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Factors causing variation in fine root biomass in forest ecosystems

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ABSTRACT

Fine roots form one of the most significant components contributing to carbon cycling in forest ecosystems. We study here the effect of variation in root diameter classes, sampling depth and the inclusion of understorey vegetation root biomass in fine root biomass (FRB) estimates. The FRB estimates for different forest biomes are updated using a database of 512 forest stands compiled from the literature. We also investigate the relationships between environmental or forest stand variables and fine root biomass (≤2 mm in diameter) at the stand ($g\,m^{-2}$) and tree level ($g\,tree^{-1}$). The FRB estimates extrapolated for the whole rooting depth were $526 \pm 321\,g\,m^{-2}$, $775 \pm 474\,g\,m^{-2}$ and $776 \pm 518\,g\,m^{-2}$ for boreal, temperate and tropical forests, respectively, and were 26–67% higher than those based on the original sampling depths used. We found significant positive correlations between ≤1 and ≤2 mm diameter roots and between ≤2 and ≤5 mm roots. The FRB estimates, standardized to the ≤2 mm diameter class, were 34–60% higher and 25–29% smaller than those standardized to the ≤1 mm and ≤5 mm diameter classes, respectively. The FRB of the understorey vegetation accounted for 31% of the total FRB in boreal forests and 20% in temperate forests. The results indicate that environmental factors (latitude, mean annual precipitation, elevation, temperature) or forest stand factors (life form, age, basal area, density) can not explain a significant amount of the variation in the total FRB and a maximum of 30% that in the FRB of trees at the stand level, whereas the mean basal area of the forest stand can explain 49% of the total FRB and 79% of the FRB of trees at the tree level.

1. Introduction

The forests of the world contain 80% of all above-ground carbon (C) and 40% of all below-ground terrestrial C (Dixon et al., 1994). It is notable, however, that the below-ground C pool in a forest ecosystem often exceeds the above-ground pool. Fine roots, i.e. non-woody, small-diameter roots and their associated mycorrhizae, are important for the water and nutrient uptake of trees. They have also been regarded as short-lived and recognised as the most important component contributing to below-ground C fluxes in forest ecosystems, accounting for up to 75% of the annual net primary production (Fogel, 1985; Keyes and Grier, 1981; Vogt et al., 1996; Gill and Jackson, 2000). Even though some recent studies suggest that the life-span of fine roots has been underestimated and their contribution to ecosystem net primary production has been overestimated (e.g. Strand et al., 2008), fine roots play an important role in the cycling and accumulation of C and nutrients in forest ecosystems (Berg, 1984; Joslin and Henderson, 1987; Hendrick and Pregitzer, 1993; Helmisaari et al., 2002). Much less is known, however, about the contribution of fine roots to soil C pools than that of the above-ground parts of the vegetation. This is partly due to methodological problems, the labour-intensive nature of such studies and the wide range of internal and external factors affecting fine root biomass (FRB) and its production (Vogt et al., 1996; Majdi et al., 2005).

The results of individual experimental studies have been gathered together and analysed in several review studies to find out the relationships between FRB and stand and environmental characteristics on larger geographical scales (Vogt et al., 1986, 1996; Cairns et al., 1997; Jackson et al., 1996, 1997; Leuschner and Hertel, 2003; Chen et al., 2004; Finér et al., 2007). Fine root biomass has been found to vary in relation to forest stand characteristics, i.e. tree species, stand age, density, basal area and soil properties, or environmental factors, chiefly air temperature, amount of precipitation, geographical location and elevation (Vogt et al., 1986, 1996; Cairns et al., 1997; Jackson et al., 1996, 1997; Leuschner and Hertel, 2003; Chen et al., 2004; Finér et al., 2007). Most reviews have found the

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relationships to be weak, the results inconsistent between studies, the datasets small and the variation in forest stand and environmental characteristics narrow. Fine roots are important for taking up water and nutrients from soil, and environmental variables such as air temperature and precipitation affect soil water and nutrient availability and the functioning of the roots. The average FRB has proved to be smaller under the cooler climatic conditions of boreal forests than under the warmer conditions of temperate and tropical forests (Vogt et al., 1986, 1996; Jackson et al., 1996, 1997), although the differences between biomes have not always been consistent (Vogt et al., 1996; Finér et al., 2007). The increase in FRB from boreal to temperate and tropical forests might be related to the availability of water and nutrients. The FRB in boreal and temperate forests has been reported to increase with the amount of precipitation (Leuschner and Hertel, 2003; Finér et al., 2007), but that relationship has not been studied in tropical forests, which receive a much higher precipitation in any case. Many experimental and review studies have shown that FRB correlates with the availability of soil nutrients and water, and it has usually been smaller in the same geographical area when nutrient availability is higher (Keyes and Grier, 1981; Vogt et al., 1983, 1986, 1996; Finér and Laine, 1998; Finér et al., 2007; Helmisaari et al., 2007) or water availability is poorer (Nisbet and Mullins, 1986; Leuschner et al., 2004; Meier and Leuschner, 2008).

