

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

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Accepted Version

Brunner, I., Bakker, M.R., Bjork, R.G., Hirano, Y., Lukac, M., Aranda, X., Borja, I., Eldhuset, T.D., Helmisaari, H.S., Jourdan, C., Konopka, B., Miguel Perez, C., Persson, H. and Ostonen, I. (2012) Fine-root turnover rates of European forests revisited: an analysis of data from sequential coring and ingrowth cores. *Plant and Soil*, 362 (1-2). pp. 357-372. ISSN 0032-079X doi: <https://doi.org/10.1007/s11104-012-1313-5> Available at <http://centaur.reading.ac.uk/29391/>

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To link to this article DOI: <http://dx.doi.org/10.1007/s11104-012-1313-5>

Publisher: Springer

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

3

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33

34 **Abstract**

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

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

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

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

51

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

54

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

60

61

62 Introduction

63 Tree fine roots, generally defined as those with a diameter of less than 2 mm, together with
64 mycorrhizas, perform the task of water and nutrient uptake from the soil. Due to the nature of
65 their function, fine roots tend to have limited lifespan and thus constitute a significant input of
66 carbon (C) into the soil profile. Given the estimated size of the C flux associated with fine root
67 turnover, thought to reach 0.5 to 3 t C ha⁻¹ y⁻¹ (Gill and Jackson 2000; Brunner and Godbold
68 2007), we clearly need accurate estimates of the rate at which fine roots die and contribute to
69 soil C pools. The amount of C annually cycled through fine roots is dependent on the standing
70 stock and on the lifespan (synonyms: 'longevity' or 'turnover time', inverse of 'turnover' or
71 'turnover rate') of fine roots (see Fig. 1).

72 The uncertainty of currently available fine root turnover values can best be illustrated by
73 the ongoing debate about how the turnover of the fine roots can be estimated and which
74 method is the most suitable (e.g. Strand et al. 2008; Trumbore and Gaudinski 2003; Majdi et al.
75 2005). Starting from the most recent developments, stable and labile C-isotopes (¹³C, ¹⁴C) may
76 be used to estimate root carbon longevity, either by using labelling techniques or natural
77 abundances in the atmosphere (e.g. Matamala et al. 2003; Gaudinski et al. 2001, 2010;
78 Endrulat et al. 2010). A more widely used method to estimate the lifespan of fine roots is the
79 use of minirhizotrons (e.g. Johnson et al. 2001; Majdi and Andersson 2005). This technique
80 allows for a direct observation of individual roots and their development. Both methods suffer
81 from several drawbacks, the main weakness of isotopic analysis for root age determination is
82 the uncertain age of organic compounds used to construct fine roots (Sah et al. 2011).
83 Meanwhile, minirhizotron studies are not able to determine the exact time of root death. In
84 addition, the installation of the minirhizotron tubes can change water and temperature regimes
85 as well as soil matrix resistance to root penetration. Moreover, fine root growth is often
86 stimulated by the conditions along the minirhizotron tube. Unsurprisingly, direct comparisons of
87 these two methods result in a discrepancy in root longevity estimates (Tierney and Fahey 2002;
88 Strand et al. 2008; Gaul et al. 2009), sometimes explained by different fractions of fine roots
89 under observation, i.e. the short-lived and the long-lived fine roots, likely to be recorded by
90 these two methods (Gaudinski et al. 2010).

