



Fine root production and turnover in forest ecosystems in relation to stand and environmental characteristics

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ABSTRACT

The production and turnover of fine roots (diameter ≤ 2 mm) contributes significantly to carbon cycling in forest ecosystems. We compiled an up-to-date global database covering 186 stands from the literature and estimated fine root production (FRP) and fine root turnover (FRT) for boreal, temperate and tropical forests in order to study the relationships between FRP or FRT and environmental and stand variables. FRP for all plants (trees + understorey) was 311 ± 259 ($n = 39$), 428 ± 375 ($n = 71$) and 596 ± 478 $\text{g m}^{-2} \text{a}^{-1}$ ($n = 32$) in the boreal, temperate and tropical forests, respectively, and the corresponding annual FRT rates were 0.77 ± 0.70 , 1.21 ± 1.04 and 1.44 ± 0.76 , respectively. When the FRP and FRT of trees were estimated separately for boreal and temperate forests the differences between the two biomes were insignificant. The mean FRP of trees for the two biomes combined was 306 ± 240 $\text{g m}^{-2} \text{a}^{-1}$ ($n = 86$) and the annual FRT was 1.31 ± 1.43 . Fine root biomass (FRB) was the most significant factor explaining the variation in FRP, and more so at the tree level than at the stand level, explaining 53% of the variation in FRP for trees at the tree level. The corresponding proportions at the stand level were 21% for all plants and 12% for trees. Latitude, mean annual temperature and annual precipitation each explained $<20\%$ of the variation in FRP or FRT. Fine root production and FRT estimates are highly dependent on the species included in the sampling, the sampling depth and the methods used for estimating FRP or calculating FRT. The results indicate that the variation in FRP on a global scale can be explained to a higher degree if we focus on tree roots separately from the roots of the understorey vegetation and on FRP at the tree level instead of FRP at the stand level or on FRT.

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1. Introduction

The forests of the world contain 80% of all the above-ground carbon (C) and 40% of all the below-ground terrestrial C (Dixon et al., 1994). It has been estimated that substantial amounts of below-ground C may be released into the atmosphere within this century, contributing significantly to global warming (Bellamy et al., 2005; Sitch et al., 2003). These estimates regarding C pools and fluxes are uncertain because the below-ground C dynamics is poorly understood (Schulze et al., 2009). Fine roots, which are short-lived, non-woody, small-diameter roots associated with mycorrhizae, are the most important component contributing to below-ground C fluxes in forest ecosystems, so that up to 75% of the annual net primary production can be allocated to fine roots (see Fogel, 1985; Keyes and Grier, 1981; Vogt et al., 1996; Gill and Jackson, 2000). Thus fine roots can play a key role in the

cycling and accumulation of C in forest ecosystems (Berg, 1984; Joslin and Henderson, 1987; Hendrick and Pregitzer, 1993; Helmisaari et al., 2002). The progress in understanding the contribution of fine roots to soil C pools has been slow partly due to methodological problems, the labor-intensive nature of such studies, and the wide range of internal and external factors affecting fine root production (FRP) and fine root turnover (FRT) (see Vogt et al., 1996; Majdi et al., 2005). So far biochemical models for below-ground C dynamics have contained simplified representations of fine root dynamics (Woodward and Osborne, 2000). Better understanding of factors affecting FRP and FRT would be important for developing global C models, and such information can be gained by collecting new data in the field or in controlled conditions and by further analyzing and generalizing on already existing bodies of data.

In this study our approach was to generalize the data from existing studies, the number of which has increased since the previous similar undertakings (Vogt et al., 1986, 1996; Gill and Jackson, 2000). That was found to be problematic, for many reasons. There

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is no clear consensus as to what is meant by fine roots or which species should be included in the FRP estimates. In most studies fine roots are defined on the basis of diameter, the diameter class ≤ 2 mm being the most commonly used (Vogt et al., 1986; Cairns et al., 1997; Chen et al., 2004b; Noguchi et al., 2007; Finér et al., 2011). Figures quoted for FRP and FRT are highly dependent on the diameter class, and arbitrary selection of the diameter class can result in biased FRP and FRT estimates (Gill and Jackson, 2000; Matamala et al., 2003; Majdi et al., 2005; Guo et al., 2007; Yuan and Chen, 2010). Studies of FRP in forest ecosystems do not always indicate clearly whether the estimates include tree roots only or the roots of both trees and the understorey vegetation. Differentiation between all roots (tree and understorey vegetation roots) and tree roots only are especially important in boreal forests, where the understorey vegetation contributes significantly to the FRP of the whole ecosystem and the FRT rates of the understorey vegetation differ from those of the trees (Finér and Laine, 1998; Helmisaari et al., 2002). It is also rare for fine root studies to cover the whole rooting depth, as most scientists limit their sampling to the uppermost soil layers (e.g. Finér et al., 2011). That will most probably give an underestimate of FRB or FRP, even though majority of roots exist in the studied layers (Stone and Kalisz, 1991; Jackson et al., 1996, 1997; Schenk and Jackson, 2002). Unlike the fine root biomass (FRB), which can be estimated with relatively high accuracy by the coring method if the number of samples is large enough to cover the high variation (Vogt et al., 1998; Park et al., 2008), the estimation of annual FRP and FRT is more complicated. The mechanisms affecting fine root dynamics are not fully understood, and fine roots grow and die continuously during growing season. Fine root production has been estimated using several direct (sequential soil coring, ingrowth cores, the minirhizotron) or indirect methods (C and nitrogen budgets, C balance and C flux, the isotopic approach), which all have their advantages and disadvantages (Vogt et al., 1998; Majdi et al., 2005; Hendricks et al., 2006; Strand et al., 2008). Comparative studies performed at the same sites indicate that FRP estimates differ significantly between methods (see Steele et al., 1997; Vogt et al., 1998; Hertel and Leuschner, 2002; Hendricks et al., 2006). Hendricks et al. (2006) found that the ingrowth core and soil coring methods gave lower estimates for FRP than the minirhizotron technique, whereas Vogt et al. (1998), who compared the methods at the same sites, did not find any consistent differences between them. It is certainly the case, however, that the C isotope technique has consistently yielded considerably lower FRT rates than any of the other methods (Gaudinski et al., 2001; Matamala et al., 2003; Guo et al., 2007; Strand et al., 2008). So far there are no studies where the results of the different FRP estimate methods have been compared by combining data from different sites.

