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RESEARCH ARTICLE

Vertical root distribution in Himalayan trees: about half of roots occur below 30 cm, the generally sampled depth

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Abstract

Almost nothing is known about the vertical root distribution for Himalayan forest trees. By providing an analysis of vertical distribution of root density of ten important central Himalayan tree species (two evergreen conifers, five evergreen broadleaf species and three deciduous broadleaf species), this paper attempts to address this gap. We used trench profile method to measure tree root density, both of fine (≤ 3 mm diameter) and coarse (> 3 mm diameter) roots. Principal Component Analysis was performed to identify the major sources of variation among species in root distribution. In ten study tree species (eg., sal, oaks, pine and *Cupressus torulosa*) the rooting depth varied from 90 to 150 cm. On average across the study species, about 49% total roots (all diameter classes) occurred below 30 cm depth and 20.6% below 60 cm depth. These percentages are almost identical to that of tropical rain forest of Amazon. The tree species varied in root density (in entire soil column) from 26.04 ± 2.66 root/100 cm^2 in *Q. floribunda* to 52.7 ± 4.96 root/100 cm^2 in *Machilus duthei*. The ordination graph indicated that tree species of a growth form and even a genus did not form groups and differed markedly in root characters. Tree water status and roots were related only partially and in a complex way. The study has shown that (1) root density measured by digging trenches gives a reasonable estimate of proportional root distribution of trees, and (2) studies which consider only top 30 cm depth can grossly misrepresent root distribution and its consequence.

Keywords Conifers · Fine roots · Himalayas · Oaks · Tree · Vertical root distribution

Introduction

Fine tree roots (< 2–3 mm in diameter) are central to belowground ecological processes, playing a major role in forest ecosystem functioning (Pregitzer 2002). They form the most active and short-lived part of the root system and influence forest carbon, soil nutrient acquisition and water cycle (Lukac 2012). Although aboveground components of forests have been investigated in detail almost for all types across the world, there are considerably fewer studies on belowground components, particularly fine roots (Clark et al. 2001; Mokany et al. 2006; Cordeiro et al. 2020). In terrestrial ecosystems across the world fine root productivity is estimated to share 22–40% of net primary productivity (Bloom et al. 1985; Aragao et al. 2009; McCormack et al. 2015), which is an important source of soil organic carbon (Russell et al. 2004; Lukac 2012). In a forest ecosystem, most large roots die only with tree itself, while the fine roots show a constant seasonal flux with a high rate of death and renewal (Persson 1979). The physiological cost

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of maintaining a fine root system for a single tree may be up to 70% of the available carbon flow (Agren et al. 1980).

Ecologists are increasingly interested in the Carbon budget of forests, as they are the major carbon sink that can help to reduce future global warming (Steele et al. 1997; Strand et al. 2008). Globally, 45% forest carbon is found as soil organic matter (FAO 2020). Changes in root depth in soil can influence vital ecosystem processes, such as mycorrhizal infestation, root chemistry and soil carbon storage (Jackson et al. 1996; Iversen 2010). In a study by Lozanova et al. (2019) in Bulgaria, two beech and two Douglas fir stands were compared for several root traits, such as standing root mass, annual production, and turnover rate, not only for analysing tree health, nutrient and water uptake, but also for carbon input to soils. Soil root profiles are important to determine changes in soil carbon and how ecosystems may respond to disturbances and a climate warming (Vogt et al. 1993; Matamala et al. 2003). Trees vary considerably in specific root length which is highly sensitive to climate change (Ostonen et al. 2007). In the region of a strongly seasonal precipitation, such as Himalayas moisture is a key determiner of fine root distribution (Metcalfe et al. 2008), and a likely driver of belowground dynamics under the climate warming (Magrin et al. 2014). Concentration of fine roots in top soil layer helps a species to rapidly derive nutrients from litter, but is prone to dying in pre-monsoon (March to June), which is a common feature in Himalayas and the area dominated by a monsoon rainfall (Singh et al. 2017). Tree roots are highly variable in morphology even across the species of same growth form such as deciduous forest trees (Rewald et al. 2014).

Almost all forest types occur in the Himalayas because of extraordinarily wide elevational range. In much of Himalayas, forests occur in an elevational range of above 4000 m (Singh 2018) and include as an example oaks (*Quercus* species), sal (*Shorea robusta*), pines (*Pinus*), firs (*Abies*), maples (*Acer*), ash (*Fraxinus*) and alder (*Alnus nepalensis*). Some of these forests and trees have been investigated thoroughly for productivity, nutrient cycling, water relations, phenology and fire adaption (Singh and Singh 1992; Zobel and Singh 1997). However, almost nothing is known about the distribution of roots in soil profiles of Himalayan forests. Worldwide, most of the studies on roots and soil carbon are restricted to top soil 0–30 cm layer (Vogt et al. 1983; Elliot and Coleman 1988; Helmisaari et al. 2002; Schenk and Jackson 2002), however, roots as the recent soil carbon studies indicate, may occur up to a considerably more soil depth (Iversen 2010; Cordiero et al. 2020). Though several tree characters are related to growth form (e.g. needle-leaved and broadleaved evergreen), its relationship with soil root distribution is hardly known (Pierett et al. 2016; Iversen et al. 2017).

The present study on vertical distribution of roots of the trees largely concerns the Himalayan temperate forests between 1950 and 2400 m elevations in the outer ranges, characterized by monsoon pattern of precipitation (~ 75–80% of annual precipitation occurring from mid-June to September). We investigated ten species of which two were conifers, five broadleaved evergreen species and three broadleaved deciduous species.

In this study our objectives were: (1) to provide a basic information on vertical root distribution for important tree species of the Central Himalayan forests and to examine whether the species of a growth form resemble in their root attributes; (2) to contribute to making generalizations with regard to the root distribution in forest trees, particularly with reference to deeper soils (below 30 and 60 cm) which are frequently sampled; and (3) to find out whether vertical distribution of roots shed any light on tree water status. Our hypotheses in this study are: (1) keeping in view the heterogeneity in topography and geological processes (Singh and Singh 1992), rooting depth in Himalayan forests is expected to vary considerably among the trees, and deeper soil layers (soil below 30 cm and 60 cm depth) may account for a substantial fraction of total roots, and (2) species with shallower roots will be more water stressed than those with deeper roots, as surface soil gets considerably dry during pre-monsoon months in Himalayas (Singh et al. 2006). The study makes a small beginning to address the gap in the ecology of Himalayan forests. For vertical root distribution, we measured root density (fine roots as well as coarse roots) across soil profiles upto the depths beyond which roots were not observed (from 90 to 150 cm across ten tree species). The tree water status was based on predawn (the period before the rising sun when plant water potential is the maximum in a diurnal cycle) tree water potential measured on the study tree species seasonally for two years in an earlier research project (Singh et al. 2006).