91 Alternatively, instead of direct observations of individual root longevity, the mean lifespan
92 can be calculated by dividing the 'pool' (standing crop or biomass) by its 'input' (annual
93 production). Because the turnover is the inverse of lifespan, it can be calculated by dividing the
94 'annual production' by the 'belowground standing crop' (Gill and Jackson 2000). There are
95 several methods used to obtain estimates of annual fine root production. A widely used method
96 to directly measure the production of fine roots is the use of ingrowth cores (e.g. Persson 1980;
97 Vogt and Persson 1991). This method measures the amount of fine roots which grow into a
98 defined volume of root-free soil over a defined period of time. The advantage of this method is
99 its relative ease and speed of application when estimating root production (Vogt and Persson
100 1991). More recently, root nets were applied instead of ingrowth cores to minimise soil
101 disturbance during the installation (Hirano et al. 2009; Lukac and Godbold 2010). An alternative
102 method to indirectly measure the production of fine roots is the sequential coring technique.
103 Here, several series of soil cores are sampled at discrete intervals over a period of at least one
104 year. Fine roots are extracted from the soil cores and the differences of the dry mass of living
105 (biomass) and dead (necromass) fine roots between two time points recorded. Taking
106 advantage of data generated by sequential coring, several methods exist to calculate the
107 production from the change of the fine-root biomass and necromass data. The production can
108 be calculated by the 'Maximum-Minimum' formula (McClagherty et al. 1982), by the 'Decision
109 Matrix' formula (Fairley and Alexander 1985), or by the 'Compartment Flow' formula
110 (Santantonio and Grace 1987). Whereas the 'Maximum-Minimum' formula uses only biomass
111 data, the other two methods require both biomass and necromass data. The 'Compartment
112 Flow' formula further requires decomposition data of fine root litter (e.g. Silver et al. 2005).
113 Thus, the values of fine root turnover can vary not only due to measurement methods but also
114 due to calculation methods applied (e.g. Vogt et al. 1998; Strand et al. 2008). A true comparison
115 of the various turnover values may only be possible by using observations from identical sites
116 where various methods were applied (e.g. Haynes and Gower 1995; Hendricks et al. 2006). As
117 for the popularity of different measurement methods, many more estimates of root turnover are
118 available from sequential coring and ingrowth cores than from the minirhizotron method (Finer
119 et al. 2011).

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

131

132 **Materials and Methods**

133

134 Data origin

135

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

147

148 Calculations of fine-root production

149

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

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

160

$$161 \quad P_{a(MM)} = B_{max} - B_{min} \quad [1]$$

162

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

166

$$167 \quad P_{a(DM)} = \sum P \quad [2]$$

168

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

173

$$174 \quad P = \Delta B + \Delta N \quad \text{a) if biomass and necromass have increased} \quad [3]$$

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

$$176 \quad |\Delta N|$$

$$177 \quad P = \Delta B \quad \text{if biomass has increased and necromass has decreased} \quad [4]$$

178 $P = 0$ a) if biomass and necromass have decreased [5]
 179 b) if biomass has decreased and necromass has increased, but $|\Delta B|$ higher than
 180 $|\Delta N|$

181

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

192

193 Calculations of fine-root turnover

194

195 The turnover $T_{B_{max}}$ of fine roots was calculated by dividing the annual fine root production (P_a)
 196 by the highest standing crop value (maximum biomass B_{max}) according to Gill and Jackson
 197 (2000):

198

$$199 \quad T_{B_{max}} = P_a / B_{max} \quad [6]$$

200

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

204

$$205 \quad B_{mean} = \sum B / n \quad (n = \text{number of samples per year}) \quad [7]$$

206

207 $T_{\text{Bmean}} = P_a / B_{\text{mean}}$ [8]

208

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

213

214 Data restrictions and limitations

215

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

221 This synthesis of fine-root turnover did not allow for detecting any effect of soil depth on
222 the turnover values, mainly due to the lack of a balanced dataset (using the data of Hertel 1999;
223 Richter 2007; Makkonen and Helmisaari 1999; Bakker 1999; Jourdan et al. 2008). Further, our
224 study did not allow for a sound comparison of the effect of the length of the observation period
225 (1, 2, or 3 years) or of the season when measurements commenced, nor were we able to
226 elucidate any influence of root diameter. Our data suggested decreasing turnover for increasing
227 root diameter, but the number of studies (2) and number of different stands (6) was very limited.
228 It would seem that turnover for the finest fraction (i.e. < 1 mm roots *versus* 1-2 mm roots) is
229 slightly higher (using the data of Hertel 1999 and Børja et al. 2008). Differences between
230 species (and/or experimental conditions) strongly affected the result (using the data of Fritz
231 1999; Bakker 1999; Lukac et al. 2003; Makkonen and Helmisaari 2001).

