japan	Karizumi 1979
Juglans nigra	3.0	silt loam	Japan	Karizumi 1979
Latrix decidua	3.4	fine silty sand at depth	New York, USA	White and Wood 1958
Nothofagus pumila	2.0	orange loam/rocks at depth	S-Argentina	Schulze et al. 1996
Platanus orientalis	2.6	medium texture	Japan	Karizumi 1979
Populus nigra	1.9	silt loam	Japan	Karizumi 1979
Populus sargentii	2.6	loam underlain with clay	Missouri, USA	Biswell 1935
Populus tremula	2.0	clay subsoil	Sweden	Persson 1975
Populus tremuloides	2.3	grey clay	Michigan, USA	Day 1944
Populus tremuloides	2.9	sandy loam	Utah, USA	Gifford 1966
Prunus yedoensis	2.1	fine texture clay	Japan	Karizumi 1979
Quercus dentata	4.3	silt loam	Japan	Karizumi 1979
Quercus macrocarpa	4.3	fine-textured loams	Nebraska, USA	Weaver and Kramer 1932
Quercus macrocarpa	4.4	upland clay	Missouri, USA	Biswell 1935
Quercus sp-Carya sp[a]	4.0	silt loam on sandstone/shale	Virginia, USA	Kochenderfer 1973
Quercus velutina	3.0	medium texture	Japan	Karizumi 1979
Salix babylonica	2.2	silt loam	Japan	Karizumi 1979
TEMPERATE GRASSLAND				
Agropyron repens	2.4	loose sandy	Nebraska, USA	Weaver 1919
Agropyron smithii	2.7	silt loam	Colorado, USA	Weaver 1958
Agropyron spicatum	1.4	med. textur. Benge series	Washington, USA	Harris 1967
Agropyron spicatum	1.5	silt loam	Washington, USA	Weaver 1919
Amorpha canescens	5.0	loose sandy	Nebraska, USA	Weaver 1919
Andropogon furcatus	1.5	Judson silt loam	Nebraska, USA	Weaver and Darland 1949
Andropogon furcatus	2.8	clay loam	Nebraska, USA	Weaver 1919
Andropogon gerardi	2.1	lilt loam	Iowa, USA	Weaver 1958
Andropogon hallii	1.8	sandy	Nebraska, USA	Tolstead 1942
Andropogon hallii	3.0	sandy	Colorado, USA	Weaver 1958
Andropogon scoparius	1.5	silt loam	Iowa, USA	Weaver 1958
Andropogon scoparius	1.8	loam sandy	Colorado, USA	Weaver 1919
Aragallus lambertii	1.4	loam sandy	Colorado, USA	Weaver 1919
Argemone platyceras	3.7	loam sandy	Colorado, USA	Weaver 1919
Artemisia frigida	1.7	dark brown soil on shales	S-Canada	Coupland and Johnson 1965
Artemisia cana	2.4	dark brown soil on shales	S-Canada	Coupland and Johnson 1965
Atriplex nuttallii	1.8	dark brown soil on shales	S-Canada	Coupland and Johnson 1965
Astragalus crassicarpus	2.0	loam soil on hard joint clay	Nebraska, USA	Weaver 1919
Berberis repens	3.0	silt loam	Washington, USA	Weaver 1919
Biscutella laevigata	2.1	–	Mid Europe	Kutschera 1960

Appendix 1 (continued)

