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 ± 321 g m^{-2}, 775 ± 474 g m^{-2} and 776 ± 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 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.

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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

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

to enter data on four environmental variables (latitude, elevation, mean annual temperature and mean annual precipitation) and four tree stand variables (dominant tree species or forest type, stand age, stand density and stand basal area) into our database, and we also collected information on the soil (soil type, soil carbon-nitrogen-ratio) and the above-ground parts of the vegetation (tree height, diameter, volume, leaf biomass or litterfall), but could not utilize that information, either because it was available only for very few stands (soil carbon-nitrogen-ratio, tree height, diameter, volume, leaf biomass or litterfall), or because we were unable to render it comparable due to the different sampling depth (soil carbon-nitrogen-ratio) or classification methods used for soil type. We grouped the forest types into boreal (at latitudes >55° in Europe and >48° on the other continents), tropical (at latitudes ≤25°, including subtropical) and temperate (between these two extremes) based on information in the original studies. The dominant tree species were used for grouping the boreal and temperate forests by life form into needleleaf or deciduous forests, and the tropical forests into evergreen and deciduous (including semi-deciduous) forests.

2.2. The database

The whole database covered 35 countries on all the forested continents, represented by a total of 512 tree stands. One hundred and six of these stands were in boreal forests, 323 in temperate forests and 83 in tropical forests (Table 1). The boreal forests were mostly needleleaf forests and the tropical forests either evergreen (69 stands) or deciduous (14 stands). There were clear decreasing gradients in mean annual temperature and mean annual precipitation from tropical to temperate, and then to boreal forests (Table 2). There was also considerable variation in stand density and stand basal area between the forest biomes, in addition to which there were more natural forests among the tropical forests and they were generally older than those in the other biomes.

2.3. Calculations and statistical analyses

When studying FRB relationships between the diameter class fractions we constructed linear regression equations for the relationships between the ≤2 mm and ≤1 mm FRB diameter classes and between the ≤2 mm and ≤5 mm classes (Fig. 1) and used these to standardize the ≤1 mm and ≤5 mm diameter class data to a single ≤2 mm diameter class and to calculate the results for the various diameter classes.

Since the FRB sampling depths recorded in the individual studies did not cover the whole rooting depths in most cases and were not as deep as the maximum rooting depth presented for forest biomes by Schenk and Jackson (2002), we extrapolated the ≤2 mm FRB for the whole rooting depth using the equation presented by Gale and Grigal (1987):

$$Y = 1 - \beta^d \tag{1}$$

where Y is the cumulative root fraction (varying between 0 and 1) from the soil surface to depth d (cm), and β the parameter values fitted to a global FRB dataset by Jackson et al. (1997): 0.943, 0.983, 0.967, 0.982, 0.972 and 0.972 for the boreal, temperate coniferous, temperate deciduous, tropical deciduous, tropical evergreen and tropical savanna biomes, respectively. When performing these calculations the stands in each biome were classified into vegetation types on the basis of the information presented in the original papers.

We calculated the FRB at the tree level (g tree^{-1}) by dividing that at the stand level (g ha^{-1}) by the stand density (trees ha^{-1}) and the mean basal area (m^2 tree^{-1}) at the tree level by dividing the basal area (m^2 ha^{-1}) at the stand level by the stand density (trees ha^{-1}). The stand density and basal area data presented in the

original papers were used as such, even though in the majority of cases we could not find any definition for these parameters.

We used analyses of variance and covariance to identify differences in FRB between the forest life forms and between the biomes, and also to evaluate the differences between FRB calculated with the original sampling depth and that extrapolated for the whole sampling depth. When the differences in FRB between biomes were significant post hoc comparisons were performed using the Tukey HSD test. Sampling depth was used as a covariate for the analyses with the original sampling depth when it was significant ($p < 0.05$). We started out by exploring the relationships between the four environmental variables (latitude, elevation, mean annual temperature and mean annual precipitation) and the four tree stand variables (life form, stand age, stand density and stand basal area) (Table 2) using principal component analysis (PCA), after which linear regression models were fitted between the stand (g m^{-2}) or tree level (g tree^{-1}) FRB by using the data with the original sampling depth and the tree stand or environmental variables. We first fitted the regression models using each of the three tree stand and four environmental variables in turn as the dependent variable and then used stepwise multiple regression analysis to study the relationships between FRB and all tree stand and environmental variables. The variable forest life form was used as a dummy variable. The number of observations available for the stepwise regression models was much smaller than for the models with a single dependent variable, since not all the data were available for all the stands. The dependent variables in the equations were chosen on the basis of information on the significance of the parameters and the whole equation, the magnitude of the error terms and the distribution of the residuals. Only significant parameters and equations were accepted ($p < 0.05$) and are presented here. Equations with a degree of determination (R^2) < 30% were excluded even though some of the equations were significant ($p < 0.05$), since the error terms were high and the FRB data were not distributed evenly in relation to the variation in the dependent variables, so that the patterns observed here could easily change with the addition of new data to the analyses. The correlation, variance, covariance and regression analyses were performed with the SPSS 16.1 software package using the bivariate correlation, general linear model (GLM) and linear regression (RLIN) procedures, respectively.

3. Results

3.1. Relationships between FRB diameter classes

We used both the FRB of trees and combined tree and understorey FRB (total FRB) data for all the biomes to study the relationships between the root diameter classes. All the data of the FRB of trees originated from temperate and boreal forests. There were significant linear correlations between the ≤2 mm and ≤1 mm FRB and between the ≤2 mm and ≤5 mm FRB for both the trees and the trees and understorey vegetation combined ($p < 0.001$, Fig. 1), but there was more variation in these relationships when the tree and understorey vegetation roots were combined. The relationships did not differ between the needleleaf and broadleaf forests ($p > 0.05$).

The data standardized to the different diameter classes indicated that the standardized mean total ≤1 mm FRB for the various biomes is 25–29% smaller than the mean total ≤2 mm FRB and that of the ≤5 mm FRB 34–60% higher (Table 3). The mean total FRB biomass estimates standardized to the ≤2 mm diameter class did not differ significantly from those calculated from the original data, which contained the different diameter classes (Table 3), in any of the biomes ($p > 0.05$).

Table 1
Distribution of the boreal, temperate and tropical forest stands in the database by forest type or dominant tree species and country. The numbers in parentheses indicate the numbers of stands.