Material and methods

Study sites

The study was conducted in the Nainital lake catchment (29° 23′ 31″ N Latitude and 79° 27′ 15″ E Longitude) of Kumaun Himalaya, Uttarakhand. Of the ten species, two were conifers, five broadleaved evergreen species and three broadleaved deciduous species (Table 1). With a characteristic monsoon pattern of rainfall, the area gets 75–80% of annual rainfall (generally between 1500 and 2500 m) from mid-June to September. The annual average temperature of Nainital at the lake level (1938 m) was recorded as 15.7 °C (Bisht et al. 2013) and it declines at the lapse rate of − 0.53 °C/100 m with elevation rise (Joshi et al. 2018). The soil is classified as

Table 1 General distribution of the studied Himalayan tree species [Source: Troup (1921); Champion and Seth (1968); and Sahni (1990); Singh et al. (2006)]

Tree species (family)	Altitudinal range (m asl)	Distribution/ habitat
Carpinus viminea Lindley[d] (Betulaceae)	1800–2400	Occurs in isolated patches mainly on the bouldery/old landslides and moist shady places of oak forests
Cornus macrophylla Wall.[d] (Cornaceae)	1800–3000	Limited to moist ravines, temperate and lower temperate mixed forests
Fraxinus micrantha Lingelsh.[d] (Oleaceae)	1800–2100	Occurs from Sikkim westwards, distributed in patches in mixed temperate forests
Machilus duthiei King[e] (Lauraceae)	1200–2400	Distributed in western Himalaya, in ravines and shady places as under-canopy of oak forests
Pinus roxburghii Sarg.[e] (Pinaceae)	1000–2000	Form extensive forests in outer ranges; common on ridges of the Siwalik Hills flanking the Himalayas, generally between 1000 and 2000 m
Quercus leucotrichophora A. Camus[e] (Fagaceae)	1200–2400	Widely distributed in western and central Himalaya, between 1000 and 2200 m
Quercus floribunda Lindley ex A. Camus[e] (Fagaceae)	2000–2400	Distributed in western Himalaya from Nepal westwards; common in Kumaun Himalaya, between 2000 and 2400 m
Shorea robusta Gaertn.[e] (Dipterocarpaceae)	300–1200	Widely distributed in the foothills of Himalaya from Himachal Pradesh in the west to eastern Himalaya
Cupressus torulosa D. Don[ee] (Cupressaceae)	1800–2700	Distributed throughout the outer and middle ranges of the Himalayas in isolated small pockets
Rhododendron arboreum Smith[ee] (Ericaceae)	1500–2400	Occurs as undercanopy in oak forests in western Himalayas; but also extends to eastern Himalaya

[d] Deciduous

[e] Evergreen with about one year leaf life span

[ee] Multi-year evergreen

forest brown earth. It is predominantly sandy loam belonging to the Krol series. Podzolization is weak if present. The organic carbon varies widely from less than 1–4%, and the pH from 5.6 to 6.5, and decreases with elevation (Gahlot et al. 2020). All study species are canopy forming, except *Machilus duthei* and *Rhododendron arboreum* which are undercanopy species of Oak forests (*Q. leucotrichophora* and *Q. floribunda*). Himalayas, particularly western and central parts are warming at rates far more than global average (Yao et al. 2012), and tree ring data suggest that the region has been drying for last several decades.

Methods

Root density

We carried out sampling for vertical distribution of roots mostly at the sites where tree-water relation sampling was conducted in an earlier study (Singh et al. 2006). The root density was measured at the end of monsoon, in September, when root mass is the highest in these Himalayan forests (Usman et al. 1997). For tree root distribution in soil we used a trench profile method similar to described by Bohm (1979). Trenches were excavated with hand tool between 1 and 3 m from the marked tree bases (2–3 trees for each species). The 100 cm wide trench was first excavated bit by bit for 30 cm depth, avoiding damage to roots. The number of root tips was counted with of 5, 10 × 10 cm randomly placed quadrats within 100 × 30 cm trench wall. The trench was further excavated by another 30 cm, and root counting was done again as described above at five random points. Diameter of roots was measured with Vernier calipers and they were divided into three categories: < 3 mm refers to fine roots, 3–5 mm moderate fine roots and > 5 mm coarse roots. By gradually removing soil with forceps and brush we tried to avoid damage to roots. However, 10–15% roots used to get damaged, and in that case their diameter could be overestimated. The depth upto which roots occurred varied across the species from 100 to 180 cm. Each of the soil layers was 30 cm deep, except the deepest one which could be 10–30 cm deep depending upon the depth upto which roots occurred. The number of soil layers/depths varied from 4 to 6 across the species. Towards the deepest-end the assessment of root presence was counted with 10 cm increment to identify the deepest point of the root occurrence precisely. Root density for each 30 cm depth class was based on 10–15, 10 × 10 cm quadrats. Three to four persons worked together for root sampling and on a day 4–5 trenches were dug. The trenches were filled with soil after root counting.

Correlation between rooting depth and percentage of fine and total roots at two depths (top 30 cm and top 60 cm) was developed in Microsoft Excel with the help of Chart-type scatter XY for all the studied tree species. Principal component analysis (PCA), a multivariate data reduction statistical technique was applied on a set of root characteristics of ten tree species of Himalayan region in order to identify major sources of variation in root characters (Gotelli and Ellison 2004). Variation with Kaiser normalization was used with PCA as extraction method.

Results

Depth distribution of roots

The rooting depth (maximum soil depth, beyond which roots did not occur) ranged from 90 cm (*Carpinus viminea* and *Fraxinus micrantha*) to 150 cm (*Cornus macrophylla, M. duthei, Q. floribunda* and *R. arboreum*). In the rest of four species roots occurred from 100 to 140 cm soil depths. On average across all tree species, 49.2 ± 1.9% of total roots (roots of all diameter classes) of the entire soil column occurred below 30 cm depth, and the percentage increased with root diameter class, being 44.1 ± 1.6% for fine roots and 65.5 ± 1.6% for coarse roots. The rooting depth was significantly correlated with percentsge of fine ($r = 0.61$; $p < 0.05$) (Fig. 1a) and total roots ($r = 0.67$; $p < 0.05$) (Fig. 1b) only at top 60 cm soil depth. The percentage of total roots in the top 30 cm of soil varied widely from 37.7% in *R. arboreum* to 60.3% in *F. micrantha* (Fig. 1b). Though root density declined rapidly with depth, a substantial proportion of total roots in soil column was present below 60 cm depth. For example, for total roots the average percentage of roots below 60 cm was 20.6 ± 2.8%, and it increased with increasing root diameter.

The top 60 cm soil layer accounted for above ~ 87% of total roots in the shallow rooted species, viz., *Carpinus viminea* and *F. micrantha*. In the others, the contribution of the top two soil layers to total root density in the entire profile ranged from 61.6 to 85.5% roots. Generally, we found that the lower the root density in soil column, the shallower the root distribution. *Pinus roxburghii, F. micrantha* and *Q. floribunda* belonged to the category of shallow root distribution (83.7% to 92.8% roots in top 60 cm soil) (Fig. 1b) and lower root density (26.0 ± 2.7–31.1 ± 4.8 ind./100 cm^2 in the entire soil column), while the *S. robusta, R. arboreum, Cornus macrophylla, Cupressus torulosa, Q. leucotrichophora* and *M. duthei* had relatively evenly distributed roots across the soil depths of soil column (61.6–81.5% roots in top 60 cm) (Fig. 1b), and higher root density (34.8 ± 3.3–52.7 ± 4.9 ind./100 cm^2).

PCA resulted in three-component model with a total variation explained to the tune of 88.69%. The first component (PCA 1) explained 52.50% of the species variance and was determined by percentage of roots below 30 cm and 60 cm soil depth (fine roots, moderately fine roots, and total roots), total soil column density of moderately fine roots and coarse roots. The second component (PCA 2) captured 18.64% of the variance of species distribution, and was determined by rooting depth (the soil depth upto which roots occurred) (Table 2). The eigenvalue of PC 1 and PC 2 was 8.43 and 1.83, respectively. Bi-plot between PC 1 and PC 2 presents a clear species separation according to root characteristics (Fig. 2). Overall the lack of species grouping in the ordination graph was quite striking, even the two oaks did not make a group with regard to root characters. Among the broadleaved deciduous species, *Cornus macrophylla* was separate from *F. micrantha* and *Carpinus viminea* because of the difference in rooting depth.

