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4 Structure and Dynamics of the Root System

Josep Canadell, Arezki Djema, Bernat López, Francisco Lloret,
Santiago Sabaté, Daniel Siscart and Carlos A. Gracia

4.1 Introduction

The belowground component of terrestrial ecosystems is much less understood than any of the aboveground components, yet important ecosystem processes such as nutrient recycling, water storage, and long-term carbon accumulation occur largely in this compartment. For instance, belowground structures accounted for up to 83% of the total biomass in 13 Mediterranean woody communities (Hilbert and Canadell 1995), and belowground primary production was 60–80% of the total net primary production in a variety of woody systems (Coleman 1976; Ågren et al. 1980; Fogel 1985). Yet both root biomass and production are infrequently studied and technical difficulties make the measurements often inaccurate. Furthermore, plant root distribution and maximum rooting depths play important roles in overall ecosystem function, but it was not until recently that ecosystem-level and global comprehensive studies have been undertaken (Canadell et al. 1996; Jackson et al. 1996).

In water-limited systems, as in the case of Mediterranean ecosystems, root growth is among the deepest of all biome-types (Canadell et al. 1996), and carbon allocation patterns strongly favour accumulation belowground (Oechel and Lawrence 1981). This pattern occurs because of the development both of deep root systems and of large subterranean structures such as lignotubers (James 1984; Canadell and Zedler 1995; Canadell and López-Soria 1998).

Ultimately, the gaps in our understanding of root system attributes and function are manifested in the poor implementation of root properties in whole-ecosystem and biospheric/atmospheric models. These models often represent the belowground compartment using a simple bucket model or two or three arbitrary layers (Prentice et al. 1992; Melillo et al. 1993; Potter et al. 1993). Furthermore, these models use maximum rooting depths between 1 and 2 m, yet we know that deep roots (> 3 m) are very common in most biomes (Stone and Kalisz 1991; Canadell et al. 1996) and have important consequences for ecosystem processes (Silva et al. 1989; Nepstad et al. 1994; Richter and Markewitz 1995; Schulze et al. 1996).

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In this chapter, we synthesize the information available on root system attributes of the Mediterranean evergreen holm oak (*Quercus ilex* L.), mainly, but not exclusively, studied in two experimental areas: Montseny (Barcelona) and Prades (Tarragona) in northeastern Spain (Chap. 2). We describe the root system structure and its distribution in the soil profile, the total root biomass, which we relate to the aboveground biomass, and the phenology of fine roots. We expect this information to contribute to a better understanding of holm oak ecology and to the efforts to model system responses under changing environmental conditions.

4.2 The Database

The data presented in this chapter are the result of various studies that have been carried out over the past 13 years: root excavation campaigns, root profiles on road cuts, soil coring, minirhizotron technology, and field observations.

At Montseny, the root systems of 32 single-stemmed holm oaks were excavated in the winter of 1985 in La Castanya (Chap. 2). Of these trees, 20 were excavated in a mesic site (north-facing slope) near the permanent plot, and 12 in a nearby xeric site (south-facing slope). In addition, three multi-stemmed holm oaks were excavated at the xeric site. At Prades, the root systems of multi-stemmed holm oaks were dug out during 1993 on the north-facing slope of Torners (Chap. 2), in the context of the thinning experiment described in Chapter 23. Here, we will use the data from the six trees excavated in the control (unthinned) plots. In all cases, roots were excavated down to 1-m depth or to the bedrock, whichever came first, and to an end diameter of 1 cm.

Biomass of roots of Ø < 1 cm was obtained by soil coring down to 0.6 m in the permanent plot at La Castanya. Profiles of roots of Ø > 1.5 mm were studied on various road cuts down to 1.5 m deep in several additional places in northeast Spain. At Prades, minirhizotron technology was used to study the dynamics of fine root for a 2.5-year period (1994–1996) in the same plots where root systems were excavated. Minirhizotron is an in situ non-destructive technique that minimizes point-to-point variation by allowing repeated measurements at the same point over time (Taylor 1987). In the stony Prades soils, rigid minirhizotron tubes would not allow a good soil-tube contact, thus preventing normal development of fine roots around the tubes. Instead, inflatable minirhizotrons were used which yielded good quality images (López et al. 1996).