Forest type/dominant species	Country	References
Boreal broadleaf (12)		
Alnus glutinosa (2), *Betula papyrifera* (1), *Populus balsamifera* (2), *Populus tremuloides* (6), *Quercus robur* (1)	Canada (6), Sweden (3), U.S.A.(3)	Bauhus and Messier (1999), Finér et al. (1997), Persson and Stadenberg (2009), Ruess et al. (1996), Steele et al. (1997)
Boreal needleleaf (94)		
Abies balsamea (3), *Picea abies* (32), *Picea glauca* (3), *Picea mariana* (5), *Picea sitchensis* (5), *Pinus banksiana* (2), *Pinus contorta* (4), *Pinus sylvestris* (38), *Pseudotsuga menziesii* (2)	Canada (14), Finland (44), Norway (6), Russia (4), Sweden (16), U.K. (5), U.S.A. (5)	Ahlström et al. (1988), Bauhus and Messier (1999), Børja et al. (2008), Brække (1992), Finér and Laine (1998), Finér et al. (1997, 2003, 2007), Helmisaari and Hallbäcken (1999), Helmisaari et al. (2002, 2007), Kimmins and Hawkes (1978), Kleja et al. (2008), Laiho and Finér (1996), McDowell et al. (2001), McKay and Malcolm (1988), Majdi and Persson (1995), Majdi and Andersson (2005), Möttönen et al. (2003), Nisbet and Mullins (1986), Nygaard and de Wit (2004), Ohashi et al. (2007), Persson (1978, 1979), Persson and Stadenberg (2009), Ruess et al. (1996), Smith et al. (2000), Steele et al. (1997), Taskinen et al. (2003), Vanninen and Mäkelä (1999), Widén and Majdi (2001)
Temperate broadleaf (115)		
Acer saccharum (15), *Betula alleghaniensis* (2), *Betula ermanii* (1), *Betula papyrifera* (1), *Betula* sp. (1), *Castanopsis cuspidata* (1), *Fagus erenata* (1), *Fagus grandifolia* (1), *Fagus sylvatica* (58), *Fraxinus americana* (1), *Fraxinus grandifolia* (1), *Fraxinus mandshurica* (1), *Populus tremuloides* (3), *Populus tristis × balsamifera* (1), *Quercus alba* (3), *Quercus cerris* (1), *Quercus crispula* (1), *Quercus ilex* (1), *Quercus petraea* (7), *Quercus phellos* (1), *Quercus robur* (4), *Quercus rubra* (4), *Quercus velutina* (1), *Quercus* sp. (4)	Austria (1), Belgium (2), China (1), France (6), Germany (49), Japan (4), Poland (1), Slovenia (5), Spain (1), Sweden (1), Netherlands (5), U.S.A. (39)	Bakker et al. (2008), Bolte and Villanueva (2006), Brække and Kozlowski (1977), Burke and Raynal (1994), Claus and George (2005), Coleman et al. (2000), Epron et al. (1999), Fahey and Hughes (1994), Farrish (1991), Finér et al. (2007), Fisk et al. (2004), Hendrick and Pregitzer (1993), Hendricks and Bianchi (1995), Hertel and Leuschner (2002), Joslin and Henderson (1987), Joslin et al. (2006), Konôpka et al. (2005), Leuschner and Hertel (2003), McClaugherty et al. (1982), Meier and Leuschner (2008), Leuschner et al. (2004), López et al. (2001), Nadelhoffer et al. (1985), Noguchi et al. (2007), Park et al. (2008), Safford (1974), Tateno et al. (2004), Tripathi et al. (2005), Van Praag et al. (1988), Wang et al. (2006), Wilczynski and Pickett (1993), Yin et al. (1989)
Temperate needleleaf (208)		
Abies amabilis (2), *Abies balsamea* (2), *Abies grandis* (2), *Calocedrus decurrens* (1), *Chamaecyparis obtusa* (6), *Cryptomeria japonica* (22), *Larix gmelinii* (1), *Larix kaempferi* (1), *Larix leptolepis* (2), *Picea abies* (57), *Picea engelmannii* (1), *Picea glauca* (2), *Picea glehnii* (1), *Picea rubens* (2), *Picea sitchensis* (1), *Pinus contorta* (11), *Pinus densiflora* (3), *Pinus eliottii* (2), *Pinus koraiensis* (1), *Pinus palustris* (1), *Pinus pinaster* (1), *Pinus radiata* (1), *Pinus resinosa* (7), *Pinus rigida* (10), *Pinus strobus* (5), *Pinus sylvestris* (16), *Pinus tabulaeformis* (3), *Pinus taeda* (3), *Pinus thunbergii* (3), *Pseudotsuga menziesii* (30), *Thujopsis dolabrata* (1)	Austria (4), Belgium (3), Canada (3), China (6), Czech Rep. (6), Estonia (2), France (6), Germany (42), Japan (36), Korea (4), New Zealand (1), Poland (4), Slovakia (1) Slovenia (1), Sweden (3), Switzerland (4), Slovakia (1), Netherlands (8), U. K. (2), U.S.A. (69)	Achat et al. (2008), Alexander and Fairley (1983), Ammer and Wagner (2005), Bakker et al. (2006), Bolte and Villanueva (2006), Borken et al. (2007), Brunner et al. (2002), Brække and Kozlowski (1977), Claus and George (2005), Coleman et al. (2000), Cronan (2003), Ehrenfeld et al. (1992), Enoki et al. (1996), Farrish (1991), Finér et al. (2007), Fujimaki et al. (2007), Genenger et al. (2003), Genet et al. (2008), Gholz et al. (1986), Godbold et al. (2003), Grier et al. (1981), Haynes and Gower (1995), Hendricks and Bianchi (1995), Hendricks et al. (2006), Hwang et al. (2007), Keyes and Grier (1981), Kinerson et al. (1977), Konôpka and Tsukuhara (2001), Konôpka et al. (2006), Leuschner and Hertel (2003), Litton et al. (2003), Lytle and Cronan (1998), McClaugherty et al. (1982), Majdi and Persson (1995), Majdi et al. (2008), Nadelhoffer et al. (1985), Noguchi et al. (2005, 2007), Ostonen et al. (2005), Park et al. (2008), Peichl and Arain (2006), Püttsepp et al. (2006), Uselman et al. (2007), Sakai et al. (2007), Santantonio and Grace (1987), Santantonio and Santantonio (1987), Satomura et al. (2003, 2006), Schmid (2002), Schmid and Kazda (2002), Shan et al. (2001), Son and Hwang (2003), Wang et al. (2006), Vanguelova et al. (2005), Van Praag et al. (1988), Vogt et al. (1983, 1987), Xu et al. (1997), Yamashita et al. (2004), Zhou and Shangguan (2007)
Tropical deciduous (14)		
Deciduous and semideciduous lowland and mountain forests, dry and moist forests	Australia (2), Costa Rica (3), Ghana (1), India (5), Mexico (1), Panama (2)	Castellanos et al. (1991), Cavalier (1992), Hertel et al. (2003), Kummerow et al. (1990), Lawson et al. (1970), Singh and Singh (1981), Srivastava et al. (1986), Sundarapandian and Swamy (1996), Zerihun et al. (2006)
Tropical evergreen (69)		
Lowland and mountain rainforests, subtropical forests, dry forests, primary and disturbed, lowland plantations, broadleaf and needleleaf	Australia (1 Brazil (1), China (1), Costa Rica (10) Ecuador (8), India (10), Indonesia (9), Malaysia (1), Mexico (7), Panama (1), Peru (1), Puerto Rico (2), U.S.A. (17)	Arunachalam et al. (1996a,b), Asbjornsen et al. (2005), Cuevas et al. (1991), Gower (1987), Graefe et al. (2008), Green et al. (2005), Herbert and Fownes (1999), Jaramillo et al. (2003), Kitayama et al. (1997), Leuschner et al. (2006), Ostertag (2001), Powers et al. (2005), Restrepo et al. (2003), Röderstein et al. (2005), Sothe et al. (2007), Sundarapandian and Swamy (1996), Valverde-Barrantes et al. (2007), Vance and Nadkarni (1992), Visalakshi (1994), Zhanghe et al. (1994)

