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SPECIAL FEATURE: INVITED REVIEW

Development and function of roots of forest trees in Japan

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Tree roots in a changing world

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Abstract Globally, forests cover 4 billion hectares or 30% of the Earth's land surface, and 20%–40% of the forest biomass is made up of roots. Roots play a key role for trees: they take up water and nutrients from the soil, store carbon (C) compounds, and provide physical stabilization. Estimations from temperate forests of Central Europe reveal that C storage in trees accounts for about 110 t C ha^{-1}, of which 26 t C ha^{-1} is in coarse roots and 1.2 t C ha^{-1} is in fine roots. Compared with soil C, which is about 65 t C ha^{-1} (without roots), the contribution of the root C to the total belowground C pool is about 42%. Flux of C into soils by plant litter (stemwood excluded) compared with the total soil C pool, however, is relatively small (4.4 t C ha^{-1} year^{-1}) with the coarse and fine roots each contributing about 20%. Elevated CO_2 concentrations and N depositions lead to increased plant biomass, including that of roots. Recent analysis in experiments with elevated CO_2 concentrations have shown increases of the forest net primary productivity by about 23%, and, in the case of poplars, an increase of the standing root biomass by about 62%. The turnover of fine roots is also positively influenced by elevated CO_2 concentrations and can be increased in poplars by 25%–45%. A recently established international platform for scientists working on woody root processes, COST action E38, allows the exchange of information, ideas, and personnel, and it has the aim to identify knowledge gaps and initiate future collaborations and research activities.

Key words Fine root turnover · Global change · Root carbon · Root morphology and physiology · Soil carbon

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Forests under changing environment

Across the biosphere, rapid and accelerating changes in land use, climate, and atmospheric composition driven primarily by anthropogenic forces are known to exert major influences on the productivity, biodiversity, and sustainable provision of ecosystem goods and services. Among the terrestrial ecosystems, forests are considered as the most important terrestrial reservoirs of biological diversity, containing as much as two thirds of all plant and animals species. Globally, forests cover 4 billion hectares or 30% of the Earth's land surface (FAO 2006).

As more scientific information about global warming accumulates, climate change is emerging as perhaps the greatest environmental challenge of the twenty-first century (FAO 2006). Global threats such as hunger, poverty, population growth, armed conflict, displacement, air pollution, soil degradation, desertification, and deforestation are intermingled with each other and all contribute to climate change. Forests have four major roles in climate change: (1) they currently contribute about one sixth of global carbon (C) emissions when cleared, overused, or degraded; (2) they react sensitively to a changing climate; (3) when managed sustainably, they produce wood fuels as a benign alternative to fossil fuels; and (4) they have the potential to absorb about one tenth of global C emissions projected for the first half of this century into their biomass, soils, and products and store them – in principle in perpetuity (FAO 2006). However, the total forest area continued to decrease by about 13 million hectares per year within the past decade, mainly due to the conversion of forests to agricultural land (FAO 2006). South America, followed by Africa, suffered the largest net loss of forests from 2000 to 2005.

The world's forests have been estimated to contain up to 80% of all aboveground C and 40% of all belowground terrestrial C (soils, litter, roots), although the C pool in forest soils (787 Gt) is about double that in the forest vegetation (359 Gt) (Dixon et al. 1994). Projected total future forest C emissions from climate-induced land-use change was predicted to be 4–6 Gt year^{-1} (Dixon et al. 1994).

New methods, skills, and terminology will be necessary in the future to assess C stocks and their changes in forests. The "clean development mechanism" (CDM) allows industrialized countries to offset part of their C emissions and to contribute toward sustainable development of a developing country through reforestation projects (FAO 2006). Estimating and accounting for the C in the aboveground and belowground compartments, dealing with forest degradation, sink enhancement through global warming, nitrogen (N) emissions, carbon dioxide (CO_2) fertilization, and the natural effect of aging remain issues that are difficult to resolve. In this context, the contribution of tree roots is essential and indispensable, and, thus, efforts have to be undertaken to improve the methodology in order to investigate roots and to include root data in future studies and scenarios.