4.3 Structure of the Root System

Taproots of holm oak usually grow quite rapidly into deep soil layers at early stages of seedling development. However, the dominance of a vertical single taproot in seedlings is often lost in mature trees. In the shallow soils of north-facing slopes in Montseny, most of the trees did not have a clear central taproot, while those growing on south-facing slopes, with deeper (> 1 m) and drier soils, frequently showed a large taproot. In Prades, where the climate is drier than in Montseny, 60% of the excavated trees had taproots. Thus, although the data are only correlational at this point, holm oak has taproots more often when growing in drier environments than in mesic sites. In any case, however, holm oak has the capacity to send roots quite deep in the soil profile when the substrate can be penetrated. Roots were observed at 3.0-m depth in a road cut on schists at Montseny and at a depth of 3.7 m in sandstone substrate elsewhere (Canadell et al. 1996). The presence of deep roots is thought to be one of the mechanisms for surviving summer drought. Maximum rooting depths of other evergreen tree species were between 2.7 and 40 m (Canadell et al. 1996) and 23 m for *Quercus wislizenii* in California (Lewis and Burgy 1964). Data for holm oak from deep root excavations (> 3 m) are not available. We have also observed plants of holm oak growing on very shallow soils with most of the root system growing in soft rocks (e.g. sandstone) or in-between the schistosity planes of slates with hardly any soil.

F. Lloret and D. Siscart (unpubl. data) described root density (Ø > 1.5 mm) distribution along 1.5-m-deep soil profiles in holm oak forests near Barcelona, taking advantage of recently made road cuts (Fig. 4.1). They compared two substrate types in which holm oak showed different drought tolerance to an extreme drought that took place in 1994. The root distribution profiles showed that more small roots were able to reach deeper layers when growing on schist – following exfoliation planes as preferred pathways – than when

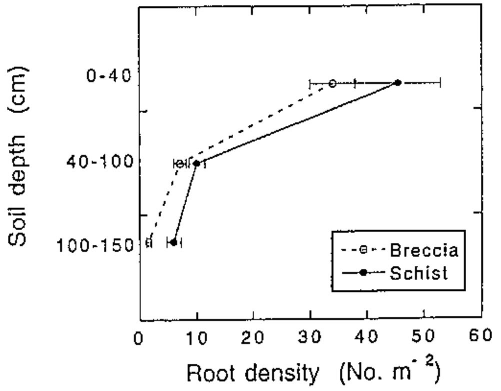

Fig. 4.1. Mean density (± SE) of holm oak roots of Ø > 1.5 mm at different soil depth intervals and substrates. Data for each substrate were obtained in a single locality from seven 5-m-wide by 1.5-m-high profiles located along the edge of a trail that were close to the transition between fault breccias and Palaeozoic schists

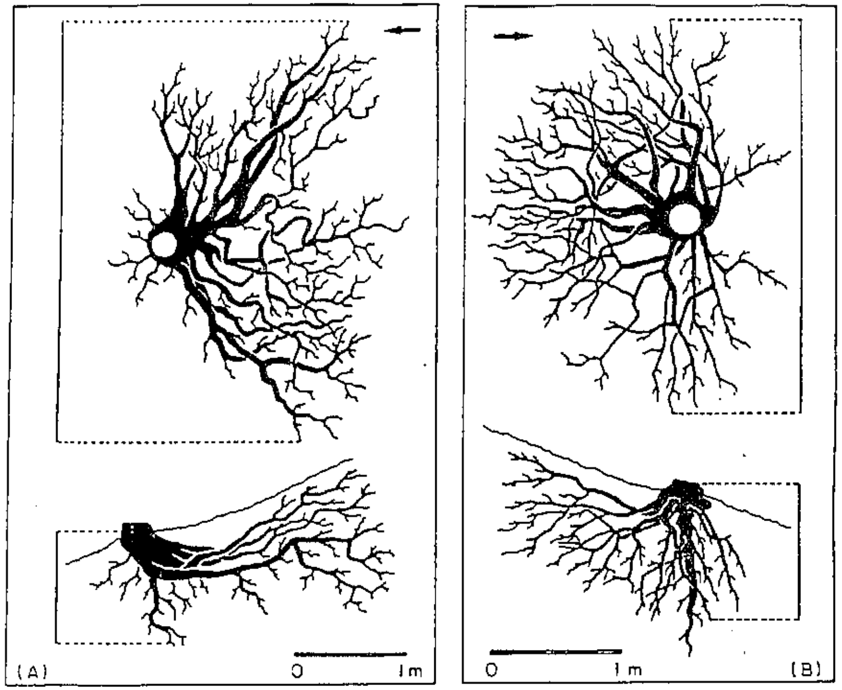

Fig. 4.2. Root systems (roots of Ø >1 cm) of single-stemmed holm oaks in A the mesic site and B the xeric site at La Castanya, Montseny. (Drawings by Mercè Cartañà)