Table 2
Descriptive statistics on the stand and environmental characteristics of the boreal, temperate and tropical forests. Data shown are the mean, standard deviation (SD), minimum (Min), maximum (Max) and number of stands (N). Data were not available for all the variables in all the forest stands. Forest life forms are not distinguished separately.

	Tree stand variables			Environmental variables			
	Age (yrs)	Basal area (m^2 ha^{-1})	Stand density (trees ha^{-1})	Latitude (degrees from equator)	Elevation (m, above sea level)	Mean annual temperature (°C)	Annual precipitation (mm)
Boreal							
Mean	75	26	1738	59	253	3.6	636
Min	10	2	199	48	3	−3.5	269
Max	250	61	9350	69	1380	7.4	1200
SD	50	12	1540	5	290	3.0	159
N	104	79	88	106	78	49	98
Temperate							
Mean	75	34	3380	45	548	8.7	1116
Min	10	0	100	30	16	1.5	462
Max	850	90	110500	58	3500	20.0	3060
SD	67	17	11782	6	567	2.8	516
N	306	187	197	320	234	244	286
Tropical							
Mean	105	36	1735	13	1224	21.7	2837
Min	11	4	150	0	60	8.6	707
Max	430	125	5730	35	3060	28.0	5000
SD	139	25	1409	8	760	5.3	1105
N	31	51	52	83	56	72	81
All together							
Mean	76	32	2703	43	580	10.5	1317
Min	10	0	100	0	3	-3.5	269
Max	850	125	110500	69	3060	28.0	5000
SD	69	18	9099	16	612	6.9	956
N	435	316	336	503	365	361	459
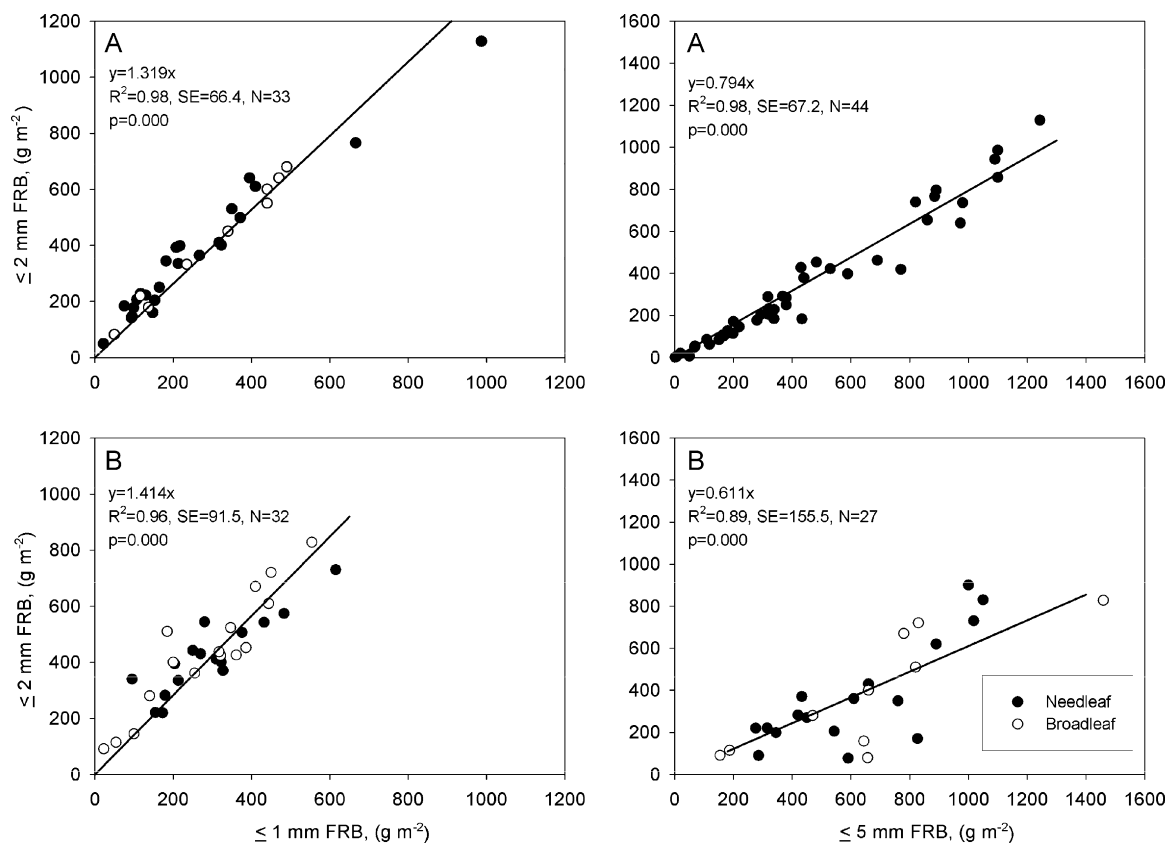
Fig. 1. Relationships between fine root biomass (FRB) ≤2 mm and ≤1 mm or ≤5 mm in needleleaf and broadleaf forest stands. (A) Tree roots only. (B) Tree and understorey vegetation roots combined. Regression lines fitted to the data are presented with the parameter values for the dependent variables, adjusted regression estimates (R^2), standard errors of the regression estimates (SE) and the total number of observations (N).