Root diameter classes

The total root density in soil column (sum of all depths of all root diameter class) per 100 cm^2 area was much lower in *Q. floribunda* (26.0 ± 2.7 ind./100 cm^2) and *F. micrantha* (31.1 ± 4.8 ind./100 cm^2) than in *M. duthei* (52.7 ± 4.9 ind./100 cm^2), *R. arboreum* (51.9 ± 2.9 ind./100 cm^2) and *Carpinus viminea* (50.5 ± 5.8 ind./100 cm^2) (Fig. 3). As for the total density of fine roots with < 3 mm diameter ranges from 16.7 ± 1.9 ind./100 cm^2 in *Q. floribunda* to 38.6 ± 4.1 ind./100 cm^2 in *M. duthei*.

From 83.4% (*R. arboreum*) to 92.5% (*F. micrantha*) roots were 5 mm or less in diameter, the rest (˃ 5 mm diameter) were coarse roots. In all species the share of fine roots in the total roots was above 50%. This percentage was the highest in *F. micrantha* (80.3%), followed by *Carpinus viminea* (75.2%). Proportionally, moderately fine roots (3–5 mm) were high in *R. arboreum* (28.4%) followed by *P. roxburghii* (24.0%), in the rest species it ranged from 12.1% (*F. micrantha*) to 23.8% in *Q. floribunda*. Coarse roots (5–25 mm diameter) accounted for 7.6% of total roots in *F. micrantha* to 16.6% in *R. arboreum*. In the other species, the percentage of coarse roots in total roots ranged from 8.9% in *M. duthei* to 15.5% in *P. roxburghii*. Species of a growth form varied in root diameter composition. For example, among the deciduous broadleaved species *F. micrantha* and *Carpinus viminea* resembled each other in having high proportions of fine roots, and they differed from *Cornus macrophylla* which had a relatively lower fraction of fine roots.

Tree water potential and rooting depth

We used two predawn water potential parameters, the lowest seasonal water potential, and the percentage of seasonal

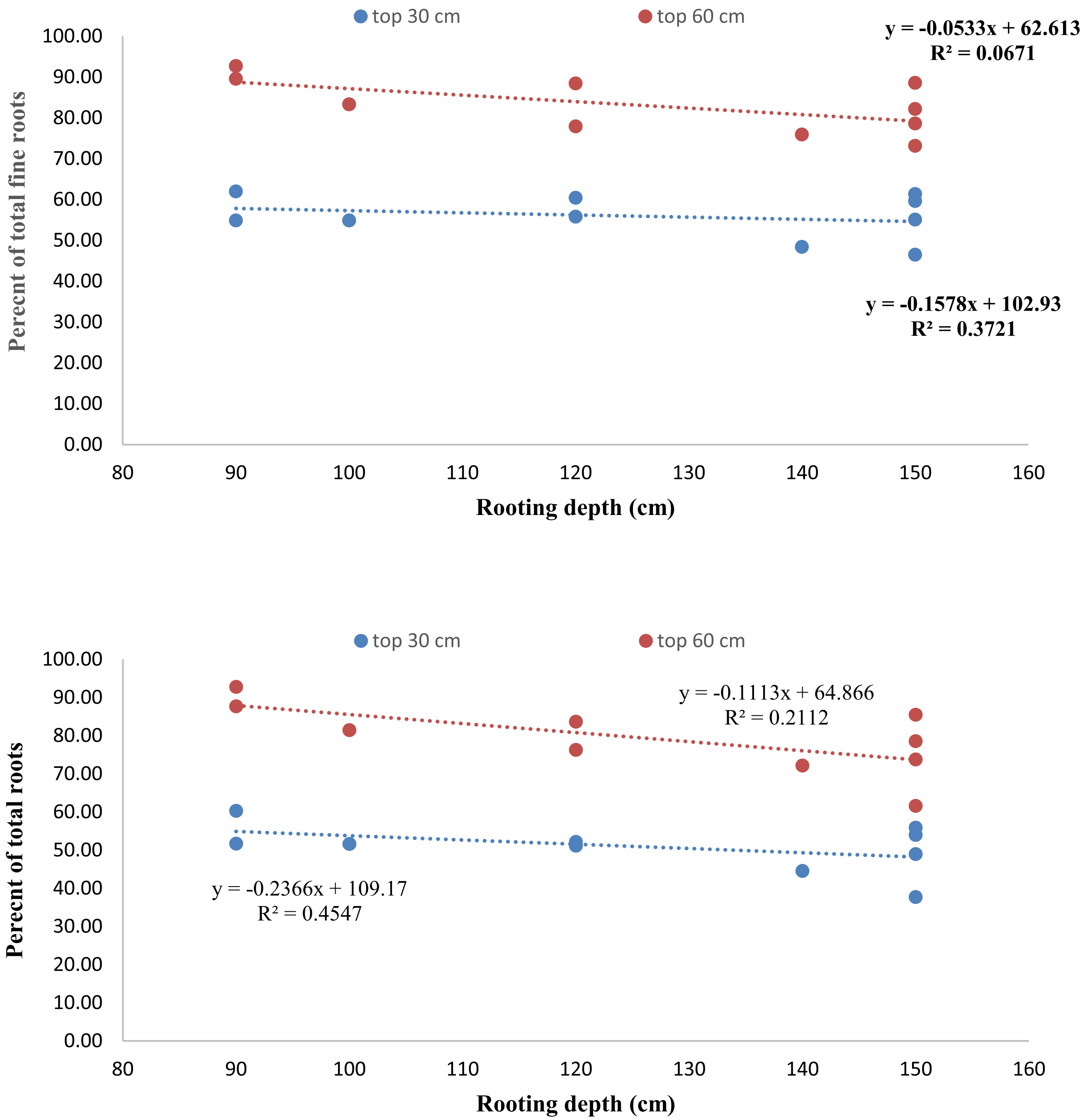


Fig. 1 Relationship between rooting depth (depth upto which roots occur) and percentage of fine and total roots in top 30 cm and 60 cm soil depth

values which were lower than − 1 MPa as an indicator of water stress. Each species was measured six times in a year, and predawn water potential values were the lowest during the pre-monsoon (March to mid-June), which is warm and dry. Among the deciduous species, the deep rooted *Cornus macrophylla* had clearly higher water potential than the shallow rooted *F. micrantha* and *Carpinus viminea*. *Pinus roxburghii* and *F. micrantha* which had the shallowest rooting depths, differed considerably in predawn water potential (Fig. 4). The two conifers, *P. roxburghii* and *Cupressus torulosa* differed in water stress, the pine maintaining relatively higher water potential than the cypress. The deep rooting habit of fine roots is advantageous for avoiding water stress by water uptake as long as water is held in deep soil layers (Yanagisawa and Fujita 1999). Of the two oaks *Q. floribunda* was more deep rooted (up to 150 cm) than *Q.*