The inclusion of FRP and FRT in national and global forest ecosystem C budget calculations require models, which are easy to use and give reliable results. The formulation of such models is problematic, since the biological mechanisms affecting FRP and FRT are still poorly understood, and the fact that several external factors have affected these variables (see Majdi, 2001) and their importance has varied on temporal and spatial scales (Vogt et al., 1996; Gill and Jackson, 2000). In global datasets the FRP or FRT have correlated with environmental factors at least in the sense that FRP has increased with mean annual air temperature and annual precipitation and FRT has increased from boreal to tropical forests (Vogt et al., 1986, 1996; Gill and Jackson, 2000). At the biome level, FRP and FRT have correlated with latitude, mean annual air temperature, precipitation and soil nutrient status (Vogt et al., 1996; Yuan and Chen, 2010). The directions of these relationships have varied depending on the factors and biomes concerned. Fine root production has correlated positively with FRB in boreal and cold temperate forests (Li et al., 2003; Chen et al., 2004b), and this relationship

has been used for modeling C budgets for national purposes (Li et al., 2003). At a more local level, FRP or FRT in individual experiments has responded to several environmental factors such as soil temperature and soil nutritional or moisture status (e.g. Keyes and Grier, 1981; Pregitzer et al., 2000; Vogt et al., 1983, 1987; Farrar and Jones, 2000; Joslin et al., 2000; Lahti et al., 2005; Hendricks et al., 2006), and stand factors such as tree species or species groups, stand age, or above-ground productivity (Keyes and Grier, 1981; Finér and Laine, 1998; Finér et al., 1997; Tingey et al., 2005; Hendricks et al., 2006). Again the directions of the responses have varied between studies. FRP and FRT estimates at particular sites are also affected by seasonal and annual variations, which may be attributed to variations in environmental factors and internal factors such as the phenological stages of roots and shoots (Vogt et al., 1998; Steiner et al., 2010). Analysis of more comprehensive datasets might reveal new or more stable relationships between FRP or FRT and stand and environmental factors.

In the present study we compiled an up-to-date global database from the literature in order to compare FRP and FRT of tree roots and all plant roots (tree roots and understorey vegetation roots combined) in boreal, temperate and tropical forests, and to study global relationships and formulate equations between FRP or FRT and stand and environmental factors. We had to limit our study mostly to relationships between FRP or FRT and the same stand and environmental factors as in the previous studies (Vogt et al., 1986, 1996; Gill and Jackson, 2000), since no new easily available and measurable variables were found from the literature. However, we assumed that more reliable and stable relationships could be found by analysing larger datasets in a more standardized way than earlier, focusing entirely on the ≤ 2 mm root diameter class and by analysing tree roots separately from all plant roots. We also aimed to find out whether different FRP estimation methods and sampling depths have impacts on the FRP or FRT estimates and their relationships to stand and environmental factors. The results of this study may prove useful for developing descriptions of fine root dynamics for inclusion in global ecosystem C models.

2. Materials and methods

2.1. Compilation of the data

Initially we compiled a database of FRP and live FRB in tree roots and/or all plant roots (tree roots and understorey vegetation roots combined) in forest stands as reported in the literature. The FRP data had been obtained by either the sequential coring, ingrowth core, N-budget or minirhizotron method. The FRP estimates obtained with the sequential coring method were based on various calculation methods, including the minimum–maximum approach, balancing changes in living and dead fine root biomass and the compartment flow method (see McClaugherty et al., 1982; Fairley and Alexander, 1985), and there was not always any information on whether the differences had been tested statistically. If more than one method had been used for determining the FRP, we selected the estimate obtained by the sequential coring method in those cases where the authors did not consider any of the estimates more realistic than the others. The results of one commonly used method were selected because the estimates obtained with one method were considered more valid for comparison. The sequential coring method and the ingrowth bag method were the most commonly used. Since the ingrowth bag method has been observed to give underestimates relative to the sequential coring method or minirhizotron method (Finér and Laine, 2000; Vogt et al., 1998), the sequential coring method was

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