Table 3
Fine root biomass (FRB) (g m^{-2}) in the various biomes: (a) value calculated using all the original data irrespective of root diameter (selected in the order ≤2 mm, ≤1 mm, ≤5 mm if data were available for more than one diameter class), (b) value calculated using the original data in each diameter class separately, (c) value obtained by standardizing all the original data to the ≤1 mm, ≤2 mm or ≤5 mm diameter class using the equations presented in Fig. 1. Data shown are the mean and standard deviation, with the number of stands in parenthesis. NS = the difference in FRB between the original diameter and the ≤2 mm diameter is not significant, $p < 0.05$. The calculations are based on the whole database.

	FRB all with the original diameter[a]	FRB using original data[b]			FRB using equations for relations between diameters[c]		
		≤1 mm	≤2 mm	≤5 mm	≤1 mm	≤2 mm	≤5 mm
Boreal	302 ± 188 (106)	169 ± 103 (21)	287 ± 177 (94)	494 ± 192 (20)	220 ± 129 (106)	295 ± 173NS (106)	396 ± 244 (106)
Temperate	379 ± 252 (323)	310 ± 200 (61)	389 ± 255 (295)	580 ± 416 (64)	288 ± 184 (323)	391 ± 254NS (323)	553 ± 399 (323)
Tropical	494 ± 483 (83)	224 ± 135 (12)	405 ± 283 (73)	1096 ± 839 (13)	322 ± 240 (83)	453 ± 339NS (83)	724 ± 558 (83)

3.2. FRB and sampling depth

The FRB sampling depths were significantly smaller in the boreal forests than in the tropical or temperate ones ($p < 0.001$) (Table 4), and there was significant positive correlation between total FRB and sampling depth in the tropical and temperate forests ($r^2 = 0.48$, $p < 0.001$, $N = 73$ and $r^2 = 0.52$, $p < 0.001$, $N = 173$, respectively). The FRB estimates extrapolated for the whole rooting depth using equation (1) were 526 ± 321 g m^{-2}, 775 ± 474 g m^{-2} and 776 ± 518 g m^{-2} for the boreal, temperate and topical forests, respectively (Table 5). These values were 26–67% higher than those based on the original sampling depths, the differences being statistically significant ($p < 0.001$, Table 5).

3.3. Contribution of understorey vegetation roots to total FRB

The proportion of the total FRB extrapolated for the whole sampling depth attributable to the understorey vegetation roots was assessed with data covering 74 temperate and 59 boreal forest stands. Tropical forests could not be included because there were no data available for the analyses. The proportion tended to be higher in the boreal forests (0.31 ± 0.26) than in the temperate forests (0.20 ± 0.29), and higher in the needleleaf forests (0.29 ± 0.28, $N = 101$) than in the broadleaf forests (0.13 ± 0.25, $N = 32$), but the differences were not statistically significant ($p > 0.05$). There were relatively more forest stands without any understorey vegetation in the temperate (40 out of 74) and broadleaf forests (22 out of 32) than in the boreal (4 out of 59) or needleleaf forests (25 out of 101). No significant relationships ($p > 0.05$) were found between FRB of trees as a proportion of total FRB and tree stand basal area (m^2 ha^{-1}), tree stand density (trees ha^{-1}) or stand age (data not shown).

3.4. Tree, understorey and total FRB in the biomes

The mean FRB of trees calculated using the original sampling depth did not differ between the temperate and boreal forests ($p > 0.05$), whereas it was significantly higher in the broadleaf than in the needleleaf forests ($p = 0.05$) (Tables 5 and 6). These differences disappeared when the mean FRB of trees by biome was calculated for the whole rooting depth ($p > 0.05$) (Tables 5 and 6).

There were no significant differences in the mean understorey FRB between the temperate and boreal forests or between the broadleaf and needleleaf forests (Tables 5 and 6).

The mean total FRB (trees + understorey) did not differ significantly between the biomes in the non-extrapolated original data ($p > 0.05$), but the extrapolated values for the whole rooting depth differed significantly between biomes ($p < 0.05$) (Tables 5 and 6), being higher in the tropical and temperate forests than in the boreal forests (Tukey HSD test, $p < 0.01$). There were no significant differences ($p > 0.05$) in the mean total FRB biomass between the broadleaf forests and needleleaf forests or between the evergreen and deciduous tropical forests (Tables 5 and 6).

3.5. Relationships between FRB and stand and environmental characteristics

We started by exploring the relationships between the eight tree stand and environmental variables by means of PCA ordination. Of the environmental variables, latitude, temperature and annual precipitation had the highest scores on the first ordination axis and only elevation on the second axis (Fig. 2), while among the tree stand variables stand density and basal area had the highest scores on the second axis and the needleleaf and broadleaf forests were located at opposite ends of the first axis.

Table 4
Mean sampling depths in the various biomes and percentages of studies in the database in which the sampling depth extended to depths covering 50% and 95% of the total fine root biomass (FRB) in the given biomes (according to Schenk and Jackson, 2002). Data shown are the mean, standard deviation (SD), minimum (Min), maximum (Max) and number of stands (N). Mean FRB values indicated with the same letter do not differ significantly from each other, $p > 0.05$.

	Sampling depth (cm)					Percentage (%) of studies covered with	
	Mean ± SD		Min	Max	N	50% FRB	95% FRB
Boreal	33.9 ± 16.6	a	3	90	106	92	8
Temperate	47.2 ± 27.0	b	6	133	317	79	3
Tropical	50.0 ± 37.1	b	10	200	83	89	19

Table 5
Mean tree, understorey vegetation and total fine root biomass (FRB, ≤2 mm, g m^{-2}) by forest life form in the boreal, temperate and tropical forests, calculated on the basis of the original sampling depth and that extrapolated to the maximum rooting depth using equation (1). The boreal and temperate forest values are calculated for broadleaf and needleleaf forests separately, and those for the tropical forests for deciduous and evergreen forests separately. Data shown are the mean and standard deviation, with the number of stands in parentheses. The data include FRB standardized from roots diameters of <1 mm or <5 mm. F and p-values are presented for the analyses of variance performed to compare the FRB of all roots calculated using the original sampling depth with those extrapolated to the whole rooting depth. For the other statistical tests, see Table 6.

