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Fine-root turnover of European forest trees revisited: an analysis of data from sequential coring and ingrowth cores

Brunner I*[1], Bakker MR[2,3], Björk RG[4], Hirano Y[5], Lukac M[6], Aranda X[7], Børja I[8], Eldhuset TD[8], Helmisaari HS[9], Jourdan C[10], Konôpka B[11], López BC[12], Miguel Pérez C[7], Persson H[13], Ostonen I[14]

[1] Swiss Federal Institute for Forest, Snow and Landscape Research WSL, CH-8903 Birmensdorf, Switzerland

[2] Bordeaux Sciences Agro, UMR 1220 TCEM, F-33175 Gradignan, France

[3] INRA, UMR 1220 TCEM, F-33883 Villenave d'Ornon, France

[4] Department of Biological and Environmental Sciences, University of Gothenburg, P.O. Box 461, SE-405 30 Gothenburg, Sweden

[5] Graduate School of Environmental Studies, Nagoya University, Nagoya 464-08601, Japan

[6] School of Agriculture, Policy and Development, University of Reading, Reading RG6 6AR, United Kingdom

[7] Ecophysiology, IRTA Torre Marimon, E-08140 Caldes de Montbui, Spain

[8] Norwegian Forest and Landscape Institute, P.O.Box 115, NO-1431 Ås, Norway

[9] Department of Forest Sciences, University of Helsinki, P.O.Box 27, FI-00014 Helsinki, Finland

[10] CIRAD, UMR Eco&Sols, 2, Place P. Viala, F-34060 Montpellier, France

[11] Forest Research Institute, National Forest Centre, SK-96001 Zvolen, Slovak Republic

[12] CREAF Center for Ecological Research and Forestry Applications, and Ecology Unit of the Department of Plant and Animal Biology and Ecology, Edifici Ciències UAB, E-08193 Bellaterra, Spain

[13] Department of Ecology, Swedish University of Agricultural Sciences SLU, P.O.Box 7044, SE-750 07 Uppsala, Sweden

[14] Institute of Ecology and Earth Sciences, University of Tartu, Vanemuise 46, EE-51014-Tartu, Estonia

*Corresponding Author: Ivano Brunner, E-mail: ivano.brunner@wsl.ch, Phone: +41-44-739-2284, Fax: +41-44-739-2215

Abstract

Background and aims Forest trees directly contribute to carbon cycling in forest soils through the turnover of their fine roots. In this study we aimed to calculate root turnover values of common European forest tree species and to compare them with established reference values.

Methods We compiled available European data and applied various turnover calculation methods to the resulting database. We used Decision Matrix and Maximum-Minimum formula in a transparent and reproducible way.

Results Mean turnover values obtained by the combination of sequential coring and Decision Matrix were 0.86 y^{-1} for *Fagus sylvatica* and 0.88 y^{-1} for *Picea abies* when maximum biomass data were used for the calculation, and 1.11 y^{-1} for both species when mean biomass data were used. Using mean standing biomass rather than maximum resulted in about 30% higher values of root turnover. Using the Decision Matrix to calculate turnover doubled the turnover values when compared to the Maximum-Minimum formula. The Decision Matrix, however, makes use of more input information than the Maximum-Minimum formula.

Conclusions We propose that calculations using the Decision Matrix with mean biomass give the most reliable estimates of root turnover in European forests and should preferentially be used in models and C reporting.

Keywords Annual production, Decision Matrix, Fine-root turnover, Ingrowth cores, Maximum-Minimum formula, Sequential coring

Abbreviations ANOVA Analysis of variance**,** B Biomass, BGC Biogeochemical cycles, C Carbon, DM Decision Matrix, GPP Gross primary production, GUESS General ecosystem simulator, LPJ Lund-Potsdam-Jena model, MAT Mean annual temperature, MM Maximum-Minimum, MRT Mean residence time, N Necromass, NPP Net primary production, P Production, PLSD Protected least significant difference, SOM Soil organic matter, T Turnover

Introduction

Tree fine roots, generally defined as those with a diameter of less than 2 mm, together with mycorrhizas, perform the task of water and nutrient uptake from the soil. Due to the nature of their function, fine roots tend to have limited lifespan and thus constitute a significant input of carbon (C) into the soil profile. Given the estimated size of the C flux associated with fine root turnover, thought to reach 0.5 to 3 t C ha^{-1} y^{-1} (Gill and Jackson 2000; Brunner and Godbold 2007), we clearly need accurate estimates of the rate at which fine roots die and contribute to soil C pools. The amount of C annually cycled through fine roots is dependent on the standing stock and on the lifespan (synonyms: ‘longevity’ or ‘turnover time’, inverse of ‘turnover’ or ‘turnover rate’) of fine roots (see Fig. 1).

The uncertainty of currently available fine root turnover values can best be illustrated by the ongoing debate about how the turnover of the fine roots can be estimated and which method is the most suitable (e.g. Strand et al. 2008; Trumbore and Gaudinski 2003; Majdi et al. 2005). Starting from the most recent developments, stable and labile C-isotopes (^{13}C, ^{14}C) may be used to estimate root carbon longevity, either by using labelling techniques or natural abundances in the atmosphere (e.g. Matamala et al. 2003; Gaudinski et al. 2001, 2010; Endrulat et al. 2010). A more widely used method to estimate the lifespan of fine roots is the use of minirhizotrons (e.g. Johnson et al. 2001; Majdi and Andersson 2005). This technique allows for a direct observation of individual roots and their development. Both methods suffer from several drawbacks, the main weakness of isotopic analysis for root age determination is the uncertain age of organic compounds used to construct fine roots (Sah et al. 2011). Meanwhile, minirhizotron studies are not able to determine the exact time of root death. In addition, the installation of the minirhizotron tubes can change water and temperature regimes as well as soil matrix resistance to root penetration. Moreover, fine root growth is often stimulated by the conditions along the minirhizotron tube. Unsurprisingly, direct comparisons of these two methods result in a discrepancy in root longevity estimates (Tierney and Fahey 2002; Strand et al. 2008; Gaul et al. 2009), sometimes explained by different fractions of fine roots under observation, i.e. the short-lived and the long-lived fine roots, likely to be recorded by these two methods (Gaudinski et al. 2010).

Alternatively, instead of direct observations of individual root longevity, the mean lifespan can be calculated by dividing the 'pool' (standing crop or biomass) by its 'input' (annual production). Because the turnover is the inverse of lifespan, it can be calculated by dividing the 'annual production' by the ‘belowground standing crop' (Gill and Jackson 2000). There are several methods used to obtain estimates of annual fine root production. A widely used method to directly measure the production of fine roots is the use of ingrowth cores (e.g. Persson 1980; Vogt and Persson 1991). This method measures the amount of fine roots which grow into a defined volume of root-free soil over a defined period of time. The advantage of this method is its relative ease and speed of application when estimating root production (Vogt and Persson 1991). More recently, root nets were applied instead of ingrowth cores to minimise soil disturbance during the installation (Hirano et al. 2009; Lukac and Godbold 2010). An alternative method to indirectly measure the production of fine roots is the sequential coring technique. Here, several series of soil cores are sampled at discrete intervals over a period of at least one year. Fine roots are extracted from the soil cores and the differences of the dry mass of living (biomass) and dead (necromass) fine roots between two time points recorded. Taking advantage of data generated by sequential coring, several methods exist to calculate the production from the change of the fine-root biomass and necromass data. The production can be calculated by the 'Maximum-Minimum' formula (McClaugherty et al. 1982), by the 'Decision Matrix' formula (Fairley and Alexander 1985), or by the 'Compartment Flow' formula (Santantonio and Grace 1987). Whereas the 'Maximum-Minimum' formula uses only biomass data, the other two methods require both biomass and necromass data. The 'Compartment Flow' formula further requires decomposition data of fine root litter (e.g. Silver et al. 2005). Thus, the values of fine root turnover can vary not only due to measurement methods but also due to calculation methods applied (e.g. Vogt et al. 1998; Strand et al. 2008). A true comparison of the various turnover values may only be possible by using observations from identical sites where various methods were applied (e.g. Haynes and Gower 1995; Hendricks et al. 2006). As for the popularity of different measurement methods, many more estimates of root turnover are available from sequential coring and ingrowth cores than from the minirhizotron method (Finer et al. 2011).