growing on a compact matrix of breccias. Interestingly, holm oak trees growing on the schist soils were more tolerant to drought events. These observations suggest that trees having more roots in deep soil horizons (where water is stored for a longer time) are better prepared to withstand extreme drought events. Under these conditions, the interaction between climate and substrate type plays a critical role in reshaping communities and allowing deep-rooted individuals to survive.

The lateral root system of holm oak can be quite extensive. Lateral roots can grow far beyond the canopy projection and were observed at 5.9 m from the main stem in Prades (Djema 1995); large roots (Ø > 1 cm), however, do not usually extend further than 2.5 m. The smaller diameter roots account for the largest fraction of root length, which is important in terms of soil occupation and water and nutrient uptake. Most of the horizontal large roots grow between 20 and 60 cm from the soil surface, and only a few roots are found close to the surface, where dry-wet cycles are more frequent and therefore where harsher environmental conditions for root growth are found. It is worth noting that when trees grow on steep slopes, most of the lateral root system grows up-slope yielding a highly asymmetrical root distribution (Fig. 4.2). In a review of 96 Mediterranean woody species from Australia, California and Chile the average radius of root horizontal extension was 1.6 ± SD 1.5 m and the maximum extension was 7.0 m (Canadell and Zedler 1995).

In La Castanya, root grafts were occasionally observed between roots of the same tree, but never between roots of different trees. On the contrary, root grafts were somewhat common between holm oak trees in Prades, although no root grafting was observed between different species. Generally, root grafting is not very common in Mediterranean ecosystems (Keeley 1988); it was observed in only one of nine species excavated in the Chilean matorral (Hoffmann and Kummerow 1978).

4.4 Lignotubers

One of the most characteristic features of the root system of holm oak is the development of a large woody swollen structure at the stem base called the lignotuber (Canadell and Zedler 1995). This structure is genetically determined and appears early during seedling development. There are no studies on lignotuber development in this species, but it is known that *Q. suber*, another evergreen western Mediterranean oak, starts developing the lignotuber structure through an accumulation of bud clusters and starch that occurs close to the cotyledonary insertion (Molinas and Verdaguer 1993a,b).

The size of lignotubers depends on plant age, environmental and edaphic conditions, and, most of all, on the disturbance history that individual plants have experienced (e.g. fire, logging, extreme drought or cold events). In general, disturbances trigger the growth of the meristematic tissue of the lignotuber, which is further enlarged by the fusion of the stem bases of the new emerging shoots. The presence of large lignotubers was common in Montseny and Prades because both forests were intensively coppiced for charcoal production until the 1950s. At both sites, individual holm oaks often allocate as much as half of their total biomass to the lignotuber (Canadell and Rodà 1991; Djema 1995; Sabaté et al. 1998). In one case at Montseny, the lignotuber dry weight was 317 kg and accounted for 66% of the total tree biomass.

It is believed that lignotubers have a dual function. The first function, which is morphologically related, is to store concealed buds that will resprout after disturbances; the lignotuber generally stores a large number of buds that enable plants to regrow even in environments subjected to multiple disturbances. The second function is to store non-structural carbohydrates and nutrients that will support regrowth after disturbances. Our understanding regarding the latter function has been inferred largely from studies of plant growth (DeSouza et al. 1986; Castell et al. 1994), anatomical structure (Montenegro et al. 1983), and tissue analysis of lignotuber nutrient and carbohydrate contents (Mullete and Bamber 1978; Dell et al. 1985). To date, very few studies have provided direct experimental data (e.g. Canadell and López-Soria 1998; Sabaté et al. 1998). These studies indicate that nutrients and carbohydrates stored in the lignotuber play an important role in providing resources for rapid regrowth during the first years after a disturbance.