	Fine root biomass			F and p values
	Broadleaf/deciduous	Needleleaf/evergreen	All	
Trees				
Original sampling depth				
Boreal	399 ± 239 (7)	281 ± 159 (77)	290 ± 168 (84)	
Temperate	362 ± 182 (69)	324 ± 222 (152)	336 ± 211 (221)	
Tropical	409 (1)	359 ± 165 (9)	364 ± 156 (10)	F = 11.766; p = 0.001
Extrapolated for the whole rooting depth				
Boreal	524 ± 349 (7)	373 ± 249 (77)	385 ± 260 (84)	
Temperate	505 ± 235 (69)	607 ± 428 (152)	576 ± 381 (221)	
Tropical	792 (1)	469 ± 214 (9)	501 ± 226 (10)	
Understorey				
Original sampling depth				
Boreal	114 ± 84 (7)	173 ± 259 (52)	166 ± 245 (59)	
Temperate	82 ± 228 (25)	189 ± 339 (49)	153 ± 309 (74)	
Tropical	–	–	–	F = 2.562; p = 0.111
Extrapolated for the whole rooting depth				
Boreal	146 ± 114 (7)	205 ± 294 (52)	198 ± 278 (59)	
Temperate	124 ± 354 (26)	325 ± 524 (49)	259 ± 482 (74)	
Tropical	–	–	–	
Total				
Original sampling depth				
Boreal	467 ± 253 (12)	411 ± 260 (69)	419 ± 258 (81)	
Temperate	480 ± 261 (71)	491 ± 379 (105)	486 ± 335 (176)	
Tropical	456 ± 285 (13)	467 ± 371 (60)	465 ± 356 (73)	F = 50.879; p = 0.000
Extrapolated for the whole rooting depth				
Boreal	593 ± 343 (12)	515 ± 318 (69)	526 ± 321 (81)	
Temperate	687 ± 414 (70)	836 ± 505 (100)	775 ± 474 (170)	
Tropical	1013 ± 456 (13)	724 ± 419 (60)	776 ± 518 (73)	

The regression models for the relationships between total FRB or the FRB of trees extrapolated for the whole rooting depth and the tree stand or environmental variables were fitted at both the stand and tree level (Figs. 3–5). We first fitted the models using one of the tree stand or environmental variables as the dependent variable, and then performed a stepwise multiple regression analysis with all eight tree stand and environmental variables. The number of observations in the latter analysis was smaller than in those with

Table 6
Results of analyses of variance and covariance performed on the data in Table 5. The fine root biomass fractions are used as the dependent variables, the biome and life form (broadlead/needleleaf) are the independent variables, and the sampling depth is a covariate for the original data only. The values are F-values, with their p-values in parentheses.

| Independent variables	Source of variation			
	Biome F-value (p-value)	Life form F-value (p-value)	Biome × Life form F-value (p-value)	Covariate-Sampling depth F-value (p-value)
Trees				
Original data	0.086 (0.318)	3.863 (**0.050**)	1.118 (0.291)	
Extrapolated data	1.403 (0.248)	0.114 (0.736)	3.008 (0.084)	
Understorey				
Original data	1.391 (0.240)	1.104 (0.295)	0.136 (0.713)	24.538 (**0.000**)
Extrapolated data	0.300 (0.585)	1.825 (0.179)	0.527 (0.469)	
Trees and understorey combined				
Original data	1.611 (0.201)	2.235 (0.136)	0.823 (0.440)	83.554 (**0.000**)
Extrapolated data	3.516 (**0.031**)	0.176 (0.675)	1.791 (0.168)	
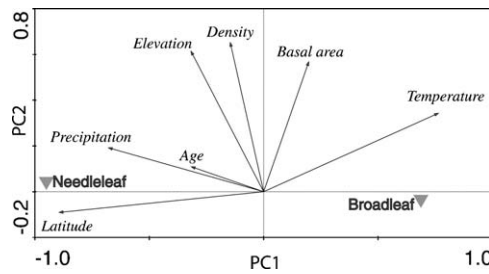
Fig. 2. Principal component analysis (PCA) ordination of the first two axes showing the relationships between the four environmental variables (latitude, elevation, mean annual temperature and mean annual precipitation) and the four tree stand variables (life form (needleleaf/broadleaf forests), stand age, stand density and stand basal area).
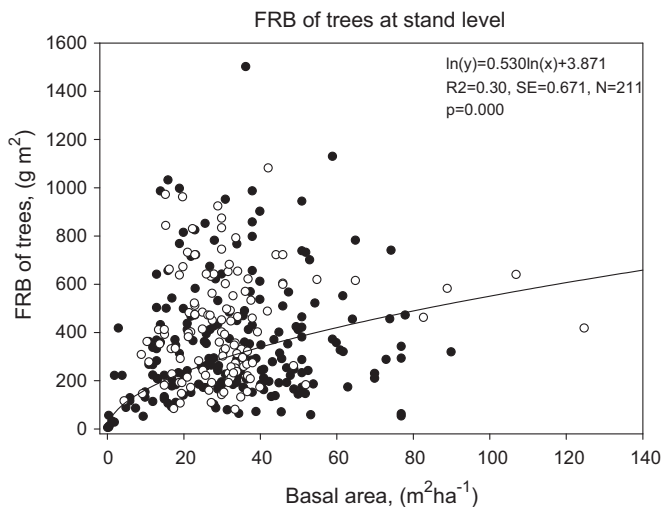