The motivation of this study is twofold: firstly, we aim to apply root turnover calculation methods to existing datasets and to compare resulting turnover values in a transparent and reproducible way. Secondly, we aim to establish reference fine root turnover values of common forest tree species. Given the uncertainty of turnover estimates and the perceived variability of turnover rates in different environments, presenting a dependable estimate with an indication of its range is of paramount importance. Root turnover values are commonly utilised to parameterise biogeochemical models, which require fine root turnover data input e.g. Biome-BGC, LPJ, or LPJ-GUESS (e.g. Pietsch et al. 2005; Sitch et al. 2003; Smith et al. 2001). Using appropriate and accurate turnover values will improve the capacity of these models to assess the change in belowground C pool in European forest and thus improve the accuracy of C reporting efforts.

Materials and Methods

Data origin

Raw fine root biomass and necromass data of forest tree species were collected from published studies. A large proportion of the data originates from doctoral theses due to the availability of raw data in this type of publication. We only included datasets where data collection was carried out for at least one full year. Fine root production was measured either directly by the use of the ingrowth core method or indirectly by the use of the sequential coring method (see Ostonen et al. 2005). Fine root standing crop was defined as the amount of living fine roots (biomass) occurring in the soil at any given time. Repeated sequential coring was used to establish standing fine root biomass in most studies, apart from the case of the ingrowth core method where standing biomass usually was estimated from a single coring. We did not consider data originating from minirhizotron studies as these are reviewed elsewhere (Børja et al., in preparation).

Calculations of fine-root production

Fine root production was calculated either with the 'Maximum-Minimum' formula or the 'Decision Matrix'. The 'Compartment Flow' method was not applied because decomposition data of root litter were not sufficiently available. As a pre-requisite of annual fine root production calculation, a single sampling campaign must have lasted for at least 12 months. At least two measurements from the same month in two consecutive years are the minimal requirement for the calculation of root production.

The Maximum-Minimum (MM) formula calculates the annual fine-root production (P_a) by subtracting the lowest biomass (B_{min}) from the highest biomass value (B_{max}) irrespectively of other biomass values recorded during a full year (McClaugherty et al. 1982). Necromass data are not required for this method:

$$P_{a\,(MM)} = B_{max} - B_{min} \qquad [1]$$

The Decision Matrix (DM) calculates the annual fine-root production (P_a) by summing all calculated productions (P) between each pair of consecutive sampling dates throughout a full year:

$$P_{a\,(DM)} = \sum P \qquad [2]$$

The production (P) between two sampling dates is calculated either by adding the differences in biomass (ΔB) and necromass (ΔN), by adding only the differences in biomass (ΔB), or by equalling P to zero (Fairley and Alexander 1985). The conditions with which of the P formulas to be used are as follows:

$P = \Delta B + \Delta N$ a) if biomass and necromass have increased [3]

b) if biomass has decreased and necromass has increased, but $|\Delta B|$ lower than $|\Delta N|$

$P = \Delta B$ if biomass has increased and necromass has decreased [4]

P = 0 a) if biomass and necromass have decreased [5]

b) if biomass has decreased and necromass has increased, but I∆BI higher than I∆NI

The Decision Matrix used as the basis for calculations is shown in Table 1. To calculate the annual production, all production values from interim periods are summed up from the start of sequential coring until the same time point in the following year (see also Table 2a, b). In the present study, all differences in biomass and necromass were taken into the account during the calculation. However, some authors suggest summing up only the statistically significant differences (e.g. Stober et al. 2000). We propose that accounting for all differences between standing root biomass in two sampling dates constitutes a better approach. The size (and therefore the significance) of the difference is clearly dependent on the duration of the interim period, as well as on the season. Including significantly different observations would skew the data coverage towards long-gap observations only.

Calculations of fine-root turnover

The turnover T_{Bmax} of fine roots was calculated by dividing the annual fine root production (P_a) by the highest standing crop value (maximum biomass B_{max}) according to Gill and Jackson (2000):

$$T_{Bmax} = P_a / B_{max} \qquad [6]$$

As an alternative, the turnover T_{Bmean} was calculated by dividing the annual fine root production (P_a) by the mean standing crop (mean biomass B_{mean}) according to McClaugherty et al. (1982) (compare also Table 2c):

$$B_{mean} = \sum B / n \qquad \text{(n = number of samples per year)} \qquad [7]$$

$$T_{Bmean} = P_a / B_{mean} \qquad [8]$$

Within the recorded datasets we further investigated whether a layer-by-layer calculation yielded different results than a one-soil layer approach and also explored any potential effects of the length or starting season of the observation period, root diameter (i.e. < 1 mm *versus* 1-2 mm), and soil depth.

Data restrictions and limitations

Several published studies were not used in the present survey because they did not fulfil all requirements, e.g. Konôpka (2005, 2009) and Ahlström et al. (1988) recorded their data over one vegetation period but not over a full year (12 months). Other studies were from areas with fertilization and irrigation (Persson 1980b; Persson and Ahlström 1994), or they did not contain data at the required level of detail (López et al. 2001).

This synthesis of fine-root turnover did not allow for detecting any effect of soil depth on the turnover values, mainly due to the lack of a balanced dataset (using the data of Hertel 1999; Richter 2007; Makkonen and Helmisaari 1999; Bakker 1999; Jourdan et al. 2008). Further, our study did not allow for a sound comparison of the effect of the length of the observation period (1, 2, or 3 years) or of the season when measurements commenced, nor were we able to elucidate any influence of root diameter. Our data suggested decreasing turnover for increasing root diameter, but the number of studies (2) and number of different stands (6) was very limited. It would seem that turnover for the finest fraction (i.e. < 1 mm roots *versus* 1-2 mm roots) is slightly higher (using the data of Hertel 1999 and Børja et al. 2008). Differences between species (and/or experimental conditions) strongly affected the result (using the data of Fritz 1999; Bakker 1999; Lukac et al. 2003; Makkonen and Helmisaari 2001).

Statistics

For statistical analyses, correlation analyses and analyses of variance (ANOVA), the software

StatView 5.0 (SAS Institute, Cary, NY, USA) was used, with the significance level of $p < 0.05$ using Fisher's PLSD test.

Results

Data sets

The most abundant data sets obtained by sequential coring were available for *Fagus sylvatica* and *Picea abies* with 13 and 11 data sets, respectively (Table 3). Data sets of other tree species, e.g. *Pinus sylvestris, Populus* spp., and *Quercus* spp., were present only in three or fewer data sets. Data sets originating from ingrowth cores were available only for *F. sylvatica, P. abies*, and *P. sylvestris*, and with only two to three data sets per tree species (Table 4).

Fine-root turnover

Turnover values obtained by the combination of sequential coring, Decision Matrix method, and the maximum biomass data varied from 0.19 to 2.04 y^{-1} for *F. sylvatica* and from 0.44 to 1.36 y^{-1} for *P. abies* (Table 3), with mean values for *F. sylvatica* and *P. abies* of 0.86 and 0.88 y^{-1}, respectively (Table 5). Using the mean biomass instead of the maximum biomass, the turnover values varied from 0.23 to 2.92 y^{-1} for *F. sylvatica* and from 0.56 to 1.77 y^{-1} for *P. abies* (Table 3), with mean values of 1.11 y^{-1} for both *F. sylvatica* and *P. abies* (Table 5). For other tree species, less than three data sets were available, e.g. only 2 data sets were available for *P. sylvestris,* and both had turnover values higher than 1.5 y^{-1} (Table 3).

Turnover values obtained by the combination of sequential coring, Maximum-Minimum method, and maximum biomass data were consistently below 0.7 y^{-1} for *F. sylvatica* and *P. abies* (Table 3), with mean turnover values of 0.41 y^{-1} and 0.44 y^{-1}, respectively (Table 5). The mean turnover value of *P. sylvestris* was 0.48 y^{-1} and did fall in a similar range (Table 5). Using the mean biomass instead of the maximum biomass, the turnover values ranged from 0.26 to

0.95 y^{-1} for *F. sylvatica* and *P. abies* (Table 3), with mean turnover values of 0.53 y^{-1} for *F. sylvatica* and 0.57 y^{-1} for *P. abies* (Table 5).

Mean turnover values obtained by ingrowth cores, the Decision Matrix method, and the maximum biomass were 1.00, 0.72, and 0.76 y^{-1} for *F. sylvatica, P. abies,* and *P. sylvestris*, respectively (Table 5). Using the Maximum-Minimum method and the maximum biomass, the mean turnover values were with 1.00, 0.62, and 0.72, respectively, in a similar range (Table 5). Using the mean biomass instead of the maximum biomass, the mean turnover values were higher, 2.58, 1.15, and 1.40 y^{-1} for *F. sylvatica, P. abies,* and *P. sylvestris*, respectively, using the Decision Matrix, and 2.58, 0.98, and 1.31 y^{-1} for *F. sylvatica, P. abies,* and *P. sylvestris*, respectively, using the Maximum-Minimum formula (Table 5).