Earlier studies have also pointed to differences in FRB depending on forest life forms and above-ground stand characteristics (Vogt et al., 1986, 1996; Jackson et al., 1996, 1997; Leuschner and Hertel, 2003; Finér et al., 2007; Noguchi et al., 2007). According to Jackson et al. (1996, 1997), needleleaf temperate forests have a higher FRB than broadleaf forests, whereas the other results (Vogt et al., 1986, 1996; Leuschner and Hertel, 2003; Finér et al., 2007; Noguchi et al., 2007) have indicated the opposite trend. Earlier studies have also suggested differences in FRB between evergreen and deciduous tropical forests (Vogt et al., 1996; Jackson et al., 1996, 1997). In addition, FRB has been found to be related to stand age and canopy closure, increasing up to the point of canopy closure and remaining constant or decreasing thereafter (Vogt et al., 1983; Vanninen et al., 1996; Helmisaari et al., 2002; Claus and George, 2005). There have been exceptions to this pattern, however (Leuschner and Hertel, 2003; Finér et al., 2007).

It is well documented at the tree level that stump and coarse root biomass (g tree^{-1}) has a close correlation with stem diameter and can be used to estimate that of trees with high accuracy (Hakkila, 1972; Marklund, 1988; Vadeboncoeur et al., 2007), and a number of studies also indicate that FRB at the tree level correlates with stem diameter or basal area, the correlations being higher than those between FRB at the stand level (g m^{-2}) and forest stand characteristics (Chen et al., 2004; Helmisaari et al., 2007; Finér et al., 2007). So far these tree-level relationships have been studied only between the FRB of trees and stand characteristics, and it therefore remains open whether these relationships also exist between total FRB and forest stand or environmental characteristics.

Most earlier works combining data from different FRB studies (e.g. Vogt et al., 1986, 1996; Jackson et al., 1996, 1997) have not analysed the effects of diameter class and sampling depth on FRB estimates. It is well known from stand-level studies that FRB estimates are highly dependent on the diameter selected (Finér and Laine, 1998). Given that the diameter classes for fine roots vary from ≤0.5 mm to ≤10 mm, (Vogt et al., 1986, 1996; Nadelhoffer and Raich, 1992), it is the ≤1 mm, ≤2 mm and ≤5 mm diameter classes that are most commonly used (Vogt et al., 1986, 1996; Cairns et al., 1997; Chen et al., 2004; Noguchi et al., 2007). Fine root biomass decreases exponentially from the soil surface to the deeper soil layers in all forest biomes, but there is some variation in rooting depths between biomes (Jackson et al., 1996, 1997; Schenk and Jackson, 2002). Very few FRB studies cover the whole rooting depth (Jackson et al., 1996, 1997; Schenk and Jackson, 2002). Fine root sampling is a very laborious undertaking, and most scientists either limit their attentions to the layer which they consider contains the majority of the roots, so that only a few try to cover the whole rooting depth. Many, in fact, do not know the actual rooting depth at their sites (Schenk and Jackson, 2002, 2005).

Since the FRB of a forest consists of the roots of both the trees and the understorey vegetation, it would also be important to study the impact of the understorey on forest ecosystem FRB estimates, since in ecosystems such as boreal forests the understorey can account for a significant proportion of total FRB (Laiho and Finér, 1996; Chen et al., 2004; Helmisaari et al., 2007). The proportion of total FRB in a forest that is attributable to tree roots increases exponentially, and in some cases tree roots completely exclude understorey vegetation roots as the stand develops and increases its basal area (Chen et al., 2004). Studies of forest FRB may determine total FRB without distinguishing between understorey vegetation roots and tree roots (Vogt et al., 1986, 1996; Nadelhoffer and Raich, 1992; Jackson et al., 1996, 1997; Kurz et al., 1996; Leuschner and Hertel, 2003; Li et al., 2003; Noguchi et al., 2007), or they may present FRB of trees estimates only (Cairns et al., 1997; Finér et al., 2007). or else they may treat the tree and understorey FRB separately, or fail to indicate clearly which vegetation categories have been included. Thus we are lacking understorey FRB estimates for different forest biomes. It would be important to determine the relationships between the various fine root categories, and to take account of the roots of both the trees and the understorey vegetation when estimating the pools and turnover rates of C in forest ecosystems.

The aim of the present work was to determine (1) how much the FRB estimates for different forest biomes and life forms are affected by variations in root diameter class, sampling depth and the inclusion of understorey vegetation in these estimates, and (2) the relationships between FRB and forest stand and environmental variables. This was done by analysing a comprehensive global FRB database compiled from the literature.

2. Material and methods

2.1. Compilation of the data

We compiled a database of live FRB in forest stands from the literature, keeping the tree and understorey vegetation data separate if they were presented separately in the original papers. When it was not clear whether the data included only tree roots, or both tree and understorey vegetation roots combined, we assumed that all roots were included.

We accepted well documented data collected by soil coring, pith or monolith methods, but not accepted data for stands affected by recent disturbances, i.e. we excluded stands that were less than 10 years old or recently managed, e.g. by irrigation, cutting or fertilization. We also excluded agroforestry systems from our analyses. If the sampling was performed several times on the same stand, the mean value was used. Some reports concerned several stands, perhaps even in the same geographical area, in which case the data for the stands were treated separately. We collected FRB data for the diameter classes ≤1 mm, ≤2 mm and ≤5 mm, since these were the most commonly used. Data for the classes ≤0.5 mm, ≤3 mm or ≤4 mm were available in only a few cases, and these were treated as ≤1 mm, ≤2 mm or ≤5 mm classes, respectively, in the biome-level and regression analyses. FRB was determined as applying to roots that were ≤2 mm in diameter in 90% of the cases. For understorey vegetation we included only data for the ≤2 mm class, due to the small amount of data available for individual diameter classes. We also recorded the sampling depth for all stands.

We used the information on the relationships between environmental and stand characteristics found in the earlier studies