Fig. 3. Significant relationships between the fine root biomass (FRB ≤2 mm) of trees alone and stand basal area. Regression line fitted to the data are presented with the parameter values for the dependent variables, adjusted regression estimates (R^2), standard errors of the regression estimates (SE) and the total number of observations (N). For the symbols see Fig. 1.
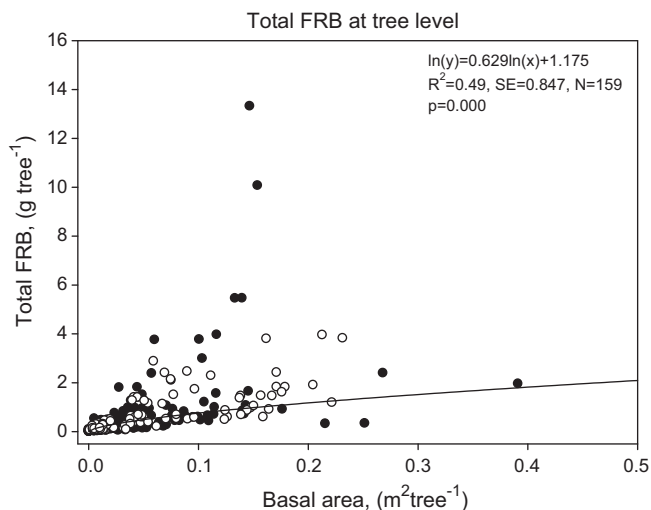

Fig. 4. Significant relationships between the fine root biomass of trees and understorey vegetation combined (total FRB ≤2 mm) at the tree level and mean stand basal area. Regression line fitted to the data are presented with the parameter values for the dependent variables, adjusted regression estimates (R^2), standard errors of the regression estimates and the total number of observations. For the symbols see Fig. 1.
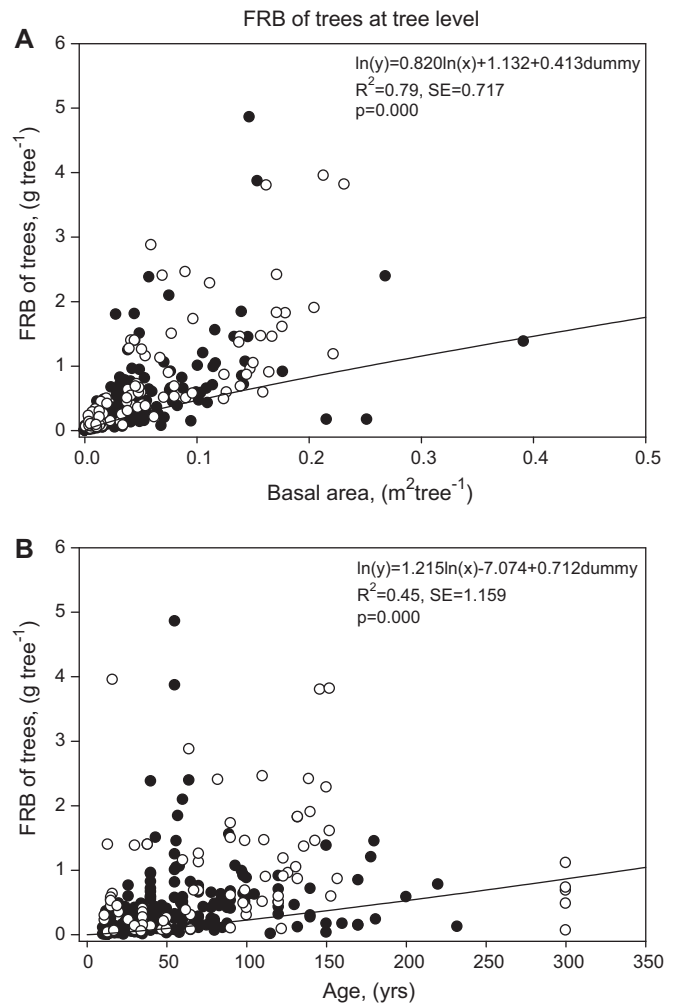

Fig. 5. Significant relationships between the fine root biomass (FRB ≤2 mm) of trees alone at the tree level and (A) mean stand basal area and (B) age. Regression lines fitted to the data are presented with the parameter values for the dependent variables, adjusted regression estimates (R^2), standard errors of the regression estimates (SE) and the total number of observations (N). Dummy = 0 for needleleaf forests and 1 for broadleaf forests. For the symbols see Fig. 1.

one dependent variable since not all the data were available for all the stands. The stand level analyses using stand variables as dependent variables showed only one significant relationship, the FRB of trees increasing with stand basal area ($p < 0.001$, Fig. 3). The stand level model explained 30% of the variation in the FRB of trees. Of the environmental variables, latitude, precipitation and elevation did not have significant relationships ($R^2 < 30\%$) with total FRB or the FRB of trees at the stand level. The degree of determination for total FRB did not increase over 30% when all the environmental and stand variables were included in the models for stepwise regression analyses (results not shown), and in the case of the FRB of trees not higher than that with the use of stand basal area as dependent variable only (Fig. 3).

The tree-level analyses showed that the mean tree basal area alone explained 49% of the variation in total FRB and 79% of that in the FRB of trees ($p < 0.001$, Figs. 4 and 5), although the standard errors of the estimates were also high in the tree-level models. The models indicated that tree-level FRB increases with increasing mean basal area (Figs. 4 and 5). We also found a significant relationship between the tree-level FRB and stand age ($p < 0.001$, Fig. 5), which could explain 45% of the variation in tree-level FRB. When all eight tree stand and environmental variables were included in the tree-level stepwise regression analyses the degree of determi-

nation did not increase from that with the mean basal area of trees only (results not shown). The relationships at the tree level differed between the needleleaf and broadleaf trees (Fig. 5).

4. Discussion

4.1. Effects of fine root diameter, sampling depth and inclusion of the understorey vegetation on FRB estimates

Despite the fact that species differ in the tissue structure and morphology of their roots, there was a clear linear relationship between the root diameter classes, and the relationships did not differ between the deciduous and needleleaf forests (Fig. 1). The close relationship between diameter classes could be a result of the autocorrelation between diameter classes, i.e. ≤1 mm was included in the ≤2 mm diameter class and ≤2 mm in the ≤5 mm class. The regression equations had a somewhat smaller error between the ≤1 mm and ≤2 mm diameter classes than between the ≤2 mm and ≤5 mm diameter classes (Fig. 1). Our results are not fully comparable to the earlier ones. Leuschner and Hertel (2003) found significant differences between tree species in the contribution of the 2–5 mm diameter class to the ≤5 mm diameter FRB when they compared only three tree species, and Chen et al. (2004) showed strong linear relationships between ≤2 mm and ≤5 mm FRB when they made the comparisons on tree level for different tree species. Our dataset was larger than the earlier ones and it covered data on several tree species at stand level.