Species/ dominant species[a]	Maximum rooting depth (m)	Soil type	Country	Reference
Bouteloua curtipendula	1.7	silt loam	Colorado, USA	Weaver 1958
Bouteloua gracilis	1.7	Colby silt loam	Nebraska, USA	Weaver and Darland 1949
Bouteloua gracilis	1.8	silt loam	Colorado, USA	Weaver 1958
Bouteloua gracilis[a]	2.1	–	Kansas, USA	Albertson et al. 1953
Brauneria pallida	2.4	clay loam	Nebraska, USA	Weaver 1919
Buchloe dactyloides	1.8	silt loam	Iowa, USA	Weaver 1958
Buchloe dactyloides	2.0	Wabash silt loam	Nebraska, USA	Weaver and Darland 1949
Bulbilis dactyloides	1.9	alluvial	Nebraska, USA	Weaver 1919
Calamovilfa longifolia	1.8	dark borwn soil on shales	S-Canada	Coupland and Johnson 1965
Calamovilfa longifolia	3.0	sandy	Colorado, USA	Weaver 1958
Carex arenaria	1.8	–	Mid Europe	Kutschera 1960
Carex filifolia	1.5	silt loam	Colorado, USA	Weaver 1958
Carlina acaulis	4.1	–	Germany	Kutschera 1960
Centaurea scabiosa	3.3	–	Germany	Kutschera 1960
Chrysopis villosa	2.4	dark brown soil on shales	S-Canada	Coupland and Johnson 1965
Equisetum arvense	3.0	sandy	Canada	Coupland and Johnson 1965
Equisetum palustre	2.5	–	Mid Europe	Kutschera 1960
Eriogonum heracleoides	2.4	silt loam	Washington, USA	Weaver 1919
Eriogonum jamesii	2.3	loam with some sand	Colorado, USA	Weaver 1919
Eriogonum microthecum	3.0	sandy	Colorado, USA	Weaver 1919
Erodium botrys	1.3	gravelly clay loam	California, USA	McKell et al. 1962
Eryngium campestre	4.2	–	Germany	Kutschera 1960
Eurotia lanata	1.8	dark brown soil on shales	S-Canada	Coupland and Johanson 1965
Festuca arizonica	1.2	sandy loam-sandy clay	Colorado, USA	Currie and Hammer 1979
Festuca arizonica	1.3	–	Colorado, USA	Schuster 1964
Festuca arundinacea	2.7	–	Germany	Kutschera 1960
Festuca pallescens[a]	2.0	alluvial sandy loam & gravel	S-Argentina	Schulze et al. 1996
Gaillardia aristata	1.7	dark brown soil on shales	S-Canada	Coupland and Johnson 1965
Geranium viscosissimum	2.9	silt loam	Washington, USA	Weaver 1919
Grindelia squarrosa	1.9	loose sand	Nebraska, USA	Weaver 1919
Heracleum sphondyleum	2.0	–	Mid Europe	Kutschera 1960
Hieracium scouleri	2.2	silt loam	Washington, USA	Weaver 1919
Hoorebekia racemosa	3.4	silt loam	Washington, USA	Weaver 1919
Kochia prostrata	6.3	–	Germany	Kutschera 1960
Kuhnia glutinosa	5.2	–	Nebraska, USA	Weaver 1919
Lepachys pinnata	1.5	brown silt loam	Illinois, USA	Sperry 1935
Lespedeza capitata	2.4	lower slopes of loess hills	Nebraska, USA	Weaver 1919
Liatris punctata	2.1	gravelly	S-Canada	Coupland and Johnson 1965
Liatris punctata	4.8	clay	Nebraska, USA	Weaver 1919
Lithospermum gmelini	2.1	sandy	Nebraska, USA	Tolstead 1942
Lupinus ornatus	4.0	silt loam	Washington, USA	Weaver 1919
Lygodesmia juncea	3.0	sandy	Nebraska, USA	Tolstead 1942
Lygodesmia juncea	3.0	dark brown soil on shales	S-Canada	Coupland and Johnson 1965
Lygodesmia juncea	6.3	loess	Nebraska, USA	Weaver 1919
Medicago falcata	4.3	–	Germany	Kutschera 1960
Muhlenbergia montana	1.3	sandy clay loam subsoil	Colorado, USA	Schuster 1964
Onobrychis natrix	2.3	–	Mid Europe	Kutschera 1960
Ononis natrix	2.3	–	Germany	Kutschera 1960
Panicum virgatum	2.7	loose sand	Nebraska, USA	Weaver 1919
Parthenium integrifolium	1.8	brown silt loam	Illinois, USA	Sperry 1935
Petalostemum purpureum	1.8	brown silt loam	Illinois, USA	Sperry 1935
Peucedanum cervaria	4.1	–	Germany	Kutschera 1960
Phalaris aquatica	1.2	granite	Spain	Joffre et al. 1987
Pimpinella saxifraga	3.7	–	Germany	Kutschera 1960
Potentilla blaschkeana	2.3	silt loam	Washington, USA	Weaver 1919
Potentilla fruticosa	3.0	gravelly	S-Canada	Coupland and Johnson 1965
Potentilla concinna	1.8	dark brown soil on shales	S-Canada	Coupland and Johnson 1965
Psoralea tenuiflora	1.8	loose sand	Nebraska, USA	Weaver 1919
Psoralea tenuiflora	3.7	loam sandy, silt loam	Colorado, USA	Weaver 1919
Redfieldia flexuosa	1.5	sandy	Colorado, USA	Weaver 1958
Ruellia ciliosa	1.5	brown silt loam	Illinois, USA	Sperry 1935
Rumex crispus	3.3	–	Germany	Kutschera 1960
Senecio riddellii	1.5	sandy soil	Nebraska, USA	Tolstead 1942
Silphium integrifolium	1.7	brown silt loam	Illinois, USA	Sperry 1935
Silphium laciniatum	1.8	brown silt loam	Illinois, USA	Sperry 1935
Solidago canadensis	3.4	loose sandy	Nebraska, USA	Weaver 1919
Solidago rigida	1.4	brown silt loam	Illinois, USA	Sperry 1935
Spartina pectinata	4.0	silt loam	Iowa, USA	Weaver 1958