4.5 Allometric Relationships Between Above- and Belowground Biomass

Root excavation studies enable us to develop allometric equations that can be used to investigate the relationships between the aboveground and belowground parts of trees. They are also used to estimate large-root biomass of individual trees by measuring their aboveground dimensions. Table 4.1 shows these equations for Montseny and Prades. Several regressors were used depending on the tree structure. Diameter at breast height (dbh) and stem diameter at 50 cm (D_{50}) were good regressors to estimate the root biomass of single-stemmed trees, which is the dominant tree structure in the Montseny mesic site (Canadell et al. 1988). On the other hand, multi-stemmed trees are dominant in Prades and the root biomass of a stool is best estimated using the total cross-sectional area (CSA), at 50 cm from the ground, of all the stems it bears (Djema 1995).

It is worth noting that trees with dbh < 20 cm at Montseny had more root biomass in the xeric site than in the mesic site, as it would be predicted according to our current understanding of carbon allocation and soil water availability. Santantonio et al. (1977) compiled alometric regressions (log-log) of large-root biomass (kg) on dbh (cm) for a number of tree species. In the dbh range 10–20 cm, which contains most of our sample trees, values of large-root biomass (Ø > 5 cm) predicted by our equation for single-stemmed holm oak are very close to those derived from their mean regression for coniferous trees, and about 2.5 times higher than those from their mean regression for deciduous trees.

Table 4.1. Allometric equations for total large-root biomass (kg dry weight, including lignotuber) for single-stemmed holm oaks at Montseny and multi-stemmed holm oaks at Prades

y[a]	x	a	b	r^2	*n*
Montseny – mesic and xeric sites (single-stemmed trees)					
Total large roots	Dbh	– 1.047	2.191	0.73	32
Total large roots	D_{50}	– 1.687	2.623	0.79	32
Total large roots	TAB	– 0.212	0.894	0.83	30
Montseny – mesic site (single-stemmed trees)					
Total large roots	Dbh	– 1.393	2.451	0.81	20
Montseny – xeric site (single-stemmed trees)					
Total large roots	Dbh	– 0.448	1.734	0.71	12
Prades (multi-stemmed trees)					
Total large roots	CSA	– 55.210	0.605	0.91	6

dbh, Stem diameter at 1.3 m from the ground (cm); D_{50}, stem diameter at 50 cm from the ground (cm); TAB, total aboveground biomass (kg dry weight); CSA, cross-sectional area at D_{50} (cm^2) of all the stool stems.

[a] The model is $\log y = a + b \log x$ for Montseny and $y = a + b \log x$ for Prades. Log indicates logarithm to base 10.

4.6 Root Biomass

The proportion of biomass allocated to belowground tissues by perennial plants usually increases as the environment becomes more severe (Rundel 1980). Thus, root systems may account for up to 90% of total plant biomass in many arctic plants and some desert shrubs (Rodin and Bazilevich 1967; Caldwell and Fernandez 1975).

In the Montseny mesic site, a holm oak stand dominated by single-stemmed trees had 28% of its total tree biomass belowground (Table 4.2). Of the 63 Mg dry wt. ha^{-1} of root biomass, 48% was in lignotubers and roots larger than 5 cm in diameter, 27% in roots of Ø 1–5 cm, and 24% in roots of Ø < 1 cm. The allocation of 28% of the total biomass into the belowground compartment is quite high, but it still falls within the range of 15–35% commonly found in temperate forest ecosystems (Rodin and Bazilevich 1967),

Table 4.2. Basal area (m^2 ha^{-1}), aboveground biomass (Mg dry wt. ha^{-1}) and various fractions of root biomass (Mg dry wt. ha^{-1}) for the Montseny mesic and xeric sites, and Prades

Site	Basal area	Above-ground biomass	Roots Ø > 5cm[a]	Roots Ø 1–5 cm	Roots Ø < 1 cm	Total roots	Root biomass (% of total)[b]
Montseny mesic[c]	26.6	160	30	17	16	63	28
Montseny xeric[d]	16.3	79	—— 91.0 ——		16[e]	108	58
Prades[f]	37.1	103	66	37	–	128[g]	55[g]

Data compiled from Canadell and Rodà (1991), Gracia et al. (1994), Djema (1995), and Sabaté et al. (1998).