We compared the difference in turnover rate estimates based on maximum or mean standing biomass as the denominator. On average in our dataset, using mean standing biomass rather than maximum resulted in about 30% higher estimate of root turnover T ($T_{Bmean} = 1.3\ T_{Bmax}$; $r^2 = 0.98$, $p < 0.001$; Fig. 2).

Soil stratification and root turnover

Our results show that a layer-by-layer approach yields a higher turnover value than a 'one soil layer' approach (Figure 3). For this comparison of the two approaches, sequential coring data, decision matrix calculations and mean biomass values were taken from Hertel (1999), Richter (2007), Makkonen and Helmisaari (1999), Bakker (1999), Ostonen et al. (2005), and Jourdan et al. (2008). Using average data for the whole of the soil profile, as opposed to using data for individual layers, does not capture all observed differences in root biomass and therefore results in a lower estimate of NPP and thus significantly lower turnover T ($T_{whole\ profile} = 0.9\ T_{layer\text{-}per\text{-}layer}$; $r^2 = 0.92$, $p < 0.001$; Figure 3).

Comparison between the Decision Matrix and the Maximum-Minimum method

Mean turnover values calculated with the Decision Matrix were significantly higher than values calculated with the Maximum-Minimum method (1.14 y^{-1} *versus* 0.57 y^{-1}, when using mean biomass data; 0.88 y^{-1} *versus* 0.43 y^{-1}, when using maximum biomass data; $p < 0.001$, Figure 4). The Decision Matrix methods yields T values approximately double the Maximum-Minimum method. Using mean biomass data resulted in significantly higher turnover values compared to the use of maximum biomass data ($p = 0.021$, Figure 4), with a mean difference of about 30%.

Relationship between the turnover and the mean annual temperature

At a global scale, turnover values are dependent on the mean annual temperature (MAT). Gill and Jackson (2000) determined the turnover $T_{Bmax} = 0.228\ e^{0.036\ MAT}$, having a significant relation with MAT ($r^2 = 0.07$, $p = 0.018$; Figure 5a). Our turnover values, calculated with the Decision Matrix and maximum biomass data, however, did not result in a significant relation with MAT (Figure 5b). If Gill and Jackson (2000) had used data only from our temperature range from 2 to 15°C, then no significant relation would be obvious.

Discussion

Decision Matrix *versus* Maximum-Minimum method

We found about two times higher root turnover values when using the Decision Matrix method compared to the Maximum-Minimum method. The observed discrepancy is best described by the fact that Decision Matrix accumulates differences between all observations – the larger the number of interim observations the larger the potential for accounting all the peaks and troughs. The Maximum-Minimum method, on the other hand, makes use only of the annual net gain in biomass. On the basis of our comparison, we suggest that the Maximum-Minimum method should be used with caution; by definition, root turnover estimates calculated by this method are bound between 0 and 1. Although this range may cover some ecosystems, it cannot correctly capture reality in systems where faster root turnover has been observed (e.g. Lukac et al.

2003). The Maximum-Minimum method is therefore only suitable for ecosystems with strong annual fluctuation of fine root biomass where turnover is not expected to exceed 1. In a forest ecosystem where root production and root death occur continuously and on a similar level all year round (‘steady state’), no differences between maximum and minimum biomass will be observed. Such an observation will result in a zero estimate of root production and subsequently a zero estimate of root turnover (compare also Kurz and Kimmins 1987). For example, this may be the case in tropical rainforests, which lack pronounced seasonality.

Moving on to the Decision Matrix method, the weak point of this method is - as with all methods using dead roots - the difficulty of accurately quantifying root necromass. The potentially rapid disappearance of root necromass may lead to underestimates (Hendricks et al. 2006). Nevertheless, we propose that if necromass observations are available or can be obtained, the Decision Matrix should be favoured over the Minimum-Maximum formula. The former considers both living and dead fine roots, the calculation is thus based on more information, reducing the scope for significant errors. However, distinguishing between biomass and necromass is often difficult, as is recognising the difference between partially decomposed fine-root and foliage litter. An important source of variation between estimates from different sources is the arbitrarily imposed root fragment size limit. Whereas Hertel (1999) used for his calculation fine-root litter fragments >0.25 mm length, other authors set the minimum fragments length either at >1 mm (Fritz 1999; Wu 2000) or >5 mm length (Richter 2007), thus varying the amount of necromass recovered from the soil. Comprehensive comparisons of the two methods have also been carried out by other authors (Vogt et al. 1998; Hendricks et al. 2006).

Even though root coring methods – whether sequential or ingrowth – do deliver dependable and comparable measurements of fine root turnover, the application of the minirhizotron technique to estimate fine-root production and turnover is still favoured over the sequential coring or the ingrowth core method in certain situations (Hendricks et al. 2006). Turnover estimates obtained by minirhizotron studies can be higher than 1 and the method allows for repeated observation of the same roots. The latest variation of the minirhizotron technique involves using a series of buried flatbed scanners. This adaptation offers the opportunity for continuous and automated monitoring of fine root growth and dieback (Dannoura et al. 2008). However, in some forest ecosystems, application of minirhizotron methods to measure fine-root production is hampered, e.g. in stony or shallow soils or on steep slopes. Sequential coring and ingrowth core methods are suitable even for these environments, giving them an advantage in terms of comparability of resulting data. In a new approach, Osawa and Aizawa (2012) complemented soil-coring techniques with litterbag experiments in order to estimate fine-root decomposition. By including decomposition rates into the calculations, the authors further improved the accuracy of the values for fine-root production.

Maximum biomass *versus* mean biomass

By definition, the denominator in the root turnover calculation equation is the representation of live standing crop present in the soil. An assumption inherent to all root turnover calculation method is that annual fine root production (obtained by whatever method) equals to fine root mortality and the system is at steady state on an annual basis. Over the course of the year, new growth replaces roots which have been died. The proportion of roots which have been replaced can therefore be calculated as root production over standing crop. At the present, both maximum and mean root biomass are used as representations of annual standing crop, with about two-thirds of studies using maximum biomass (Gill and Jackson 2000). They justified the use of the maximum biomass "…because it is an extensively used model of root turnover and because of its heuristic value". When constructing models of root allocation in forests, it is possible that maximum biomass may be the preferred parameter over mean or minimum values because of the importance of setting an upper limit for the allocation rate. Fine root allocation rate may depend on sink strength (C demand), but might ultimately be limited by the maximum fraction of GPP which trees can allocate to root systems (Astrid Meyer, personal communication). Having said that, and bearing in mind that the root turnover calculation assumes an ecosystem at steady state, a mean value is indicative of the long-term average as it evens out seasonal variation in standing crop. Maximum biomass, on the other hand, is substantially more susceptible to between-year fluctuations due to climatic variation, which occur even if a forest ecosystem is at a steady state. Thus, we propose that mean standing crop rather than the maximum is more representative of the annual live biomass present in the soil. The use of mean biomass in our calculations increased the turnover values by about 30% compared to the use of the maximum biomass.

An additional factor significantly affecting the results of the turnover calculations is the use of summed up values of biomass, necromass, and productivity for the whole soil profile *versus* using these data for individual soil layers (horizons). We acknowledge that using individual horizons should be preferable as the rate of root turnover may be affected by differing physical and chemical characteristics of individual horizons. We established that basing root turnover calculation on individual horizon data increases the overall turnover rate – probably because it allows for better capture of biomass and necromass variations over time. We are, however, aware that root biomass and production observation on a horizon basis constitute a significant technical challenge and contend that using whole-soil data is acceptable. Further factors potentially influencing the turnover, e.g. soil depth, length of study, or root diameter class, however, could not be tested in this study because the available European dataset did not allow for this. Thus, besides the uncertainties due to climatic and calculation reasons, many other external factors may potentially affect the estimates of root turnover values. At present, no available technique can solve this predicament and we put forward that our root turnover values represent the best approximation obtained by using soil or ingrowth cores.

Turnover values of European tree species

Our review of published studies from European forest stands revealed that most data for fine-root turnover originate from sequential coring, with the prevalence of *Fagus sylvatica* or *Picea abies* as the species of interest. Studies performed in forest stands with other dominating tree species such as *Quercus* spp., *Pinus* spp. were far less abundant. Similarly, turnover studies where ingrowth cores were used instead of employing the sequential coring method to measure fine-root production, were far less abundant. Whereas in our study the data sets of *F. sylvatica* derived mainly from Central Europe, the data sets of *P. abies* originated from Central as well as from Northern Europe. Trees from Southern European countries were represented only by a few data sets, and no conclusive turnover values can be suggested for this environment yet. Overall, we propose that only the fine root turnover values in our study for the following species may be recommended for further use in biogeochemical models with a reasonable degree of accuracy: *F. sylvatica* and *P. abies*. We established turnover values of 1.11 y^{-1} for both *F. sylvatica* and *P. abies,* using the Decision Matrix formula and the mean biomass data from sequential coring.