Table 2 Correlation of the variable (descriptors) with individual PCA axes

Variable	PC 1	PC 2
Rooting depth	0.03	0.93
Percentage of fine roots (< 30 cm)	0.87	0.11
Percentage of fine roots (< 60 cm)	0.80	0.37
Total fine root density in soil column	0.02	0.05
Percentage of intermediate roots (< 30 cm)	0.80	0.49
Percentage of intermediate roots (< 60 cm)	0.84	0.47
Total intermediate root density in soil column	0.80	0.33
Percentage of coarse roots (< 30 cm)	0.52	0.31
Percentage of coarse roots (< 60 cm)	0.67	0.69
Total coarse root density in soil column	0.93	0.18
Percentage of total roots (< 30 cm)	0.94	0.16
Percentage of total roots (< 60 cm)	0.88	0.43
Total root density in soil column	0.40	0.08
Variation explained (%)	52.50	18.64
Eigen value	8.43	1.83

leucotrichophora (up to 120 cm), but below 60 cm soil profile, *Q. leucotrichophora* had more roots (3.2/100 cm^2 in 60–90 cm soil depth and 1.8/100 cm^2 in 90–120 cm soil depth) while roots were negligible below 60 cm soil depth profile (1.0 and 0.38/100 cm^2 in 60–90 cm and 90–120 cm depths, respectively) in *Q. floribunda*. Consequently, the percentage of values below − 1 MPa predawn was higher (38%) in *Q. floribunda* than in *Q. leucotrichophora* (18%). *Shorea robusta* growing in foothills had the least water stress as none of its predawn water potential values in a year was below − 1 MPa, and its leaf conductance values were generally the highest among the ten study species. Its total root density (47.3/100 cm^2 in soil column) was towards the higher side of range of density across the ten species.

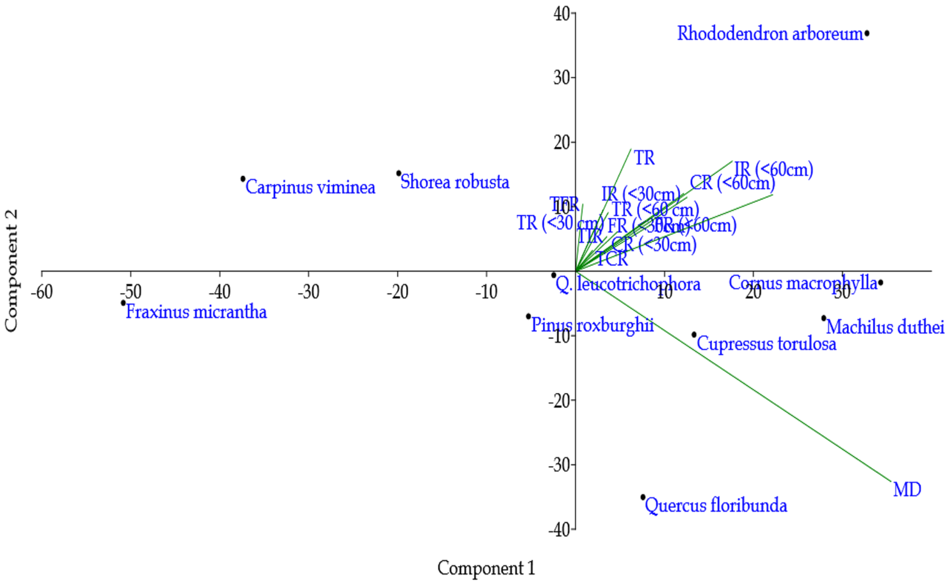
Discussion

Substantial fractions of roots in deeper soil layers

Contrary to historical assumption that fine roots largely occur in the top 30 cm soil layer, the soil deeper than 30 cm depth of the present study, accounted for a considerable fraction of soil root column. Of all diameter classes, on average across the ten study tree species, 49.2 ± 1.9% of total roots (of all diameter classes in the entire soil column) occurred below 30 cm soil layer, and this percentage increased with increasing root diameter. A global meta-analysis indicates that in woody vegetation coarse roots occur deeper than fine roots (Schenek and Jackson 2002). These values are quite similar to that of a Central Amazon forest in which 53.9% of standing fine-root length is reported to be in the top 30 cm soil layer (Cordeiro et al. 2020). In the Amazon forest study, root length was measured precisely with a minirhizotron, thus indicating that root density, as measured in the present study gave a reasonably precise estimate of proportional depth distribution of roots. The average percentage of the total roots in the top 30 cm soil (50.8%) in the present study is almost same as that of temperate forest (50%) (Jackson et al. 1996).

Since root turnover in deeper layers is less than in shallower layers, carbon in deeper layers could stay longer. In a study on soil carbon distribution in banj oak (*Q. leucotrichophora*), Singh et al. (2011) found that of the total carbon in top 1 m soil, 50% occurred below 20 cm depth,