The equations allowed us to standardize all the FRB data in our database to the ≤2 mm diameter class, and to render the results published for the ≤1 mm, ≤2 mm and ≤5 mm diameter classes comparable (Table 3). Attempts have been made to introduce a common definition for fine roots (Böhm, 1979; Zobel and Waisel, 2009), but there is no consensus, and many recent studies have focused more on ≤0.5 mm roots because they are physiologically more active than larger ones (Pregitzer et al., 1998; Joslin et al., 2006; Yanai et al., 2006; Park et al., 2008; Makita et al., 2009).

The various fine root fractions were treated together in many of the earlier reviews, and this undoubtedly increased the variation and resulted in biased estimates for FRB (Leuschner and Hertel, 2003). In our database, however, the standardized ≤2 mm FRB estimates did not differ significantly from those calculated using the original data, which contained diameter classes ≤1 mm, ≤2 mm and ≤5 mm ($p > 0.05$) (Table 3). This was probably due to the fact that most of the data sets we used included FRB data for the ≤2 mm diameter class, and the effect of the ≤1 mm FRB data could be offset by that of the ≤5 mm FRB data. The total FRB estimates would have been 25–29% smaller if we had standardized the results to the ≤1 mm diameter class, and 34–60% higher in the case of the ≤5 mm diameter class (Table 3).

We were able to find data to produce estimates for the mean understorey vegetation FRB for needleleaf and deciduous forests in both the temperate and boreal zones. Since the FRB production and turnover rates of different species groups vary (Finér et al., 1997; Finér and Laine, 1998; Majdi and Andersson, 2005), it is important to determine FRB separately for the trees and the understorey vegetation, as the roots of the latter contributed 10–30% of the total FRB (Table 5), this proportion being highest in the boreal and needleleaf forests. The observation that there were relatively more temperate broadleaf than needleleaf forests without any understorey FRB indicates that the FRB sampling was carried out in dense temperate forest stands where there is not enough light for any understorey vegetation to grow. Sampling in spring, before the full development of the leaves, could probably have given different estimates. We did not find any studies from tropical forests in which the FRB of trees had been determined separately from that of the understorey veg-

etation, but the diversity of species and canopy layers are much higher in pristine tropical forests than that in temperate or boreal forests or the understorey can mostly consist of juvenile trees, which makes separation too laborious and somewhat arbitrary. There was large variation in the proportion of total FRB attributable to trees, and in contrast to the results of Chen et al. (2004), we did not find any correlation between this proportion and tree stand characteristics. Chen et al. (2004) also studied the relationship between the proportion of FRB attributable to trees in boreal and temperate forests, and one reason why they found a correlation and we did not may be that they made separate calculations for shade-tolerant and shade-intolerant species, which we could not do. Studies on the dynamics of above-ground biomass have shown clear relationships between the understorey vegetation biomass and tree stand characteristics such as basal area, stand age and stand density, and these relationships have varied between understorey species groups (Alaback, 1982; Muukkonen and Mäkipää, 2006). Such species-specific relationships may counteract the relationship between the proportion of total FRB accounted for by trees and the FRB for the understorey vegetation.

According to the review by Schenk and Jackson (2002), rooting depths of 58 cm in boreal forests, 104–121 cm in temperate forests and 91–94 cm in tropical forests include 95% of FRB on average, the corresponding depths for 50% of FRB being 12 cm, 21–23 cm and 14–16 cm, respectively. This suggests that the studies included in our database covered 50% of the FRB in most cases and seldom the whole rooting depth (Table 4). The sampling depth was deeper in the temperate and tropical forests than in the boreal forests (Table 4), which could indicate that the rooting depth in the boreal forests was not as deep as in the other biomes. These rooting depths are generalizations over wide geographical scales and there is much variation within each biome caused by soil properties like soil type, stoniness and impermeable layers (e.g. Schenk and Jackson, 2002) and species (Stone and Kalisz, 1991), which we could not take into account in our analyses.

Our FRB estimates based on the original sampling depths fell within the same range as reported in the earlier studies in the case of the temperate and tropical forests but were higher for the boreal forests (Tables 6 and 8), whereas our estimates extrapolated for the whole rooting depth were in general higher than those reported earlier, even including the reports that also covered deeper soil layers (Jackson et al., 1996, 1997; Leuschner and Hertel, 2003). Our results, like the earlier ones based on the original sampling depths, are most probably underestimates of the true FRB. The FRB estimates extrapolated with the equations and parameters presented by Gale and Grigal (1987) and Jackson et al. (1997) are higher than those based on the original sampling depths, but then Jackson et al. (1997) produced their parameters with only a small body of data and without separating the tree roots from the understory vegetation roots. We introduced error into our estimates when we applied the equations and parameters, and more studies on FRB covering the whole rooting depth in different forest biomes would be needed to estimate the magnitude of this error, so that the present results must be interpreted with caution. Most of the earlier studies nevertheless indicate that the FRB is higher in temperate broadleaf forests than in temperate needleleaf forests, and higher in evergreen tropical forests than in deciduous ones (Table 7). In our analyses the FRB of trees based on the original rooting depth was significantly higher in the temperate broadleaf forests than in the temperate needleleaf forests and the total FRB extrapolated to the whole rooting depth was significantly smaller in the boreal zone than in the other zones, the results depending greatly on the rooting depth used for calculating the FRB. The results do not fully confirm that there are differences in FRB between the biomes and more data covering the whole rooting depth are needed to find that out.

Table 7
Fine root biomass (FRB, g m^{-2}) by forest life form in the various biomes, according to previous reviews. Data shown are means and numbers of forest stands (*N*).