[a] Biomass of roots of Ø >5 cm and lignotuber.

[b] Percentage of total root biomass respect to total aboveground and belowground biomass.

[c] Data for the permanent plot at La Castanya, using the tree sizes of 1978.

[d] Data for a 0.03-ha plot, tallied in 1990.

[e] Roots of Ø <1 cm were not measured at the xeric site, but their biomass was assumed equal to the mesic site.

[f] Data for three control plots on the north-facing slope of Torners, tallied in 1992.

[g] Does not include roots of Ø <1 cm.

and it falls at the high end of the range of 15–25% given by Harris et al. (1980). Thus, the Montseny holm oak forest is not strikingly different from temperate forest ecosystems in its pattern of root to shoot biomass allocation, at least in an undisturbed mesic site without major water stress during the dry season and dominated by single-stemmed trees. At the tree level, and not taking into account roots of Ø < 1 cm, the mean root:shoot ratio of single-stemmed holm oaks was 0.41 (SE 0.02, $n = 30$) for all excavated trees in Montseny.

A very different picture emerges for stands dominated by multi-stemmed holm oak (as in Prades and the Montseny xeric site). Through repeated resprouting after fire and coppicing, current stems are here much younger than the stools bearing them. Under these conditions, holm oak, a long-lived species, develops massive lignotubers in which belowground biomass keeps accumulating while aboveground biomass is burned or harvested at different frequencies. Belowground biomass in these multi-stemmed stands can exceed the aboveground biomass, as is the case at the Montseny xeric and Prades sites where 58 and 55% of total biomass is belowground, respectively (the latter figure representing an underestimation of the actual belowground biomass because roots of Ø < 1 cm were not accounted for; Canadell and Rodà 1991; Djema 1995). Belowground biomass accounted for 45 and 46% of the total biomass for two small- and medium-sized multi-stemmed trees in La Castanya, and 66% for the largest excavated tree.

4.7 Fine Roots

Fine roots of trees (Ø < 2.5 mm) are the most dynamic fraction of the root system, having turnover times of between a few weeks and more than 8 years (Hendrick and Pregitzer 1992). Fine roots are responsible for nutrient and water uptake. However, fine root distribution, phenology and turnover have only recently been studied for holm oak. The following account is based on repeated observations with inflatable minirhizotrons placed down to 60-cm depth at Prades (López et al. 1996, 1998).

Fine root density, averaged over 2 years of study (excluding the first 3 months after minirhizotron installation), was greatest in the upper soil layers, with 32% of the roots counted down to 60-cm depth being in the top 10 cm of soil, 60% in the top 20 cm and 80% in the top 30 cm. Root biomass, however, was more evenly distributed along the soil profile, with only 51% of the biomass in the top 30 cm. Only 7.4% of the fine root biomass was found between 50 and 60 cm deep. Deep fine roots, although representing small quantities of the total amount of biomass, may play a key role in extracting deep soil moisture during dry periods (Canadell et al. 1996; Hendrick and Pregitzer 1996), which are an important feature of the Mediterranean climate. Roots of Ø < 0.5 mm accounted at Prades for 95% of the total number of fine roots, which is in agreement with other species such as *Acer saccharum* (Hendrick and Pregitzer 1992; Burke and Raynal 1994) and *Picea sitchensis* (Ford and Deans 1977), and is similar to the root diameter distribution of a northern hardwood forest, where two thirds of the total root length was found in the 0.2- to 0.3-mm diameter class (Fahey and Hughes 1994).