Fig. 2 Bi-plot based on root characters of ten Himalayan tree species



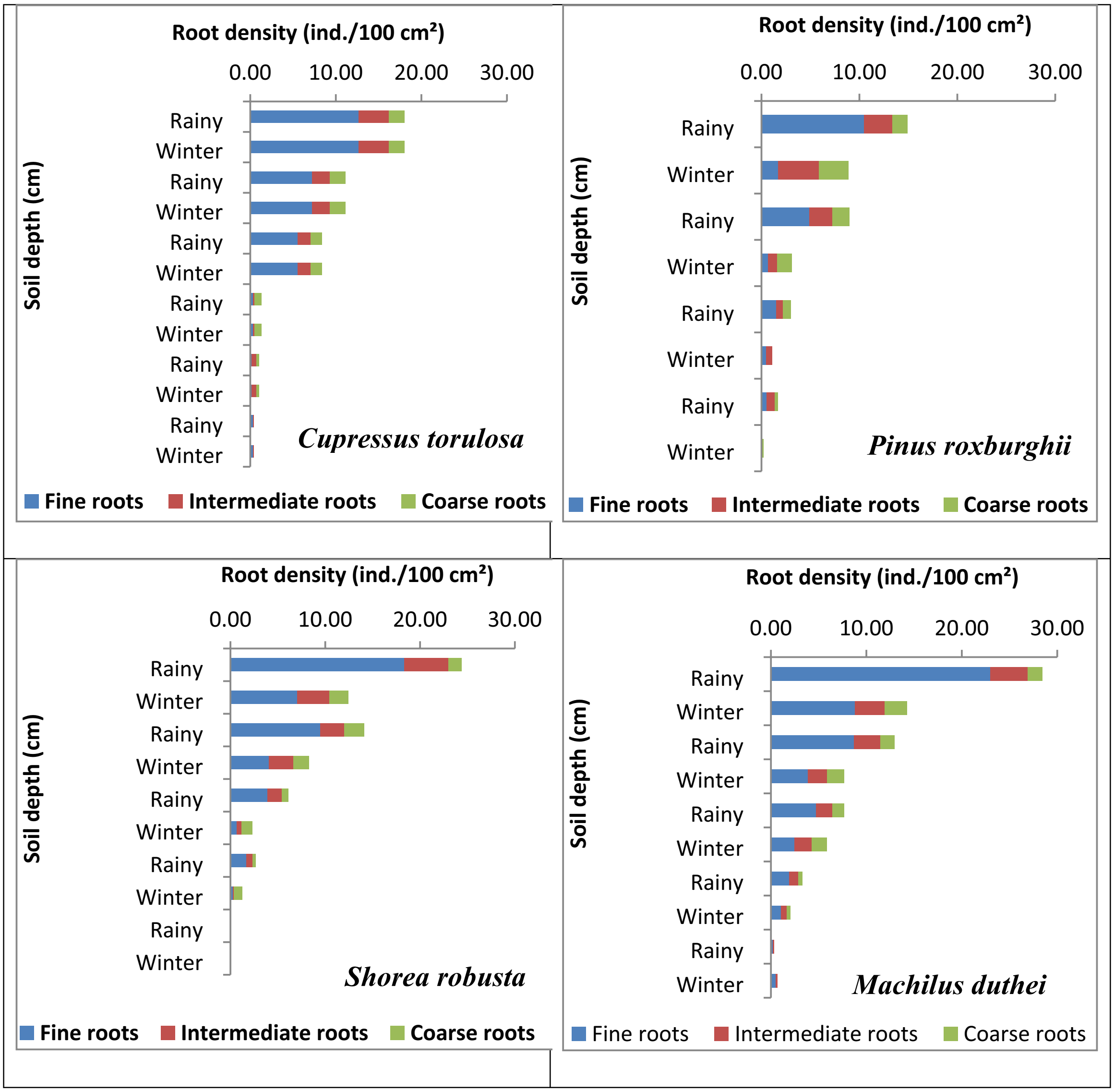


Fig. 3 Vertical distribution of fine, intermediate and coarse root in ten Himalayan tree species, Evergreen conifers: **a** *Cupressus torulosa;* **b** *P. roxburghii*; Evergreen broadleaved: **c** *S. robusta*; **d** *M. duthei*; **e** *Q. leucotrichophora*; **f** *Q. floribunda*; and **g** *R. arboreum*; Deciduous broadleaved: **h** *Carpinus viminea*; **i** *F. micrantha*; **j** *Cornus macrophylla*

and the carbon in the next 1 m soil layer was sizeable, accounting for 56% of that in first 1 m soil layer.

In the ordination field based on root characters, species were scattered and even the two oaks did not form a group. *Pinus roxburghii* and *Q. leucotrichophora*, the two regionally dominant species occupied Central portion of the field, in which root characters tended to change diagonally (Fig. 4). Our data on vertical root distribution suggest that the tree species even within a catchment differ substantially in vertical root distribution and root diameter composition. Among the three broadleaved deciduous species, *Cornus macrophylla* differed from the other two deciduous species in root depth, root density and percentage of roots below 30 cm and 60 cm depths (Fig. 4). Likewise the two conifers had little silmilarity in their root distribution. Compared to *Cupressus torulosa*, the *P. roxburghii* had distinctly lower root density and percentage of roots below 30 cm depth. The two conifers also differed in the extent water stress they are subjected to. The broadleaved evergreen species too were scattered in the ordination graph developed on the basis of root characters, even the two oaks occupied different locations. Among the ten tree species sal (*S. robusta*) was least water stressed, all of the predawn water potential values being higher than − 1 MPa. Vertical root distribution in *S. robusta* was close to the average values recorded for the ten species. For example, the percentage of all roots

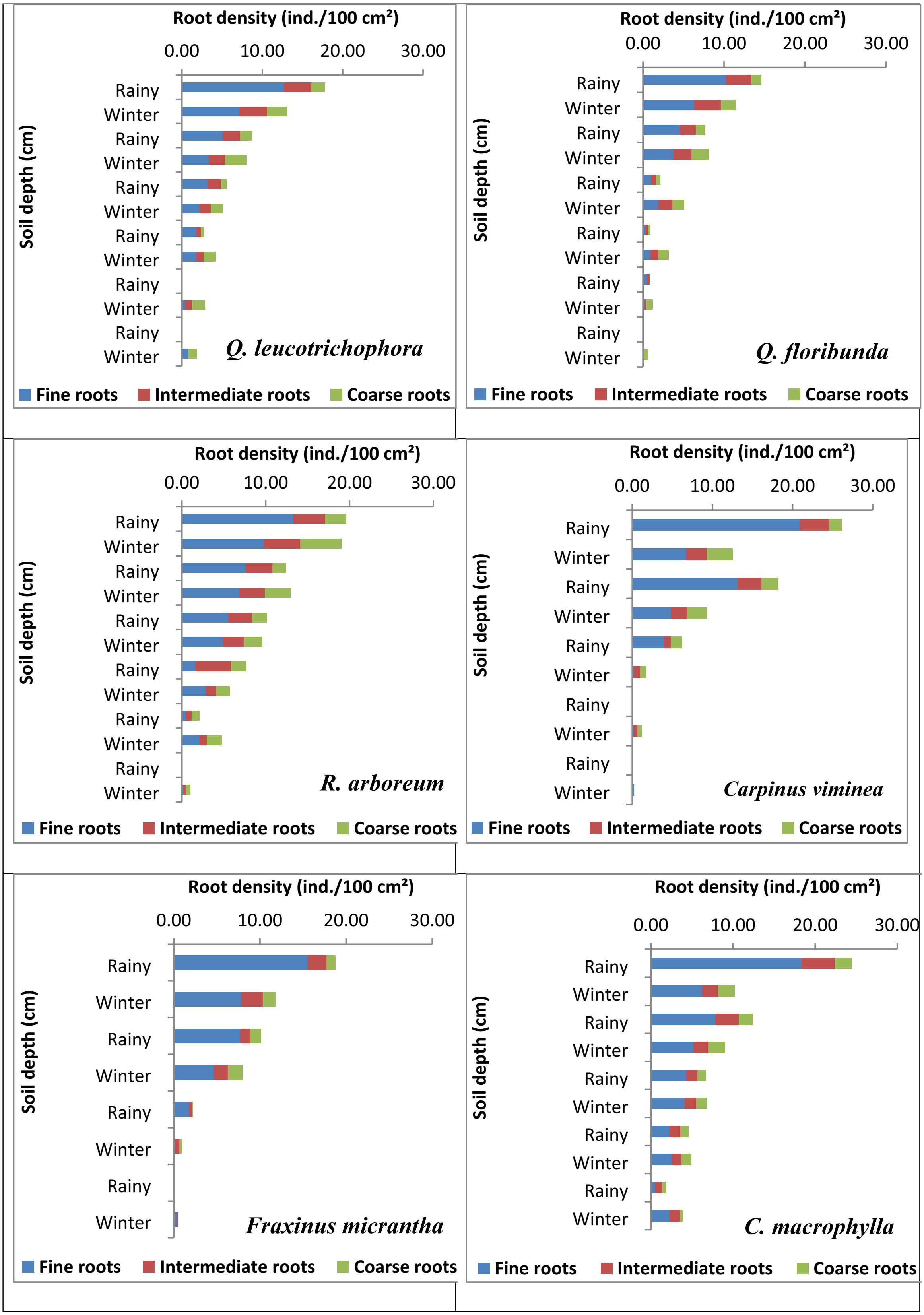


Fig. 3 (continued)