Roots of forest trees

Root systems of forest trees are important, but often poorly investigated elements in ecosystems. Roots take up water and nutrients from the soil, they store C compounds, and they provide physical stabilization. While the fine roots are evident in the uptake of water and nutrients, both fine and structural roots are relevant in tree stability. Furthermore, fine roots of trees undergo constant replacement in root turnover and provide a large biomass input to the soil containing both C and mineral nutrients. Hence, fine roots, including the structures of mycorrhizal fungi, are important in C fluxes to soils and thus C storage in soils, as well as in belowground recycling of nutrients such as N, phosphorus (P), magnesium (Mg) and calcium (Ca).

The mean amount of C in temperate and boreal forests is estimated to be 57–64 t C ha^{-1}, while that for tropical ecosystems is estimated to be about 121 t C ha^{-1} (Table 1; Dixon et al. 1994). Roots account for about 20%–40% of the total forest C. The C content in roots is higher in tropical and temperate forests (21–22 t C ha^{-1}), and is lower in boreal forests (14 t C ha^{-1}) (Table 1; Jackson et al. 1997). The C data of Jackson et al. (1997) were calculated by dividing the total root biomass by the land area and by considering a C concentration of 48.8% in living fine roots. In all forest types, tree fine root C accounts for about 10%–20% of the total amount of tree root C, with the highest values in the temperate and boreal forests and the lowest values in the tropical forest ecosystems (Table 1; Jackson et al. 1997). The amount of C in forest soils (soils, litter, roots) strongly depends on the latitudinal zones with 100–120 t C ha^{-1} in tropical and temperate forests and 340 t C ha^{-1} in boreal forests (Table 1; Dixon et al. 1994). Thus, tree roots in forest soils make up about 4%–20% of the total C in the soils.

Estimations from temperate forest stands of Central Europe showed that about 82 t C ha^{-1} is aboveground tree parts (stemwood, branches, foliage), 26 t C ha^{-1} is coarse tree roots, and 1.2 t C ha^{-1} is fine tree roots (Table 2; Perruchoud et al. 1999). Compared with the soil C, which is about 65 t C ha^{-1} (litter, soil humus; Table 2), the contribution of the root C to the total belowground C pool is about 42%. Flux of C into soils by plant litter (stemwood excluded) compared with the total soil C pool, however, is relatively small with 4.4 t C ha^{-1} $year^{-1}$ of which the fine roots contribute about 0.9 t C ha^{-1} $year^{-1}$ (Table 2).

Table 1. Mean C content of forests and forest soils of various latitudinal zones

Component	Boreal (t C ha^{-1})	Temperate (t C ha^{-1})	Tropical (t C ha^{-1})
Forests[a]	64	57	121
Total roots	14	21	22
Fine roots	3	4	3
Soils[a]	343	96	123

Data from Dixon et al. (1994) and Jackson et al. (1997)
[a] Including roots

Table 2. Mean C pools and C fluxes of forests and forest soils of temperate zones in Central Europe

Component	Pool (t C ha^{-1})	Flux (t C ha^{-1} $year^{-1}$)
Trees aboveground	82	2.3[a]
Stemwood	60	nd
Branches	19	1.0
Foliage	3.3	1.3
Trees belowground	27	1.7
Coarse roots	26	0.8
Fine roots	1.2	0.9
Soil (without roots)	65	0.4
Litter	16	0.1
Soil humus	49	0.3

Data from Perruchoud et al. (1999)
nd, not determined
[a] Without stemwood

Root dynamics and global change

In recent decades, humans have strongly affected ecosystems due to atmospheric and climatic changes, such as rising atmospheric CO_2 concentrations, elevated temperatures, altered precipitation, or N deposition (Norby and Jackson 2000). Soils of forest ecosystems, in particular, have been affected by high atmospheric inputs of acidifying pollutants (S and N compounds) originating from the combustion of fossil fuels in power generation, industry, and transportation (Fowler et al. 1999; Nadelhoffer et al. 1999; Rennenberg and Gessler 1999). These inputs have led to an acceleration of soil acidification, loss of basic cations, and release of Al ions into soil solution as a consequence of proton-buffer processes (Blaser et al. 1999). Besides its effect on soil acidification, excessive inputs of atmospheric N result in nitrate leaching and relative shortage of other nutritional elements for plants (Magill et al. 1997; Högberg et al. 2006). Nevertheless, a trend of increasing aboveground growth of trees in European forests over a long term can be observed (Spiecker 1999). These positive trends are at-

tributed mainly to the increased contents of CO_2 in the atmosphere and to enhanced N depositions. Both elevated CO_2 concentrations and N depositions lead to increased plant biomass, including that of roots (Tingey et al. 2000; Nadelhoffer 2000). Recent analysis in experiments with elevated CO_2 concentrations have shown increases of the forest net primary productivity (NPP) by about 23% (Norby et al. 2005), and, in the case of poplars, an increase of the standing root biomass between 47%–76% (Lukac et al. 2003) and 113% (King et al. 2002).