	FRB	N	Reference
Boreal			
Boreal evergreen needleleaf	135	23	Vogt et al. (1986)[a]
Boreal deciduous	129	1	Vogt et al. (1996)[b]
Boreal needleleaf evergreen	152	25	Vogt et al. (1996)[b]
Boreal	290	5	Jackson et al. (1996)[c]
Boreal	230	5	Jackson et al. (1997)[d]
Picea abies and *Pinus sylvestris*	275	53	Finér et al. (2007)[e]
Temperate			
Cold temperate evergreen needleleaf	502	12	Vogt et al. (1986)[a]
Warm temperate deciduous broadleaf	705	4	Vogt et al. (1986)[a]
Cold temperate deciduous	654	18	Vogt et al. (1996)[b]
Cold temperate needleleaf evergreen	509	26	Vogt et al. (1996)[b]
Warm temperate broadleaf deciduous	750	7	Vogt et al. (1996)[b]
Temperate deciduous	420	11	Jackson et al. (1996)[c]
Temperate coniferous	440	12	Jackson et al. (1996)[c]
Temperate deciduous	440	14	Jackson et al. (1997)[d]
Temperate coniferous	500	10	Jackson et al. (1997)[d]
Temperate broadleaf*	482	60	Leuschner and Hertel (2003)[f]
Temperate coniferous*	407	69	Leuschner and Hertel (2003)[f]
Temperate broadleaf**	637	56	Leuschner and Hertel (2003)[f]
Temperate coniferous**	544	61	Leuschner and Hertel (2003)[f]
Fagus sylvatica	389	36	Finér et al. (2007)[e]
Picea abies and *Pinus sylvestris*	303	61	Finér et al. (2007)[e]
Temperate deciduous broadleaf	746	2	Noguchi et al. (2007)[g]
Temperate evergreen broadleaf	470	1	Noguchi et al. (2007)[g]
Temperate coniferous	439	11	Noguchi et al. (2007)[g]
Tropical			
Broadleaf evergreen (live + dead)	407	20	Vogt et al. (1986)[a]
Tropical deciduous	532	8	Vogt et al. (1996)[b]
Tropical evergreen	904	24	Vogt et al. (1996)[b]
Tropical deciduous	410	5	Jackson et al. (1996)[c]
Tropical evergreen	490	14	Jackson et al. (1996)[c]
Tropical deciduous	280	6	Jackson et al. (1997)[d]
Tropical evergreen	330	12	Jackson et al. (1997)[d]

[a] Global database, diameter classes up to 6 mm, depth varying according to the original papers, no clear information on root diameter classes.
[b] Global database, diameter classes up to 5 mm, depth varying according to the original papers, no clear information on root diameter classes.
[c] Global database, diameter classes up to 2 mm, depth varying according to the original papers, but <50 cm, no clear information on root diameter classes.
[d] Global database, diameter classes up to 2 mm, depth varying according to the original papers, partly <1 m partly <25 cm, no clear information on root diameter classes.
[e] European database, diameter classes up to 2 mm, depth varying according to the original papers, tree roots.
[f] Global database, diameter classes up to 3 mm, *depth varying according to the original papers, minimum forest floor + 15 cm, maximum 100 cm and **standardized to 70 cm, mainly tree roots.
[g] Japanese database, diameter classes up to 2 mm, depth varying according to the original papers, maximum 60 cm, tree roots, no clear information on root categories.

4.2. Variation in FRB in relation to stand and environmental characteristics

To analyse the relationships between FRB and stand or environmental characteristics we used a larger dataset with more variation in the dependent variables (Table 2) than had been done earlier (Vogt et al., 1986, 1996; Leuschner and Hertel, 2003; Chen et al., 2004; Finér et al., 2007) and found only one significant relationship between the tree stand (age and basal area) and the environmental variables (latitude, elevation and precipitation) and the stand level FRB. That was less than in the earlier studies, since we accepted only statistically significant results and equations where the degree of determination was ≥30%. The combination of all the tree stand and environmental variables in the regression models could not explain more than that achieved with any of the tree stand or environmental variables alone. Also, only a small proportion of the variation in the stand level FRB had been explained with these variables in the previous works. Additional explanatory variables, ones related to soil e.g. nutrition, water availability, permeability or above-ground biomass characteristics, or else more comparable data, could probably increase the degree of determination somewhat (Li et al., 2003; Helmisaari et al., 2007; Vogt et al., 1996).

The stand variables age or stand density did not explain the variation in total FRB or the FRB of trees in our material. Total FRB did not have any relationship with stand basal area and the FRB

of trees increased with the stand basal area. In earlier studies in which the relationships were studied by tree species or species groups the FRB has either increased or decreased with stand age and decreased with stand basal area (Leuschner and Hertel, 2003; Finér et al., 2007). Chen et al. (2004), who also combined data on different tree species in the temperate and boreal zones, found that FRB increased with stand basal area. We did not find significant relationships between the environmental variables and FRB opposite to earlier studies (Vogt et al., 1986, 1996; Leuschner and Hertel, 2003; Finér et al., 2007). Our results were not fully comparable with earlier ones since we combined several species in our analyses, our data had wider variations in latitude, elevation and annual precipitation.

Our results confirmed earlier observations that the variation in FRB at the tree level can be explained on the basis of tree stand variables to a higher degree than at the stand level (Chen et al., 2004; Finér et al., 2007; Helmisaari et al., 2007). This was true for both total FRB and that of the trees alone. At the tree level, almost 80% of the FRB of trees was explained by the mean basal area of the tree stand, and almost half (49%) of the total FRB. The weaker, but still significant relationship of the mean basal area of the tree stand with total FRB than with the FRB of trees may indicate that the roots of the understorey vegetation are not affected by the above-ground parts of trees as much as are the tree roots. The tree-level FRB increased with an increase in the mean basal area of the for-

est stand, as has earlier been reported for single tree species (Chen et al., 2004; Finér et al., 2007; Helmisaari et al., 2007). As the above-ground biomass in forest stands is closely related to the basal area, our results support the findings which show that there is a relationship between FRB and above-ground biomass (Kurz et al., 1996; Li et al., 2003). Stand age also explained a significant proportion (45%) of the variation in the tree-level FRB of trees, whereas the environmental variables did not explain the variation in the tree-level FRB. An increase in the tree level FRB of trees by age has also been found earlier for single tree species (Finér et al., 2007). The relationships found in this study might change with the addition of new FRB data and explanatory variables. The regression models presented in this study give an underestimate of the true FRB since most of the data behind the models do not represent the whole rooting depth.

5. Conclusions

The results indicate that only a small proportion of the variation in stand-level FRB can be explained by environmental or tree stand variables, whereas there seems to be a higher correlation between the tree-level FRB and the mean basal area of the forest stand. The clear relationships between the ≤1 mm and ≤2 mm diameter classes and between the ≤2 mm and ≤5 mm enabled us to standardize the FRB data to the ≤2 mm diameter class. The analysis indicated that the sampling depth in most reports did not cover the whole rooting depth. If this is not taken into account, biased underestimates might be obtained for the FRB in some biomes. A more consistent determination of fine root parameters and reporting of stand and environmental characteristics in the future would facilitate the use of the results of the fine root studies for gaining a better understanding of the C cycle in forest ecosystems.

Acknowledgements

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