The mean turnover values for temperate and boreal forests in our study were distinctly higher compared to the values in the Gill and Jackson (2000), who compiled a data set of about 190 papers. Mean turnover values in our study, using maximum biomass data, were estimated to be 0.81 y^{-1} for temperate forests at mean annual temperature (MAT) 7.9°C, and 1.25 y^{-1} for boreal forest at MAT 3.3°C. Gill and Jackson (2000), however, estimated turnover values of 0.59 y^{-1} at MAT 9.8°C for temperate forests and of 0.25 y^{-1} at MAT 0.6°C for boreal forests. Yuan and Chen (2010) found a similarly high turnover value for boreal forest (0.76 y^{-1}). In contrast to our study, other reviews on turnover have shown significant but weak relations between root turnover and MAT, e.g. Yuan and Chen (2010; r^2 = 0.25, p = 0.001) in boreal forests, Finer et al. (2011; r^2 = 0.15, p = 0.001) and Gill and Jackson (2000; r^2 = 0.07, p = 0.018) in a global datasets (see also Figure 5). Giving the low r^2 of these studies, one may assume other environmental factors than MAT that act as large-scale drivers of root turnover in forests.

Turnover values applied in biogeochemical models

One of the aims of the present study was to deliver suitable fine-root turnover data of European tree species, which may be used by modellers to construct ecosystem or biogeochemical models. Such models are applied in many European countries to report the change of belowground C in European forests as a reporting requirement for the Kyoto protocol signatories. A brief overview of the models applied so far shows that a wide variety of root turnover values are used, some resembling measured values, others less so. In one of the first applications, the fine-root turnover value was set to 1.0 y^{-1} for deciduous broad-leaf and deciduous needle-leaf trees and to 0.26 y^{-1} for evergreen needle-leaf trees (White et al. 2000, using the Biome-BGC model). The distinct difference between deciduous trees and evergreen needle-leaf trees mainly originated from the notion that fine-root turnover is equal to leaf turnover, with 1.0 y^{-1} for deciduous leaves and 0.26 y^{-1} for evergreen needles/leaves. These values are themselves derived from the mean age of foliage, which is one year for deciduous trees and about four years for evergreens. A compilation of the various turnover values applied in European modelling studies is shown in Table 6. Most recent studies applied a universal fine-root turnover value of 0.7 y^{-1} to all forest tree species (Hickler et al. 2008, using the LPJ-GUESS model). This assumption is based on Vogt et al. (1996) and on Li et al. (2003) (Thomas Hickler, personal communication). Li et al. (2003) found a linear relationship between fine root production and fine root biomass, with the turnover value 0.64 y^{-1} which was lower than the original estimate of 0.73 y^{-1} from a previous analysis (Kurz et al. 1996). Using 'universal' turnover values, however, should be discouraged if country-based C budgets have to be reported within the frame to the Kyoto protocol and species-specific and biome based values of root turnover are available.

Conclusions

The present synthesis in fine-root turnover of European tree species reveals that only *Fagus sylvatica* and *Picea abies* have sufficient data availability to suggest turnover values obtained by soil coring to be used by National C reporters (0.86 y^{-1} for *F. sylvatica,* 0.88 y^{-1} for *P. abies*, when maximum biomass data are used; 1.11 y^{-1} for both species, when mean biomass data are used*)*. Data sets of other European tree species or obtained by alternative methods such as ingrowth cores were too small to allow for distinct conclusions on the turnover values. Based on our calculations, we put forward that usage of mean rather than maximum root biomass in turnover calculations is preferable as it better reflects long-term quantity of biomass.

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References

Ahlström K, Persson H, Börjesson I (1988) Fertilization in a mature Scots pine (*Pinus sylvestris* L.) stand - effects on fine roots. Plant Soil 106:179-190.

Bakker MR (1999) The effect of lime and gypsum applications on a sessile oak (*Quercus petraea* (M.) Liebl.) stand at La Croix Scaille (French Ardennes) II. Fine root dynamics. Plant Soil 206:109-121

Børja I, De Wit HA, Steffenrem A, Majdi H (2008) Stand age and fine root biomass, distribution and morphology in a Norway spruce chronosequence in southeast Norway. Tree Physiol 28:773-784

Brunner I, Godbold DL (2007) Tree roots in a changing world. J For Res 12:78-82

Brunner I, Graf Pannatier E, Frey B, Rigling A, Landolt W, Zimmermann S, Dobbertin M (2009) Morphological and physiological responses of Scots pine fine roots to water supply in a dry climatic region in Switzerland. Tree Physiol 29:541-550

Chertov OG, Komarov AS, Nadporozhskaya M, Bykhovets SS, Zudin SL (2001) ROMUL - a model of forest soil organic matter dynamics as a substantial tool for forest ecosystem modeling. Ecol Model 138:289-308

Cienciala E, Tatarinov FA (2006) Application of BIOME-BGC model to managed forests. 2. Comparison with long-term observations of stand production for major tree species. For Ecol Manag 237:252-266

Dannoura M, Kominami Y, Oguma H, Kanazawa Y (2008) The development of an optical scanner method for observation of plant root dynamics. Plant Root 2:14-18

Eldhuset TD, Lange H, de Wit HA (2006) Fine root biomass, necromass and chemistry during seven years of elevated aluminium concentrations in the soil solution of a middle-aged *Picea abies* stand. Sci Total Environ 369:344-356

Endrulat T, Saurer M, Buchmann N, Brunner I (2010) Incorporation and remobilization of ^{13}C within the fine-root systems of individual *Abies alba* trees in a temperate coniferous stand. Tree Physiol 30:1515-1527

Fairley RI, Alexander IJ (1985) Methods of calculating fine root production in forests. In: Fitter AH, Atkinson D, Read DJ. (eds) Ecological interactions in soil: plants, microbes and animals. Blackwell. Oxford, pp 37-42

Finer L, Ohashi M, Noguchi K, Hirano Y (2011) Fine root production and turnover in forest ecosystems in relation to stand and environmental characteristics. For Ecol Manag 262:2008-2023

Fritz HW (1999) Feinwurzel-Verteilung, -Vitalität, -Produktion und -Umsatz von Fichten (*Picea abies* (L.) Karst.) auf unterschiedlich versauerten Standorten. Ber Forsch Zent Waldökosyst, Reihe A, 165:1-138

Gaudinski JB, Tom MS, Riley WJ, Dawson TE, Joslin JD, Majdi H (2010) Measuring and modeling the spectrum of fine-root turnover times in three forests using isotopes, minirhizotrons, and the Radix model. Glob Biogeochem Cycles 24:GB3029

Gaudinski JB, Trumbore SE, Davidson EA, Cook AC, Makrewitz D, Richter DD (2001) The age of fine-root carbon in three forests of the eastern United States measured by radiocarbon. Oecologia 129:420-429

Genenger M, Zimmermann S, Hallenbarter D, Landolt W, Frossard E, Brunner I (2003) Fine root growth and element concentrations of Norway spruce as affected by wood ash and liquid fertilisation. Plant Soil 255:253-264

Gill RA, Jackson R (2000) Global patterns of root turnover for terrestrial ecosystems. New Phytol 147:13-31

Hendricks JJ, Hendrick RL, Wilson CA, Mitchell RJ, Pecot SD, Guo D (2006) Assessing the patterns and controls of fine root dynamics: an empirical test and methodological review. J Ecol 94:40-57

Hertel D (1999) Das Feinwurzelsystem von Rein- und Mischbeständen der Rotbuche: Struktur, Dynamik und interspezifische Konkurrenz. Diss Bot 317:1-185

Hickler T, Smith B, Prentice C, Mjöfors K, Miller P, Arnetz A, Sykes MT (2008) CO_2 fertilization in temperate FACE experiments not representative of boreal and tropical forests. Glob Change Biol 14:1531-1542

Hickler T, Prentice IC, Smith B, Sykes MT, Zaehle S (2006) Implementing plant hydraulic architecture within the LPJ dynamic global vegetation model. Glob Ecol Biogeogr 15:567-577