To obtain biomass on a ground area basis from the minirhizotron observations, root growth was assumed to be isotropic, i.e. biomass density (g mm^{-2}; all biomass and production data are on dry weight basis), observed from the minirhizotron window, was supposed to be the same as the biomass density one would see from above the soil. The 2-year average fine-root biomass obtained was 94.8 ± 6.8 g m^{-2} (mean ± SE), which is similar to other reported fine root biomasses (white oak: 115 g m^{-2}, Aber et al. 1985; white pine: 97 g m^{-2}, Aber et al. 1985; European beech: 150 g m^{-2}, Ellenberg et al. 1986; American beech: < 100 g m^{-2}, Liu and Tyree 1997; lowlands of montane rainforest: 144 g m^{-2}, Cavelier 1992), but substantially lower than estimates from some northern hardwood forests (range: 510–990 g m^{-2}, Harris et al. 1977; McClaugherty et al. 1982; Joslin and Henderson 1987; Farrish 1991; Burke and Raynal 1994). A possible explanation for these differences is that a large portion of the soil volume at Prades is composed of coarse gravel. Root production between time t_i and time t_{i+1} was calculated by summing the biomass of new roots and the positive increments of biomass of existing roots. To obtain annual fine root production we summed the production of all the field campaigns for the given year and then averaged the 2 years of observations. Root production (Fig. 4.3, top) was found to be 500 ± 4.4 g m^{-2} year^{-1}, thus giving a turnover rate of 5.27 year^{-1} or a mean fine root lifespan of 68.3 days. However, longevity of individual roots ranged from 5 to more than 475 days.

The cost of fine root formation has been estimated assuming that 1 g of carbohydrates produces 0.68 g of new root tissues (Chap. 12), which means a cost of 7.35 kcal g^{-1} of new root. Similarly, the average maintenance cost has been estimated under the soil temperature at Prades as 50 cal g^{-1} day^{-1} (Chap. 12). Using these simplifications, the formation cost of fine roots was 3675 kcal m^{-2}, and the calculated cost of maintenance was 1730 kcal m^{-2} year^{-1} (Fig. 4.3, bottom). Fine root and leaf metabolic costs represent, in this forest, more than 60% of total carbon fixed in gross primary production. Fine root formation cost, on a ground area basis, is more than twice the leaf formation cost, while the maintenance of fine roots is only 15.8% of leaf maintenance cost. The high formation cost of fine roots is related to their high turnover. Death of fine roots represents a very active mechanism of carbon transport from the atmosphere to soil. This mechanism has been evaluated in Prades as 166 g C m^{-2} year^{-1}, 66% more than the carbon lost in leaf litterfall, making fine roots the most important channel of carbon loss from these holm oak trees.

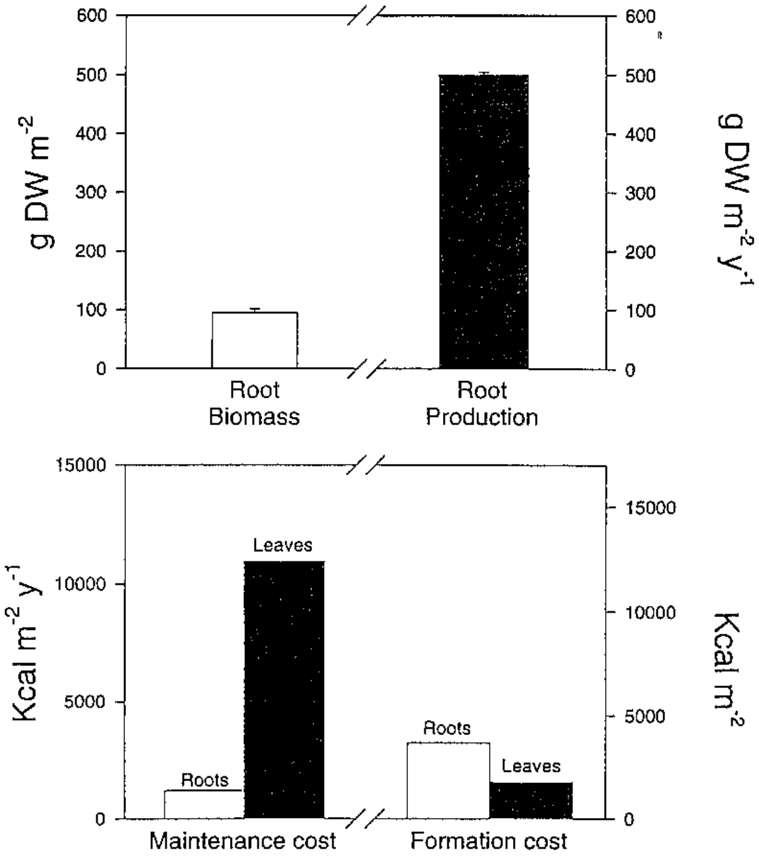

Fig. 4.3. *Above:* Fine root biomass and annual production; *below:* annual metabolic cost of fine root formation and maintenance compared with formation and maintenance costs of leaves

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