Fine root turnover

Assuming that fine roots turn over once a year, as much as 33% of the global annual NPP is used for the production of fine roots, which, after death, begin to decompose (Jackson et al. 1997). It seems, therefore, that the turnover of the fine roots is a key component of the C and nutrient cycling in ecosystems and that it is sensitive to many global change factors (Gill and Jackson 2000; Eissenstat et al. 2000). Turnover rates of fine roots in forests increase exponentially with the mean annual temperature (Gill and Jackson 2000; Pregitzer et al. 2000). Under elevated CO_2 concentrations, the mean turnover rates of fine roots of poplars increased from 1.4–1.6 $year^{-1}$ to 1.8–2.3 $year^{-1}$ by about 25%–45% (Table 3; Lukac et al. 2003). In addition, there is evidence that soil acidification also enhances fine root turnover in coniferous forests (Godbold et al. 2003).

Root turnover varies widely within and among species and across ecosystems, but the ability to predict root life span for particular species or systems is still poor (Majdi et al. 2005). Understanding the factors controlling root production and mortality, which is collectively called turnover, is therefore important for understanding element fluxes in ecosystems. Several methods have been used to calculate rates of root production and mortality (e.g., sequential coring, minirhizotrons, isotopes) and, thus, no standard approach for defining root turnover is accepted and applied (Gill and Jackson 2000; Hertel and Leuschner 2002; Tierney and Fahey 2002; Majdi et al. 2005). As a result, the contribution of fine root turnover and associated mycorrhiza to total ecosystem C and nutrient budgets remains uncertain (Trumbore and Gaudinski 2003).

Table 3. Mean annual fine root production and turnover (calculated as the ratio of fine roots production in ingrowth cores and maximum standing fine root biomass per year) of three *Populus* species under ambient and elevated CO_2 concentrations

Species	Condition	Production ($g\,m^{-2}\,year^{-1}$)	Turnover ($year^{-1}$)
Populus alba	Ambient	159	1.6
	Elevated	226	2.3
Populus nigra	Ambient	165	1.6
	Elevated	311	2.0
Populus × *euramericana*	Ambient	219	1.4
	Elevated	356	1.8

Data from Lukac et al. (2003)

Recently, advanced ecosystem models such as Biome-BGC, which require indispensable fine root parameters such as annual fine root turnover rate, C/N ratio of fine roots, or fine root labile/cellulose/lignin proportions, have been developed and parameterized (White et al. 2000). Thus, Biome-BGC allows the simulation of fluxes and pools of C and N of ecosystems aboveground and belowground. Recent applications of that model in forest ecosystem studies (e.g., Hibbard et al. 2005; Pietsch et al. 2005) have used fine root turnover rates which were set to 1.0 $year^{-1}$ for deciduous broadleaf and deciduous needleleaf trees, to 0.18–0.25 $year^{-1}$ for evergreen needleleaf trees, and to 0.5 $year^{-1}$ for juniper woodland. However, it would be of advantage if future studies included turnover rates measured *in situ*. In particular, when deciduous needleleaf trees such as *Larix decidua* are investigated, fine root turnover rates are likely to be similar to the rates for evergreen needleleaf trees, and, thus, distinctly lower than the proposed 1.0 $year^{-1}$.