Hickler T, Smith B, Sykes MT, Davis M, Sugita S,Walker K (2004) Using a generalized vegetation model to simulate vegetation dynamics in northeastern USA. Ecology 85:519-530

Hirano Y, Noguchi K, Ohashi M, Hishi T, Makita N, Fujii S, Finér L (2009) A new method for placing and lifting root meshes for estimating fine root production in forest ecosystems. Plant Root 3:26-31

Johnson MG, Tingey DT, Phillips DL, Storm MJ (2001) Advancing fine root research with minirhizotrons. Environ Exp Bot 45:263-289

Jourdan C, Silva EV, Goncalves JLM, Ranger J, Moreira RM, Laclau JP (2008) Fine root production and turnover in Brazilian *Eucalyptus* plantations under contrasting nitrogen fertilization regimes. For Ecol Manag 256:396-404

Konôpka B, Yuste JC, Janssens IA, Ceulemans R (2005) Comparison of fine root dynamics in Scots pine and Pedunculate oak in sandy soil. Plant Soil 276:33-45

Konôpka B (2009) Differences in fine root traits between Norway spruce (*Picea abies* (L.) Karst.) and European beech (*Fagus sylvatica* L.) - A case study in the Kysucké Beskydy Mts. J For Sci 55:556-566

Kurz WA, Kimmins JP (1987) Analysis of some sources of error in methods used to determine fine root production in forest ecosystems: a simulation approach. Can J For Res 17:909-912

Li Z, Kurz WA, Apps MJ, Beukema SJ (2003) Belowground biomass dynamics in the carbon budget model of the Canadian forest sector: recent improvements and implications for the estimation of NPP and NEP. Can J For Res 33:106-126

López B, Sabaté S, Gracia CA (2001) Annual and seasonal changes in fine root biomass of a *Quercus ilex* L. forest. Plant Soil 230:125-13

Lukac M, Godbold DL (2010) Fine root biomass and turnover in southern taiga estimated by root inclusion nets. Plant Soil 331:505-513

Lukac M, Calfapietra C, Godbold DL (2003) Production, turnover and mycorrhizal colonization of root systems of three *Populus* species grown under elevated CO_2 (POPFACE). Glob Change Biol 9:838-848

Majdi H, Andersson P (2005) Fine root production and turnover in a Norway spruce stand in northern Sweden: effects of nitrogen and water manipulation. Ecosystems 8:191-199

Majdi H, Pregitzer K, Morén AS, Nylund JE, Ågren GI (2005) Measuring fine root turnover in forest ecosystems. Plant Soil 276:1-8

Makkonen K, Helmisaari HS (1999) Assessing fine-root biomass and production in a Scots pine stand - comparison of soil core and root ingrowth core methods. Plant Soil 210:43-50

Makkonen K, Helmisaari HS (2001) Fine root biomass and production in Scots pine stands in relation to stand age. Tree Physiol 21:193-198

Matamala R, Gonzalez-Meler MA, Jastrow JD, Norby RJ, Schlesinger WH (2003) Impacts of fine root turnover on forest NPP and soil C sequestration potential. Science 302:1385-1387

McClaugherty CA, Aber JD, Melillo JM (1982) The role of fine roots in the organic-matter and nitrogen budgets of two forested ecosystems. Ecology 63:1481-1490

Miguel Pérez C (2010) Respuestas ecofisiologicas y estructurales a la recurrencia, duracion e intensidad de la sequia en plantaciones y bosques mixtos de *Quercus ilex, Quercus pubescens* y *Quercus cerrioides*. Dissertation, Institut de Recerca i Tecnologia Agroalimentaries IRTA, Universitat Autonoma de Barcelona UAB

Osawa A, Aizawa R (2012) A new approach to estimate fine root production, mortality, and decomposition using litter bag experiments and soil core techniques. Plant Soil (in press). DOI: 10.1007/s11104-011-1096-6

Ostonen I, Lohmus K, Pajuste K (2005) Fine root biomass, production and its proportion of NPP in a fertile middle-aged Norway spruce forest: Comparison of soil core and ingrowth core methods. For Ecol Manag 21:264-277

Persson H (1980a) Fine-root production, mortality and decomposition in forest ecosystems. Vegetatio 41:101-109

Persson H (1980b) Fine-root dynamics in a Scots pine stand, with and without near optimum nutrient and water regimes. Acta Phytogeogr Suec 68:101-110.

Persson H, Ahlström K (1994) The effects of alkalizing compounds on fine-root growth in a Norway spruce stand in southwest Sweden. J Environ Sci Health A 29:803-820

Persson HÅ, Stadenberg I (2010) Fine-root dynamics in a Norway spruce forest (*Picea abies* (L.) Karst) in Eastern Sweden. Plant Soil 330:329-344

Pietsch SA, Hasenauer H, Thornton PE (2005) BGC-model parameters for tree species growing in central European forests. For Ecol Manag 211:264-295

Publicover DA, Vogt KA (1993) A comparison of methods for estimating forest fine root production with respect to sources of error. Can J For Res 23:1179-1186

Richter A (2007) Fine root growth and vitality of European beech in acid forest soils with a low base saturation. Dissertation, ETH Zürich

Sah SP, Jungner H, Oinonen M, Kukkola M, Helmisaari H-S (2011) Does the age of fine root carbon indicate the age of fine roots in boreal forests? Biogeochemistry 104:91-102.

Santantonio D, Grace JC (1987) Estimating fine-root production and turnover from biomass and decomposition data: a compartment-flow model. Can J For Res 17:900-908.

Silver WL, Thompson AW, McGroddy ME, Varner RK, Dias JD, Silva H, Crill PM, Keller M (2005) Fine root dynamics and trace gas fluxes in two lowland tropical forest soils. Glob Change Biol 11:290-306

Sitch S, Smith B, Prentice IC, Arneth A, Bondeau A, Cramer W, Kaplan J, Levis S, Lucht W, Sykes M, Thonicke K, Venevsky S (2003) Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ Dynamic Global Vegetation Model. Glob Change Biol 9:161-185

Smith B, Prentice IC, Sykes MT (2001) Representation of vegetation dynamics in the modelling of terrestrial ecosystems: comparing two contrasting approaches within European climate space. Glob Ecol Biogeogr 10:621-637

Stober C, George E, Persson H (2000) Root growth and response to nitrogen. In: Schulze ED (ed) Carbon and nitrogen cycling in European forest ecosystems. Springer, Berlin, pp 99-121

Strand AE, Pritchard SG, McCormack ML, Davis MA, Oren R (2008) Irreconcilable differences: fine-root life spans and soil carbon persistence. Science 319:456-458

Tatarinov FA, Cienciala E (2006) Application of BIOME-BGC model to managed forests 1. Sensitivity analysis. For Ecol Manag 237:267-279

Tierney G, Fahey T (2002) Fine root turnover in a northern hardwood forest: a direct comparison of the radiocarbon and minirhizotron methods. Can J For Res 32:1692-1697

Trumbore SE, Gaudinski JB (2003) The secret lives of roots. Science 302:1344-1345

Vogt KA, Vogt DJ, Palmiotto PA, Boon P, O'Hara J, Asbjornson H (1996) Review of root dynamics in forest ecosystems grouped by climate, climatic forest type and species. Plant Soil 187:159-219

Vogt KA, Persson H (1991) Measuring growth and development of roots. In: Lassoie JP, Hinkley TM (eds) Techniques and approaches in forest tree ecophysiology. CRC Press, Boca Raton, pp 477-501

Vogt KA, Vogt DJ, Bloomfield J (1998) Analysis of some direct and indirect methods for estimating root biomass and production of forest at ecosystem level. Plant Soil 200:71-89

White MA, Thornton PE, Running SW, Nemai RR (2000) Parametrization and sensitivity analysis of the BIOME-BGC terrestrial ecosystem Model: Net primary production controls. Earth Interact 4:1-85

Wu K (2000) Fine root production and turnover and its contribution to nutrient cycling in two beech (*Fagus sylvatica* L.) forest ecosystems. Ber Forsch Zent Waldökosyst, Reihe A, 170:1-130

Yuan ZH, Chen HYH (2010) Fine root biomass, production, turnover rates, and nutrient contents in boreal forest ecosystems in relation to species, climate, fertility, and stand age: Literature review and meta-analyses. Crit Rev Plant Sci 29:204-221

Table 1 Decision Matrix according to Fairley and Alexander (1985)

	Biomass increase	Biomass decrease
Necromass increase	$P = \Delta B+\Delta N$	$P = \Delta B+\Delta N$[1] or $P = 0$[2]
Necromass decrease	$P = \Delta B$	$P = 0$