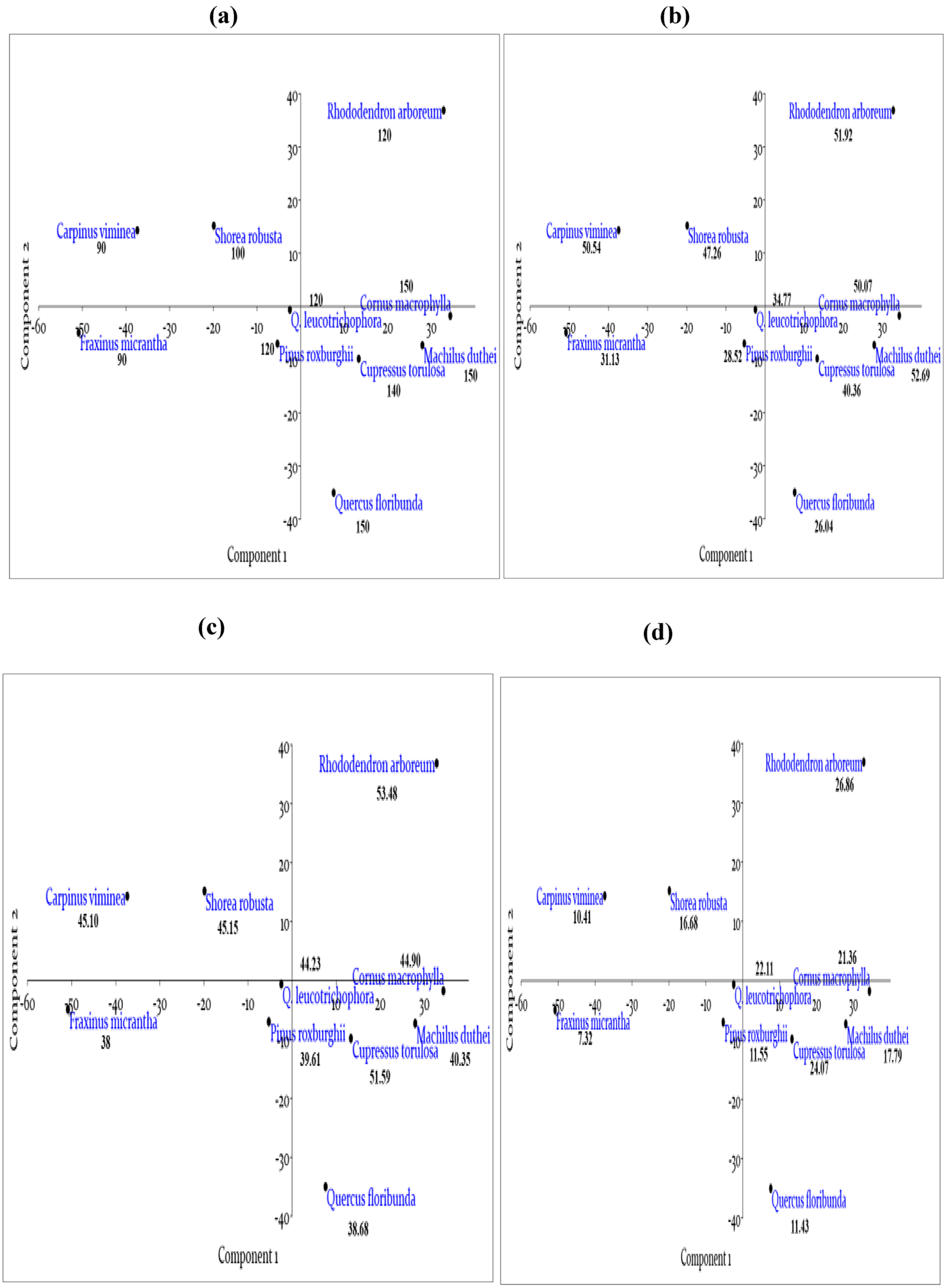


Fig. 4 Ordination graph of ten Himalayan trees species for **a** maximum rooting depth (cm); **b** total root density (ind./100 cm^2); **c** percentage of fine roots below 30 cm; **d** percentage of fine roots below 60 cm; **e** percentage of total roots below 30 cm; **f** percentage of total roots below 60 cm; **g** lowest mean tree water potential (MPa); and **h** percentage tree water potential less than – 1.0 MPa

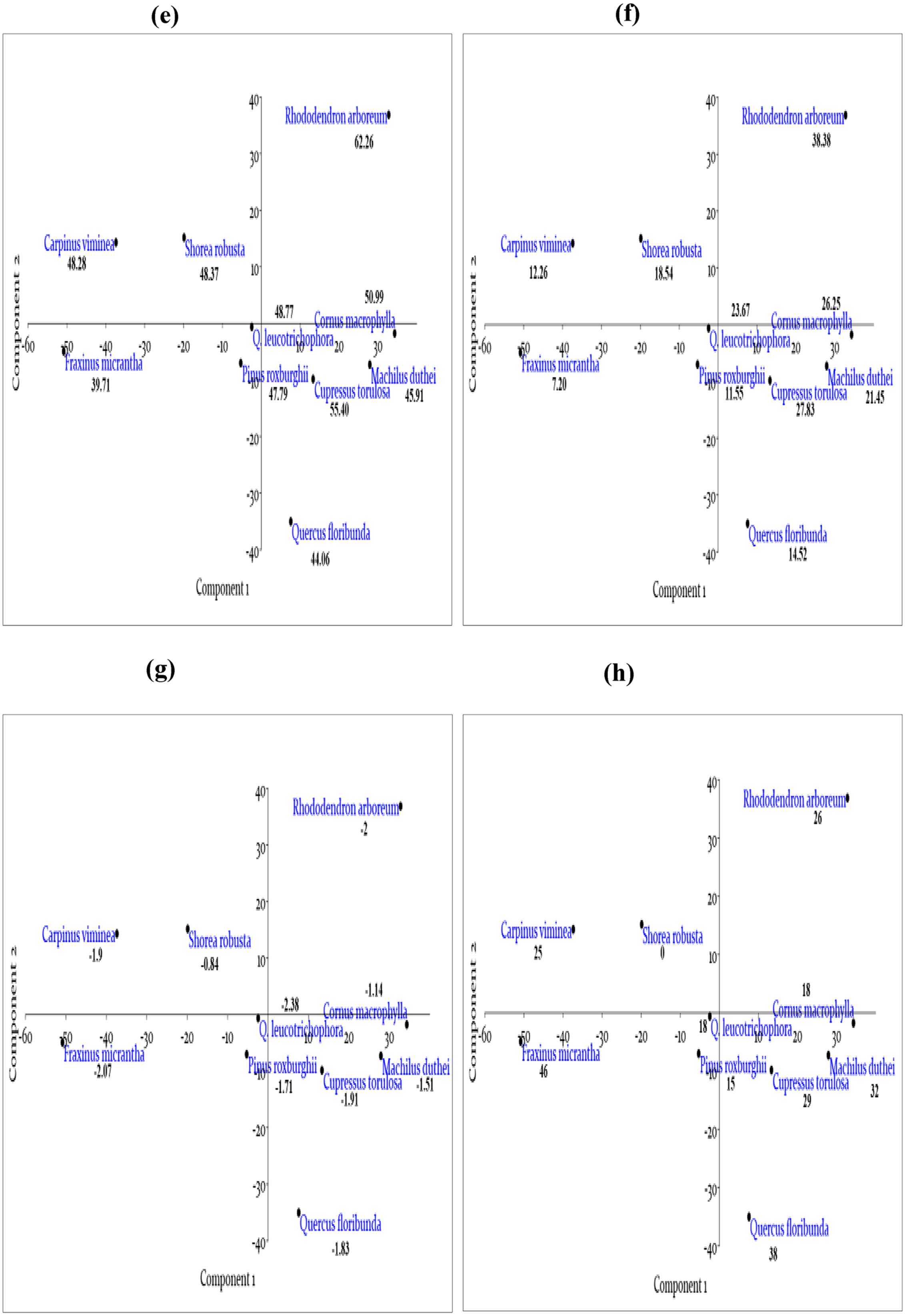


Fig. 4 (continued)

below 30 cm depth was 48.4% in *S. robusta*, compared to the mean of 49%. However, its total root density was towards the higher side of the range for the study species. Like other species root density declined substantially from rainy season to winter season, the total root density in soil column during winter being about 49% of that in rainy season. Roots were relatively shallow (upto 100 cm depth), but dense and trees often seemed to have access to moist soils. The individualistic nature of tree species with regard to root characters is quite striking, and thus needs to be examined by considering more root characters like specific root length (Ostonen et al. 2007), root tissue attributes and adequate number of representative sites.