Appendix 1 (continued)

Species/ dominant species[a]	Maximum rooting depth (m)	Soil type	Country	Reference
Sporobolus cryptandrus	1.5	deeply eroded loess	Nebraska, USA	Weaver 1919
Sporobolus heterolepsis	1.5	silt loam	Iowa, USA	Weaver 1958
Stipa spartea	1.8	silt loam	Iowa, USA	Weaver 1958
Taraxacum serotinum	4.6	–	Germany	Kutschera 1960
Thermopsis rhombifolia	2.1	gravelly	S-Canada	Coupland and Johnson 1965
Tradescantia reflexa	1.6	brown	Illinois, USA	Sperry 1935
Vernonia baldwinii	3.5	loose sand	Nebraska, USA	Weaver 1919
TROPICAL DECIDUOUS FOREST				
Antiaris toxicaria	3.5	red soil	China	Bang-Xing 1991
Baccaurea ramiflora	3.7	red soil	China	Bang-Xing 1991
Gironniera subaequalis	4.7	red soil	China	Bang-Xing 1991
Symplocos cochinchinensis	2.0	red soil	China	Bang-Xing 1991
Xauthophyllum siamense	4.6	red soil	China	Bang-Xing 1991
TROPICAL EVERGREEN FOREST				
Apodytes dimidiata	8.2	sandy loam on schists	Kenya	Kerfoot 1963
Chlorophora excelsa	2.0	ferralitic	Ghana	Mensah and Jenik 1968
Chlorophora excelsa	3.0	ferralitic	Ghana	Jenik 1971
Community	18.0	clay	Brazil	Nepstad et al. 1994
Community	5.0	–	Brazil	Poels 1987
Community	2.5	Turraeantho on sandy soil	Ivory Coast	Huttel 1975
TROPICAL GRASSLAND AND SAVANNA				
Acacia erioloba	60.0	Kalahari sands	Botswana	Jennings 1974
Anacardium pumilum	10.0	–	Brazil	Ferri 1961
Andira humilis	18.0	reddish loamy earth	Brazil	Rawitscher 1948
Andira spp.	19.0	–	Brazil	Rawitscher et al. 1943
Aristolachia giberti	1.8	redish loamy earth	Brazil	Rawitscher 1948
Boscia albitrunca	68.0	Kalahari sands	Botswana	Jennings 1974
Brachiaria brizantha[a]	8.0	clay	Brazil	Nepstad et al. 1994
Brachystegia sp.	1.8	–	Zimbabwe	Strang 1969
Capparis sp.	1.6	sandy clay loam	Ghana	Okali et al. 1973
Curatella americana	4.0	–	Venezuela	Foldats and Rutkis 1975
Jacaranda decurrens[a]	11.0	–	Brazil	Rawitscher et al. 1943
Ochna pulchra	2.2	structureless sand	South Africa	Rutherford 1983
Panicum maximum[a]	12.0	clay	Brazil	Nepstad et al. 1994
Stipagrostis amabilis[a]	5.0	Kalahari sands	South Africa	J. Canadell, unpublished work
Stryphnodendron sp.	2.0	reddish loamy earth	Brazil	Rawitscher 1948
TUNDRA				
Cares aquatilis[a]	0.3	–	Alaska, USA	Dennis et al. 1978
Dryas punctata[a]	0.5	permafrost at 40–55 cm	N-Russia	Khodachek 1971
Dupontia fischeri[a]	0.3	organic matter on sediments	Alaska, USA	Dennis 1977
Eriophorum vaginatum[a]	0.6	silty soil on permafrost	Alaska, USA	Wein and Bliss 1974
Betula nana	0.5	permafrost at 50 cm	Alaska, USA	S. Hobbie, unpublished work
Luzula confusa	0.3	loams	N-Canada	Bliss and Svoboda 1984
Salix glauca	0.5	permafrost at 45–60 cm	W-Russia	Ignatenko and Khakimzy 1971
Salix planifolia	0.9	coarse textured/bottom pit	Colorado, USA	Webber and May 1977

[a] Maximum rooting depth is not linked to the species name but to the dominant species in the community

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