[1] if $|\Delta B| < |\Delta N|$

[2] if $|\Delta B| > |\Delta N|$

Table 2 Worked sample with a data set from sequential coring (data from Ostonen et al. 2005). Formulas are according to the Material and Methods section

a) Calculation of the production P using the Decision Matrix

Sampling date	Biomass ($g\ m^{-2}$)	Necromass ($g\ m^{-2}$)	Formula	Calculation	Production P ($g\ m^{-2}\ t^{-1}$)
June 1996	127	130			
July 1996	161	178	[3]	(161-127)+(178-130)	82
Aug. 1996	166	114	[4]	166-161	5
Sept. 1996	165	174	[3]	(165-166)+(174-114)	59
Oct. 1996	199	198	[3]	(199-165)+(198-174)	58
Nov. 1996	64	159	[5]	0	0
June 1997	110	125	[4]	110-64	46
Mean [7]:	141			Sum [2]:	250

b) Calculation of the annual production P_a

Method	Formula	Calculation	Annual production P_a ($g\ m^{-2}\ y^{-1}$)
Decision Matrix	[2]	82+5+59+58+0+46	250
Maximum-Minimum	[1]	199-64	135

c) Calculation of the turnover T (using mean biomass B_{mean} or maximum biomass B_{max})

Method	Formula	Calculation		Turnover T
		Using B_{mean}	Using B_{max}	(y^{-1})
Decision Matrix	[6]	250 / 141	-	1.77
Decision Matrix	[8]	-	250 / 199	1.26
Maximum-Minimum	[6]	135 / 141	-	0.95
Maximum-Minimum	[8]	-	135 / 199	0.68

Table 3 Sequential coring: Mean and maximum biomass, annual production, and turnover of tree fine roots recorded with sequential coring. The annual production is calculated with the 'Decision Matrix' or the 'Maximum-Minimum' formula, and the turnover is calculated by dividing the annual production by the mean biomass (B_{mean}) or by the maximum biomass (B_{max}). (a = adult trees)

Country	Mean	Soil	Depth	Diam.	Age	Biomass (B)		Decision Matrix			Maximum-Minimum			References
-Site	annual	layers				Mean	Max.	Production	Turnover		Production	Turnover		
	temp.								B_{mean}	B_{max}		B_{mean}	B_{max}	
	(°C)		(cm)	(mm)	(y)	($g\ m^{-2}$)	($g\ m^{-2}$)	($g\ m^{-2}\ y^{-1}$)	(y^{-1})	(y^{-1})	($g\ m^{-2}\ y^{-1}$)	(y^{-1})	(y^{-1})	
Eucalyptus grandis:														
Brasil	19.0		0-30	<2	8	89	120	153	1.71	1.28	48	0.54	0.40	Jourdan et al. (2008)
Fagus sylvatica:														
CH-Entl.	6.7	A,B	0-25	<2	a	422	580	395	0.94	0.68	290	0.69	0.50	Richter (2007)
CH-Krau.	8.2	A,B	0-25	<2	a	480	710	476	0.99	0.67	356	0.74	0.50	Richter (2007)
CH-Nied.	8.7	A,B	0-25	<2	a	413	501	281	0.68	0.56	217	0.53	0.43	Richter (2007)
CH-Walt.	7.4	A,B	0-25	<2	a	348	441	193	0.55	0.44	171	0.49	0.39	Richter (2007)
CH-Vord.	8.8	A,B	0-25	<2	a	807	957	597	0.74	0.62	356	0.44	0.37	Richter (2007)
CH-Zofi.	8.2	A,B	0-25	<2	a	517	600	144	0.28	0.24	142	0.27	0.24	Richter (2007)
DE-Gött.	8.7	A	0-15	<2	a	177	219	41	0.23	0.19	75	0.42	0.34	Hertel (1999)
DE-Lüne.	8.1	O,A	0-5	<2	a	279	312	458	1.64	1.47	97	0.35	0.31	Hertel (1999)
DE-Soll.	6.9	O,A	0-5	<2	a	134	149	226	1.68	1.51	45	0.33	0.30	Hertel (1999)
DE-Zieg.	8.6	O,A	0-10	<2	a	70	100	203	2.92	2.04	46	0.66	0.46	Hertel (1999)
DE-Gött.	7.0	A,B	0-20	<2	a	195	282	218	1.12	0.77	157	0.81	0.56	Wu (2000)
DE-Soll.	6.4	O,A,B	0-40	<2	a	328	373	211	0.64	0.57	85	0.26	0.23	Wu (2000)
FR-Aubu.	6.0	O,A,B	0-30	<1	a	83	120	165	2.00	1.38	77	0.93	0.64	Stober et al. (2000)

Table 3 (continued)

Picea abies:														
DE-Ficht.	5.3	O,A,B	0-60	<2	a	175	224	304	1.74	1.36	104	0.60	0.47	Gaul et al. (2009)
DE-Barb.	8.0	O,A	0-40	<2	a	182	235	116	0.63	0.49	124	0.68	0.53	Fritz (1999)
DE-Eber.	7.8	A,M	0-40	<2	a	150	188	83	0.56	0.44	90	0.60	0.48	Fritz (1999)
DE-Fich.	5.5	O,A,B	0-40	<2	a	245	340	156	0.64	0.46	160	0.65	0.47	Fritz (1999)
DE-Harz	6.0	O,A,B	0-40	<2	a	204	241	278	1.36	1.15	63	0.31	0.26	Fritz (1999)
EE-Roel.	5.4		0-40	<2	a	142	199	251	1.77	1.26	135	0.95	0.68	Ostonen et al. (2005)
FR-Aubu.	6.0	O,A,B	0-30	<1	a	57	70	89	1.56	1.27	30	0.52	0.43	Stober et al. (2000)
NO-Nordm.	3.8		0-40	<2	50	462	603	298	0.65	0.49	282	0.61	0.47	Eldhuset et al. (2006)
NO-Nordm.	3.8		0-60	<2	60	56	62	63	1.13	1.02	17	0.31	0.27	Børja et al. (2008)
NO-Nordm.	3.8		0-60	<2	120	50	63	70	1.40	1.11	22	0.48	0.35	Børja et al. (2008)
SE-Forsm.	5.5		0-40	<2	a	304	410	241	0.79	0.59	186	0.61	0.45	Persson and Stadenb. (2010)
Pinus sylvestris:														
FI-Ilom.	1.9	O,E,B	0-30	<2	a	278	363	862	3.10	2.37	181	0.65	0.50	Makkonen and Helm. (1999)
SE-Ivan	5.2	F,H	-	<2	a	120	153	242	2.03	1.58	69	0.58	0.45	Persson (1980a)
Populus spp.:														
IT-P. alba	14.4			<2	2	110	143	55	0.50	0.39	56	0.51	0.40	Lukac et al. (2003)
IT-P. nigra	14.4			<2	2	109	158	84	0.77	0.53	84	0.77	0.53	Lukac et al. (2003)
IT-P. eura.	14.4			<2	2	146	187	55	0.37	0.29	89	0.61	0.48	Lukac et al. (2003)
Quercus ilex / Q. cerrioides:														
ES-Bages	14.4		0-50	<5	10	858	1336	-	-	-	812	0.95	0.61	Miguel Pérez (2010)
Quercus petraea:														
FR-La Croix	8.0		0-55	<2	a	310	346	53	0.17	0.15	63	0.29	0.18	Bakker (1999)

Table 4 Ingrowth cores: Mean and maximum biomass, annual production, and turnover of tree fine roots recorded with ingrowth cores. The annual production is calculated with the 'Decision Matrix' or the 'Maximum-Minimum' formula, and the turnover is calculated by dividing the annual production by the mean biomass (B_{mean}) or by the maximum biomass (B_{max})(a=adult)

Country	Mean	Depth	Year	Diam.	Age	Biomass (B)		Decision Matrix			Maximum-Minimum			References
-Site	annual temp. (°C)	(cm)	after install. (y)	(mm)	(y)	Mean (g m^{-2})	Max. (g m^{-2})	Production (g m^{-2} y^{-1})	Turnover B_{mean} (y^{-1})	Turnover B_{max} (y^{-1})	Production (g m^{-2} y^{-1})	Turnover B_{mean} (y^{-1})	Turnover B_{max} (y^{-1})	
Fagus sylvatica:														
DE-Gött.	7.0	0-20	2	<2	a	42	107	107	2.58	1.00	107	2.58	1.00	Wu (2000)
DE-Soll.	6.4	0-20	2	<2	a	48	123	123	2.57	1.00	123	2.57	1.00	Wu (2000)
Picea abies:														
CH-Schl.	9.6	0-10	2	<2	a	80	106	65	0.81	0.62	65	0.81	0.62	Genenger et al. (2003)
EE-Roel.	5.4	0-30	2	<2	a	52	100	89	1.70	0.89	74	1.41	0.74	Ostonen et al. (2005)
EE-Roel.	5.4	0-30	3	<2	a	70	100	66	0.94	0.65	51	0.73	0.51	Ostonen et al. (2005)
Pinus sylvestris:														
CH-Pfyn.	9.2	0-10	2	<2	a	44	62	37	0.84	0.59	37	0.84	0.59	Brunner et al. (2009)
SE-Ivan.	5.2	-	2	<2	a	65	136	126	1.96	0.93	115	1.78	0.84	Persson (1980a)