The relationship between vertical distribution and tree water potential

Between the two shallow rooted trees, *P. roxburghii* grows widely in Himalayas across a wide range of habitat, differing in soil water status, as it is able to effectively conserve water status through stomatal regulation. In contrast, the deciduous species, *F. micrantha* is subject to considerable water stress with similar rooting depth, hence distributed only in patches along water courses (Fig. 2). The two conifers differ considerably in spite of having common characters like leaf schlerophylly, and narrow tracheids. In *P. roxburghii* the lowest mean tree water potential was − 1.71 MPa and only 15% of monthly mean predawn water potential values were lower than –1.0 MPa, while in *F. micrantha*, the lowest mean tree water potential was − 2.07 MPa and 46% of the predawn water potential values were less than − 1.0 MPa; this percentage was the highest among the ten species studied (Singh et al. 2006). *Pinus roxburghii* shuts its stomata at a relatively higher water potential by raising the concentration of Abscisic Acid (Singh et al. 2006). *Pinus roxburghii* is an opportunistic species which is able to grow in some of the extremely dry areas as well as in moist slopes of Himalaya. In contrast, *F. micrantha* which largely occurs in semi-arid to arid areas is confined to sites along streams and springs.

The deep rooting habit of fine roots is advantageous for avoiding water stress by water uptake as long as water is held in deep soil layers (Yanagisawa and Fujita 1999). In the present study, *P. roxburghii* which occurs in upper slope and ridge deep roots have no use as soil gets drier. In comparison, the oaks generally occur at hill base and lower slopes (Singh and Singh 1992) where soil and water accumulate and are available even during a dry period, so their deep roots serve thus well.

However, as the ordination graph based on some root characters indicate even the two oaks differ. As for water relation, the lowest predawn tree water potential was more negative in *Q. leucotrichophora* (− 2.38 MPa) than *Q. floribunda* (− 1.83 MPa) contrarily, the percentage value below − 1.0 MPa was lower (18%) in *Q. leucotrichophora* than *Q. floribunda* (38%). When these oaks occur together, *Q. floribunda* occurs largely on north facing moist and cool slope, while *Q. leucotrichophora* occupies relatively drier. A tendency for maintaining high leaf conductance at a low water potential separates *Q. leucotrichophora* from *Q. floribunda*, and results in the lower extreme water potential value of this oak (*Q. leucotrichophora*).

The three deciduous species which differed considerably in root distribution, also differed substantially in water relations. As expected, the lowest seasonal predawn water potential in the deep rooted *Cornus macrophylla* was higher (− 1.14 MPa with 18% lower than − 1.0 MPa) than the shallow rooted *F. micrantha* (− 2.07 MPa with 46% below − 1.0 MPa). Thus, the two species which often occur together along water courses seem to employ different adaptional traits. *Carpinus viminea,* the third deciduous species is also shallow rooted (up to 90 cm depth) and suffers from water stress.

The two conifers which occupied different habitat and differed strikingly in root distribution, also differed significantly in water status. While *P. roxburghii* occurs extensively in lower elevations (below 2000 m), *Cupressus torulosa* is limited in distribution to rocks on steep south facing slopes of limestone between 2000 and 2600 m (Champion and Seth 1968; Singh and Singh 1992). The deep roots of *Cupressus torulosa* seem to enable is to survive even on rocks, by maintaining predawn tree water potential above − 2 MPa (− 1.91 MPa with 29% value lower than − 1.0 MPa). *Pinus roxburghii* (− 1.71 MPa and 15% below − 1.0 MPa), on the other hand tends to keep high safety margin which enables to form extensive forests.

In brief, root depth has substantial high influence on tree water status, but it is subjected to several other overriding adaptational factors dealing with competition and community structure. *Cupressus torulosa* is confined to steep and eroding sites because on gentle slopes it is outcompeted by oaks (Miehe et al. 2015). So, despite being fairly deep rooted, it is water stressed. High tree water potential (never below − 1 MPa predawn water potential) and high leaf conductance values (upto 500 mMol m^{-2} s^{-1}, compared to upto 222 mMol m^{-2} s^{-1} for other species) indicate that *S. robusta* is the least water stressed species, and its dense root system was in touch with moist soils.

Conclusion

The comparison of our data with those of other studies based on sophisticated methods indicates that root density measured with digging trenches gives a fairly accurate assessment of proportional vertical root distribution. This method can be applied for this purpose to prepare a large data set, necessary for making generalizations on vertical root distribution. Our data show that by restricting sampling to top 30 cm soil depth, we can grossly and mis-represent tree root distribution, and underestimate the role of roots in ecosystem carbon dynamics and related processes. Distribution of species based on root characters in an ordination field indicates that species of same growth forms and even of same genera differ considerably in root characters, and thus emphasize individualistic behaviour.

The relationship between root distribution and tree water potential is complex because trees employ several mechanisms to maintain tree water potential other than rooting depth.

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References

Agren GI, Axelsson B, Flower-Ellis JG, Linder S, Persson H, Staaf H, Troeng E (1980) Annual Carbon budget for a young scots pine. Ecol Bull 32:307–313

Aragão LE, Malhi Y, Metcalfe DB, Silva-Espejo JE, Jiménez E, Navarrete D, Almeida S, Costa AC, Salinas N, Phillips OL, Anderson LO, Alvarez E, Baker TR, Goncalvez PH, Huaman-Ovalle J, Mamani-Solorzano M, Meir P, Monteagudo A, Patino S, Penuela MC, Prieto A, Quesada CA, Rozas-Davila A, Rudas A, Silva JA Jr, Vásquez R (2009) Above-and below-ground net primary productivity across ten Amazonian forests on contrasting soils. Biogeosciences 6:2759–2778

Bisht H, Nain AS, Gautum S, Puranik HV (2013) Agro-climatic zonation of Uttarakhand using remote sensing and GIS. J Agrometerol 15:30–35

Bloom AJ, Chapin FS, Mooney HA (1985) Resource limitation in plants-an economic analogy. Annu Rev Ecol Syst 16:363–392

Bohm W (1979) Methods of studying root systems. Springer, Heidelberg

Champion HG, Seth SK (1968) A revised survey of forest types of India. Govt. of India Press, New Delhi

Clark DA, Brown S, Kicklighter DW, Chambers JQ, Thomlinson JR, Ni J (2001) Measuring net primary production in forests: concepts and field methods. Ecol Appl 11:356–370

Cordeiro AL, Norby RJ, Andersen KM, Valverde-Barrantes O, Fuchslueger L, Oblitas E, Hartley IP, Iversen CM, Goncalves NB, Takeshi B, Lapola DM, Quesada CA (2020) Fine-root dynamics vary with soil depth and precipitation in a low-nutrient tropical forest in the Central Amazonia. Plant-Environ Interact 1:3–16

Elliot ET, Coleman DC (1988) Let the soil work for us. Ecol Bull 39:23–32

FAO (2020) Global Forest Resources Assessment – Main report, Rome

Gahlot T, Joshi P, Rawat YS (2020) Stand structure and regeneration status of tree species in four major forest types along an altitudinal gradient in Kumaun Himalaya, Uttarakhand. Trop Plant Res 7:176–189