Root morphology and physiology

While roots vary widely in morphology and physiology, little is known about what environmental factors govern this variation or how this variation may be related to plant function. Several theories on plant growth strategies exist to explain the variation in tissue morphology and metabolic activity (Comas and Eissenstat 2004). An underlying assumption is that allocation of resources to tissue structure and function is governed by biotic and abiotic selection pressures. Whereas in leaves, tissue structure and function clearly correlate with the growth rate, in roots it is more or less unknown because broad studies of root traits are limited (Comas and Eissenstat 2004). However, preliminary investigations have shown that roots of fast-growing species, constructed for fast growth into new soil areas, have a high specific root length (SRL) but a low root-tissue density (RTD) (Comas et al. 2002). However, SRL and RTD can vary widely within one tree species depending on the horizons at various soil depths (Table 4; Brunner et al. 2004a). Mechanical stresses, on the one hand, can initiate a strong change in the structure of the roots (e.g., Danjon et al. 2005), and chemical and physical stresses, on the other hand, can initiate a strong change in the physiology of the roots, such as the induction of the 1,3-β-glucan callose with toxic Al (Hirano et al. 2006) or the strong reduction of the activity of the respiratory chain by drought (Richter et al. 2006). The value of the Ca/Al molar ratio of the fine roots is used to indicate the degree of soil acidification because it reflects the occurrence of toxic Al (Cronan and Grigal 1995; Brunner et al. 2004b).

Direct measurements of coarse roots are in general resource demanding and destructive and require large-scale facilities. To obtain coarse root data, either trees are excavated (e.g., Soethe et al. 2006; Oppelt et al. 2005) or the roots investigated by ground penetrating radar (e.g., Barton and Montagu 2004; Butnor et al. 2003). While radar imaging can mainly be used for biomass estimation in specific types

Table 4. Mean vertical biomass distribution of fine roots of *Abies alba* in Switzerland and its morphological properties

Horizon	Depth (cm)	Biomass ($t\,ha^{-1}$)	Length ($km\,ha^{-1}$)	Surface ($ha\,ha^{-1}$)	Volume ($m^3\,ha^{-1}$)	SRL ($m\,g^{-1}$)	RTD ($g\,cm^{-3}$)
F	0–3	1.30	7457	2.69	7.73	5.97	0.17
Ah	3–11	1.43	4682	2.36	9.66	3.30	0.17
B	11–25	0.77	2138	1.27	6.01	3.21	0.13
B	25–50	0.79	1694	1.26	7.64	2.19	0.11
B	50–75	0.58	1127	0.74	3.90	2.26	0.19
B	75–100	0.64	1499	1.02	5.66	2.42	0.16
B	100–125	0.50	1385	1.00	5.86	3.79	0.09
B	125–150	0.26	929	0.71	4.48	5.40	0.20
Sum	0–150	6.27	20911	11.05	50.94	–	–
Mean	–	–	–	–	–	3.57	0.15

Data from Brunner et al. (2004a) and Brunner (unpublished results)
SRL, specific root length; RTD, root-tissue density

of soils, a large number of parameters can be computed as a result of digitizing data after root excavation. These parameters include basal root cross sectional areas (CSA), bulk root volume distribution, and root volume in the root compartments (Danjon et al. 2005). A high correlation is documented between CSA and root weight, allowing the prediction of the root biomass. A recent improvement of that model utilized site-specific data in order to reduce the stand bias (Nielsen and Hansen 2006). A new approach for the representation and modeling of root architecture was reported by Dupuy et al. (2005). This model is based on the mathematical representation of the distribution of root properties such as number, angle, or diameter. Recent applications using three-dimensional digitizing methods enabled the link between three-dimensional root architecture and tree stability (Danjon et al. 2005).

International platform and knowledge gaps

One of the main objectives of the research on tree roots is to enhance the knowledge base and to improve the methodology of measuring root processes in relation to environmental change. Further needs in this area are to collect, evaluate, and categorize the available data on the response of root processes to global environmental change, to compare and evaluate methods and models for estimating fine root dynamics and coarse root structure, to establish the value of fine roots and coarse root structure as indicators of global environmental change, and to develop new methodologies for studying roots.

Starting in 2003, an international platform on the research of roots of woody plants was initiated as a common base for scientists working on woody root processes, which has allowed the exchange of information, ideas, and personnel [European Cooperation in the field of Scientific and Technical Research (COST action E38), www.cost38.net]. The platform provides workshops and symposia to bring together researchers, allowing integration of research from the cellular scale to the ecosystem scale. Beyond this, the platform identifies knowledge gaps, determines current and future research needs, and analyzes how they may be incorporated into research programs. The aim is the establishment of a core network of scientists operating at the cutting edge of woody root processes. Three areas were identified for which activities of research should be focused on to improve knowledge: (1) to identify properties of roots that can be used as indicators for environmental change, (2) to measure the dynamics of fine roots to assess C fluxes to soils, and (3) to model the coarse roots to estimate the biomass of the root systems. These issues are currently addressed within three working groups of the COST action E38.

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