Table 5 Summary of biomass, annual production, and turnover values (±SE) of fine roots of common European tree species. The annual production is calculated with the 'Decision Matrix' or the 'Maximum-Minimum' formula, and the turnover is calculated by dividing the annual production by the mean biomass (B_{mean}) or by the maximum biomass (B_{max})

	Biomass (B)		Decision Matrix			Maximum-Minimum		
	Mean	Maximum	Production	Turnover		Production	Turnover	
				B_{mean}	B_{max}		B_{mean}	B_{max}
	(g m^{-2})	(g m^{-2})	(g m^{-2} y^{-1})	(y^{-1})	(y^{-1})	(g m^{-2} y^{-1})	(y^{-1})	(y^{-1})
Sequential coring method								
Fagus sylvatica (n=13)								
	327	411	278	1.11	0.86	163	0.53	0.41
	(±57)	(±71)	(±44)	(±0.21)	(±0.16)	(±31)	(±0.06)	(±0.03)
Picea abies (n=11)								
	184	240	177	1.11	0.88	110	0.57	0.44
	(±37)	(±49)	(±30)	(±0.14)	(±0.11)	(±24)	(±0.05)	(±0.04)
Pinus sylvestris (n=2)								
	199	258	552	2.57	1.98	125	0.62	0.48
	(±80)	(±105)	(±310)	(±0.54)	(±0.40)	(±56)	(±0.04)	(±0.02)
Ingrowth cores method								
Fagus sylvatica (n=2)								
	45	115	115	2.58	1.00	115	2.58	1.00
	(±3)	(±8)	(±8)	(±0.01)	(±0.00)	(±8)	(±0.01)	(±0.00)
Picea abies (n=3)								
	67	102	73	1.15	0.72	63	0.98	0.62
	(±8)	(±2)	(±8)	(±0.28)	(±0.09)	(±7)	(±0.21)	(±0.07)
Pinus sylvestris (n=2)								
	55	99	82	1.40	0.76	76	1.31	0.72
	(±11)	(±37)	(±45)	(±0.56)	(±0.17)	(±39)	(±0.47)	(±0.12)

Table 6 Fine-root turnover values of European trees used in biogeochemical models

Tree type	Tree species	Turnover (y^{-1})	Model	Reference
Broad- / Deciduous needle-leaved		1.0	Biome-BGC	White et al. (2000)
Broad-leaved summergreen		1.0	LPJ-GUESS	Smith et al. (2001)
Broad-leaved		1.0	LPJ-GUESS	Hickler et al. (2004)
Broad-leaved		0.7	LPJ-GUESS	Hickler et al. (2006, 2008)
	Fagus sylvatica	1.023	Biome-BGC	Ciencela and Tatarinov (2006)[1]
	Fagus sylvatica	1.0	Biome-BGC	Pietsch et al. (2005)
	Quercus robur	1.023	Biome-BGC	Ciencela and Tatarinov (2006)[1]
	Quercus robur	1.0	Biome-BGC	Pietsch et al. (2005)
	Quercus petraea	1.023	Biome-BGC	Ciencela and Tatarinov (2006)[1]
	Quercus petraea	1.0	Biome-BGC	Pietsch et al. (2005)
	Larix decidua	1.0	Biome-BGC	Pietsch et al. (2005)
Evergreen needle-leaved		0.26	Biome-BGC	White et al. (2000)
Needle- / Broad-leaved evergreen		0.5	LPJ-GUESS	Smith et al. (2001)
Needle-leaved		0.5	LPJ-GUESS	Hickler et al. (2004)
Needle-leaved		0.7	LPJ-GUESS	Hickler et al. (2006, 2008)
	Picea abies	0.811	Biome-BGC	Ciencela and Tatarinov (2006)[1]
	Picea abies	0.195	Biome-BGC	Pietsch et al. (2005)
	Pinus sylvestris	0.18	Biome-BGC	Pietsch et al. (2005)
	Pinus cembra	0.18	Biome-BGC	Pietsch et al. (2005)

[1] and Tatarinov and Ciencela (2006)

Figure Captions

Fig 1 Simplified scheme of the relevant processes and terms of the belowground C turnover in forest soils (modified according to Santantonio and Grace 1987 and Chertov et al. 2001, and excluding mycorrhiza)

Fig 2 Relationship between turnover values using mean biomass (B_{mean}) or maximum biomass data (B_{max}). Turnover values were calculated from the whole data set of sequential coring and using the Decision Matrix and the Maximum-Minimum method

Fig 3 Relationship between turnover values calculated per whole soils profiles or per individual soil layers (summed *versus* individual layers). Turnover values were calculated the whole data set of sequential coring and using the Decision Matrix method and maximum biomass data (data from Hertel 1999; Richter 2007; Makkonen and Helmisaari 1999; Bakker 1999; Ostonen et al. 2005; Jourdan et al. 2008). Mean soil depth is 44 cm, and the average number of individual soil layers is 4

Fig 4 Mean turnover values calculated from the whole data set of sequential coring and using the Decision Matrix or the Maximum-Minimum method using mean biomass B_{mean} (□) or maximum biomass data B_{max} (■).

Fig 5 Relationship between turnover and mean annual temperature, and divided into the three vegetation zones boreal/alpine (∆), temperate (●), and tropical (◊). a) Data from a global study (redrawn from Appendix 1 of Gill and Jackson 2000). b) Present study (turnover values were calculated from the whole data of sequential coring and using the Decision Matrix method and maximum biomass data)

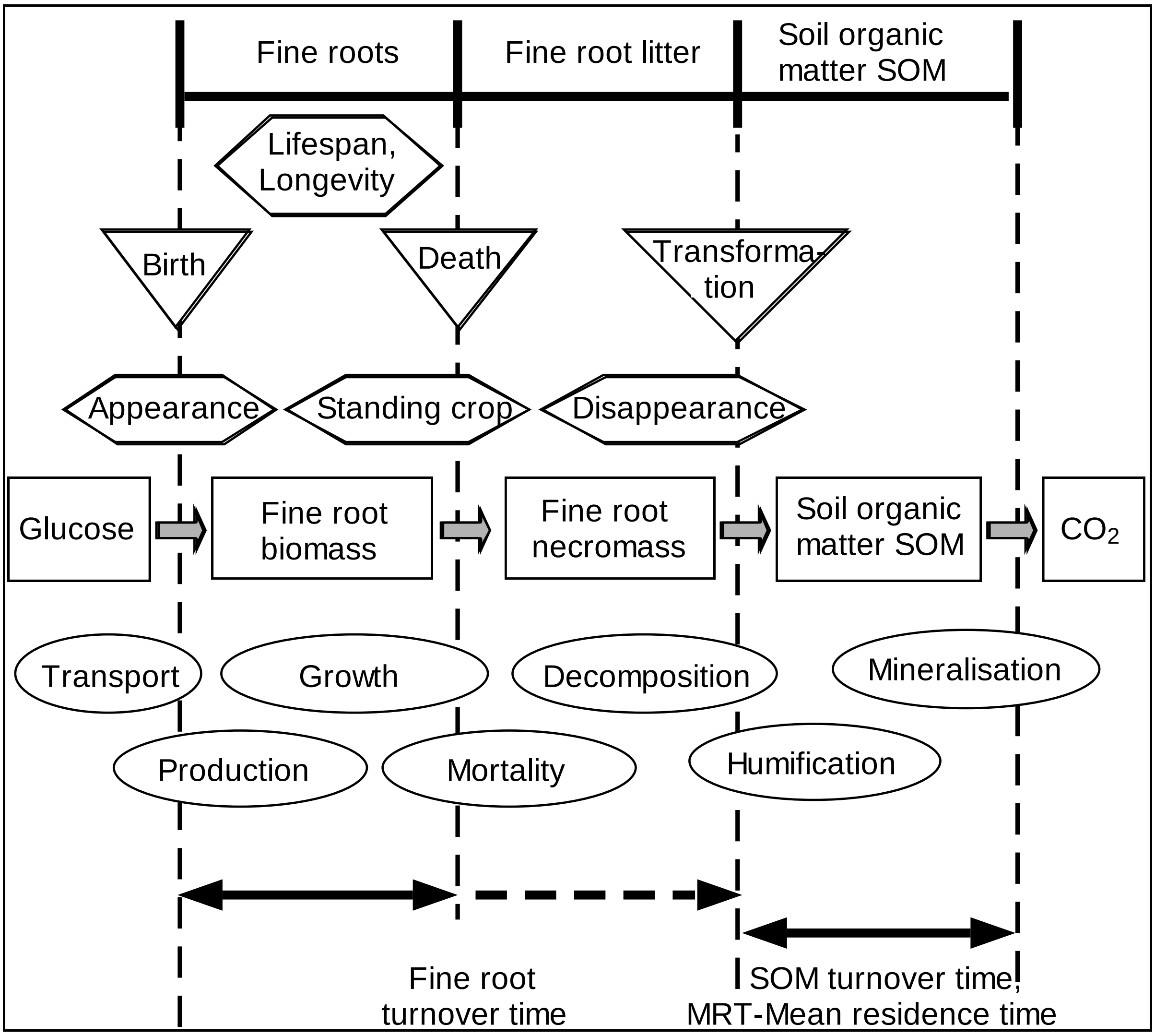
Fine roots
Fine root litter
Soil organic matter SOM
Lifespan, Longevity
Birth
Death
Transforma-tion
Appearance
Standing crop
Disappearance
Glucose
Fine root biomass
Fine root necromass
Soil organic matter SOM
CO2
Transport
Growth
Decomposition
Mineralisation
Production
Mortality
Humification
Fine root turnover time
SOM turnover time, MRT-Mean residence time