Gotelli NJ, Ellison AM (2004) A primer of ecological statistics. Sinauer Associates, Inc., Sunderland, p 510

Helmisaari HS, Makkonen K, Kellomaki S, Valtonen E, Malkonen E (2002) Below-and above-ground biomass, production and nitrogen use in Scots pine stands in eastern Finland. For Ecol Manage 165:317–326

Iversen CM (2010) Digging deeper: fine-root responses to rising atmospheric CO2 concentration in forested ecosystems. New Phytol 186:346–357

Iversen CM, McCormack ML, Powell AS, BlackwoodCB FGT, Kattge J, Roumet C, Stover DB, Soudzilovskaia NA, Valverde-Barrantes OJ, Van Bodegom PM, Violle C (2017) A global fine-root ecology database to address below-ground challenges in plant ecology. New Phytol 215:15–26

Jackson RB, Canadell J, Ehleringer JR, Mooney HA, Sala OE, Schulze ED (1996) A global analysis of root distributions for terrestrial biomes. Oecologia 108:389–411

Joshi R, Sambhav K, Singh SP (2018) Near surface temperature lapse rate for treeline environment in western Himalaya and possible impacts on ecotone vegetation. Trop Ecol 59:197–209

Lozanova L, Zhiyanski M, Vanguelova E, Doncheva S, Marinov MP, Lazarova S (2019) Dynamics and vertical distribution of roots in European Beech forests and Douglas Fir plantations in Bulgaria. Forests 10:1123

Lukac M (2012) Fine root turnover. In: Mancuso S (ed) Measuring roots. Springer, Berlin, Heidelberg, pp 363–373

Magrin GO, Marengo JA, Boulanger JP, Buckeridge MS, Castellanos E, Poveda G, Scarano FR, Vicuna S (2014) Central and South America. In: Barros VR, Field CB, Dokken DJ, Mastrandrea MD, Mach KJ, Bilir TE, Chatterjee M, Ebi KL, Estrada YO, Genova RC, Girma B, Kissel ES, Levy AN, MacCracken S, Mastrandrea PR, White LL (ed) Climate change: Impacts, adaptation, and vulnerability. Part B: Regional aspects. Contribution of Working Group II to the Fifth Assessment Report on the Intergovernmental Panel on Climate change. Cambridge University Press, Cambridge, New York, pp 1499–1566

Matamala R, Gonzalez-Meler MA, Jastrow JD, Norby RJ, Schlesinger WH (2003) Impacts of fine root turnover on forest NPP and soil C sequestration potential. Science 302:1385–1387

McCormack ML, Dickie IA, Eissenstat DM, Fahey TJ, Fernandez CW, Guo D, Helmisaari HS, Hobbie EA, Iversen CM, Jackson RB, Leppalammi-Kujansuu J, Norby RJ, Phillips RP, Pregitzer KS, Pritchard SG, Rewald B, Zadworny M (2015) Redefining fine roots improves understanding of below-ground contributions to terrestrial biosphere processes. New Phytol 207:505–518

Metcalfe DB, Meir P, Aragão LE, da Costa AC, Braga AP, Gonçalves PH, Junior J de AS, de Almeida SS, Dawson LA, Malhi Y, Williams M (2008) The effects of water availability on root growth and morphology in an Amazon rainforest. Plant Soil 311:189–199

Miehe G, Pendry CA, Chaudhary RP (eds) (2015) Nepal: An Introduction to the Natural History, ecology and human environment of the Himalayas. Royal Botanic Garden, Edinburgh

Mokany K, Raison RJ, Prokushkin AS (2006) Critical analysis of root:shoot ratios in terrestrial biomes. Glob Change Biol 12:84–96

Ostonen I, Puttsepp U, Biel C, Alberton O, Bakker MR, Lohmus K, Majdi H, Metcalfe D, Olsthoorn AF, Pronk A, Vanguelova E, Weih M, Brunner I (2007) Specific root length as an indicator of environmental change. Plant Biosyst 141:426–442

Persson H (1979) Fine root production mortality and decomposition in forest ecosystem. Vegetatio 41:101–109

Pierret A, Maeght JL, Clément C, Montoroi JP, Hartmann C, Gonkhamdee S (2016) Understanding deep roots and their functions in ecosystems: an advocacy for more unconventional research. Ann Bot 118:621–635

Pregitzer KS (2002) Fine roots of trees-a new perspective. New Phytol 154:267–273

Rewald B, Rechenmacher A, Godbold DL (2014) It's Complicated: Intraroot system variability of respiration and morphological traits in four deciduous tree species. Plant Physiol 166:736–745

Russell AE, Cambardella CA, Ewel JJ, Parkin TB (2004) Species, rotation, and life-form diversity effects on soil carbon in experimental tropical ecosystems. Ecol Appl 14:47–60

Sahni KC (1990) Gymnosperms of India and Adjacent Countries. Bishen Singh Mahendra Pal Singh, Dehradun

Schenk HJ, Jackson RB (2002) The global biogeography of roots. Ecol Monogr 72:311–328

Singh SP (2018) Research on Indian Himalayan treeline ecotone: an overview. Trop Ecol 59:163–176

Singh SP, Singh JS (1992) Forests of the Himalayas: structure, function and impact of man. Gyanodaya Prakashan, Nainital

Singh SP, Zobel DB, Garkoti SC, Tewari A, Negi CM (2006) Patterns in water relations of central Himalayan trees. Trop Ecol 47:159–182

Singh SP, Tewari A, Phartiyal P (2011) Community Carbon forestry to counter forest degradation in Indian Himalayas. In: Skutsch MM (ed) Community forest monitoring for the carbon market. Opportunities Under REDD. Earthscan, pp 118–133

Singh SP, Singh RP, Gumber S, Bhatt S (2017) Two principal precipitation regimes in Himalayas and their influence on tree distribution. Trop Ecol 58:679–691

Steele SJ, Gower ST, Vogel JG, Norman JM (1997) Root mass, net primary production and turnover in aspen, jack pine and black spruce forests in Saskatchewan and Manitoba, Canada. Tree Physiol 17:577–587

Strand AE, Pritchard SG, McCormack ML, Davis MA, Oren R (2008) Irreconcilable differences: fine-root life spans and soil carbon persistence. Science 319:456–458

Troup RS (1921) The Silviculture of Indian Trees. Vol III Lauraceae to Coniferae. Oxford University Press, Oxford

Usman S, Rawat YS, Singh SP, Garkoti SC (1997) Fine root biomas production and turnover in evergreen forests of Central Himalaya, India. Oecol Mont 6:4–8

Vogt KA, Moore EE, Vogt DJ, Redlin MJ, Edmonds RL (1983) Conifer fine root and mycorrhizal root biomass within the forest floors of Douglas-fie stands of different ages and site productivities. Can J For Res 13:429–437

Vogt KA, Publicover DA, Bloomfield J, Perez JM, Vogt DJ, Silver WL (1993) Belowground responses as indicators of environmental change. Environ Exp Bot 33:189–205

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

Yao T, Thompson L, Yang W, Yu W, Gao Y, Guo X, Yang X, Duan K, Zhao H, Xu B, Pu J, Lu A, Xiang Y, Kattel DB, Joswiak D (2012) Different glacier status with atmospheric circulations in Tibetan Plateau and surroundings. Nat Clim Change 2:663–667

Zobel DB, Singh SP (1997) Himalayan forests and ecological generalizations. Bioscience 47:735–745