Figure 1.

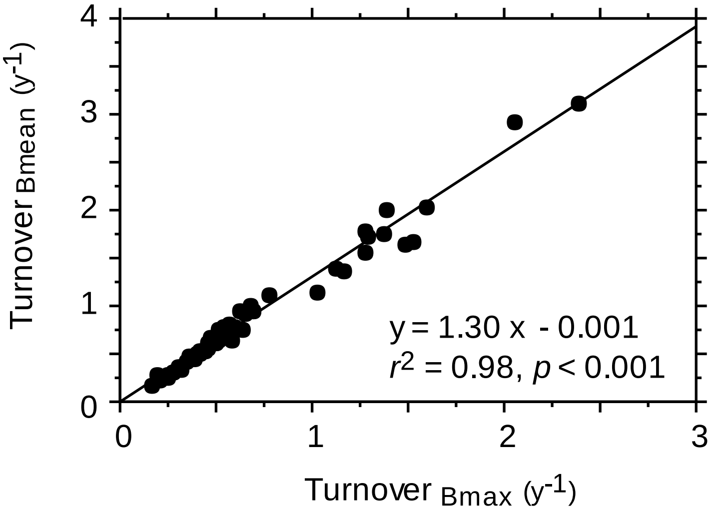
0
1
2
3
4
0
1
2
3
Turnover Bmean (y-1)
Turnover Bmax (y-1)
y = 1.30 x - 0.001
r2 = 0.98, p < 0.001

Figure 2.

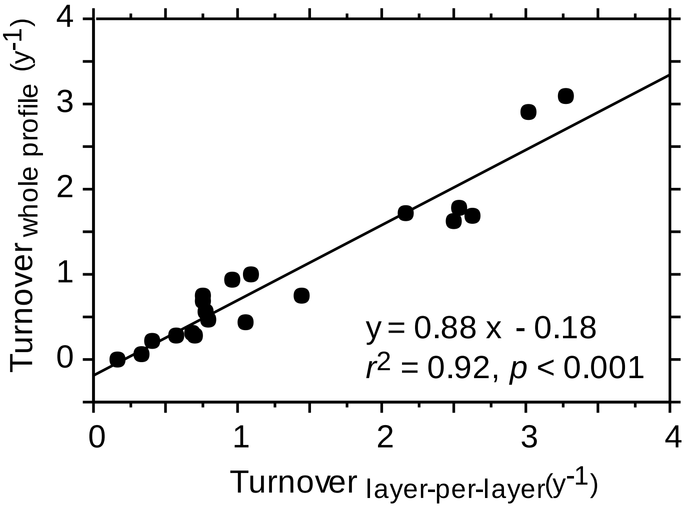
Turnover whole profile (y-1)
Turnover layer-per-layer (y-1)
0
1
2
3
4
0
1
2
3
4
y = 0.88 x - 0.18
r2 = 0.92, p < 0.001

Figure 3.

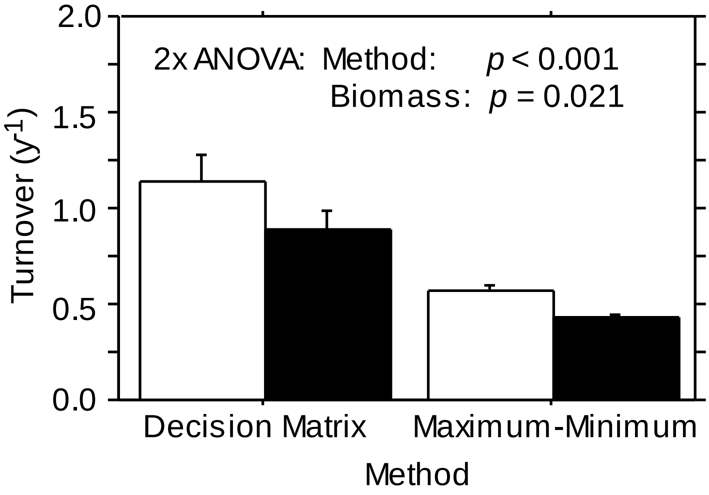
2x ANOVA: Method: p < 0.001
Biomass: p = 0.021
Turnover (y-1)
2.0
1.5
1.0
0.5
0.0
Decision Matrix
Maximum-Minimum
Method

Figure 4.

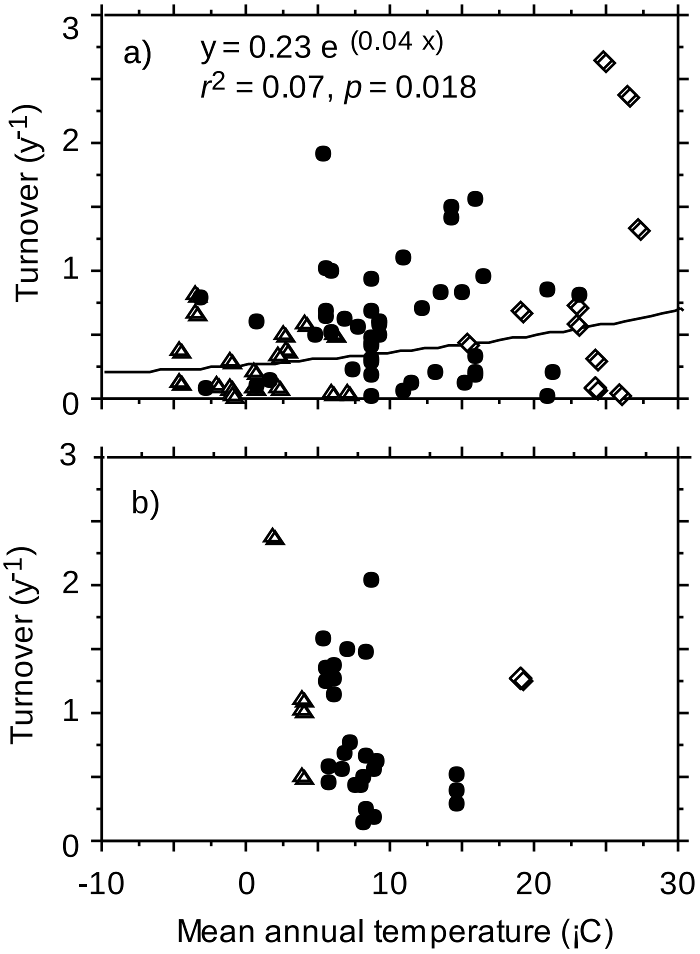
a)
y = 0.23 e (0.04 x)
r2 = 0.07, p = 0.018
b)
Turnover (y-1)
Turnover (y-1)
0
1
2
3
-10
0
10
20
30
Mean annual temperature (¡C)

Figure 5.