232

233 Statistics

234

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

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

238

239 **Results**

240

241 Data sets

242

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

248

249 Fine-root turnover

250

251 Turnover values obtained by the combination of sequential coring, Decision Matrix method, and
252 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}
253 for *P. abies* (Table 3), with mean values for *F. sylvatica* and *P. abies* of 0.86 and 0.88 y^{-1} ,
254 respectively (Table 5). Using the mean biomass instead of the maximum biomass, the turnover
255 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
256 3), with mean values of 1.11 y^{-1} for both *F. sylvatica* and *P. abies* (Table 5). For other tree
257 species, less than three data sets were available, e.g. only 2 data sets were available for *P.*
258 *sylvestris*, and both had turnover values higher than 1.5 y^{-1} (Table 3).

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

264 0.95 y^{-1} for *F. sylvatica* and *P. abies* (Table 3), with mean turnover values of 0.53 y^{-1} for *F.*
265 *sylvatica* and 0.57 y^{-1} for *P. abies* (Table 5).

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

274 We compared the difference in turnover rate estimates based on maximum or mean
275 standing biomass as the denominator. On average in our dataset, using mean standing
276 biomass rather than maximum resulted in about 30% higher estimate of root turnover T ($T_{B_{mean}}$
277 $= 1.3 T_{B_{max}}$; $r^2 = 0.98$, $p < 0.001$; Fig. 2).

278

279 Soil stratification and root turnover

280

281 Our results show that a layer-by-layer approach yields a higher turnover value than a 'one soil
282 layer' approach (Figure 3). For this comparison of the two approaches, sequential coring data,
283 decision matrix calculations and mean biomass values were taken from Hertel (1999), Richter
284 (2007), Makkonen and Helmisaari (1999), Bakker (1999), Ostonen et al. (2005), and Jourdan et
285 al. (2008). Using average data for the whole of the soil profile, as opposed to using data for
286 individual layers, does not capture all observed differences in root biomass and therefore results
287 in a lower estimate of NPP and thus significantly lower turnover T ($T_{whole\ profile} = 0.9 T_{layer-per-layer}$;
288 $r^2 = 0.92$, $p < 0.001$; Figure 3).

289

290 Comparison between the Decision Matrix and the Maximum-Minimum method

291

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

298

299 Relationship between the turnover and the mean annual temperature

300

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

307

308 **Discussion**

309

310 Decision Matrix versus Maximum-Minimum method

311

312 We found about two times higher root turnover values when using the Decision Matrix method
313 compared to the Maximum-Minimum method. The observed discrepancy is best described by
314 the fact that Decision Matrix accumulates differences between all observations – the larger the
315 number of interim observations the larger the potential for accounting all the peaks and troughs.
316 The Maximum-Minimum method, on the other hand, makes use only of the annual net gain in
317 biomass. On the basis of our comparison, we suggest that the Maximum-Minimum method
318 should be used with caution; by definition, root turnover estimates calculated by this method are
319 bound between 0 and 1. Although this range may cover some ecosystems, it cannot correctly
320 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

350 et al. 2008). However, in some forest ecosystems, application of minirhizotron methods to
351 measure fine-root production is hampered, e.g. in stony or shallow soils or on steep slopes.
352 Sequential coring and ingrowth core methods are suitable even for these environments, giving
353 them an advantage in terms of comparability of resulting data. In a new approach, Osawa and
354 Aizawa (2012) complemented soil-coring techniques with litterbag experiments in order to
355 estimate fine-root decomposition. By including decomposition rates into the calculations, the
356 authors further improved the accuracy of the values for fine-root production.

357

358 Maximum biomass *versus* mean biomass

359

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

379 rather than the maximum is more representative of the annual live biomass present in the soil.
380 The use of mean biomass in our calculations increased the turnover values by about 30%
381 compared to the use of the maximum biomass.

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

397

398 Turnover values of European tree species

399

400 Our review of published studies from European forest stands revealed that most data for fine-
401 root turnover originate from sequential coring, with the prevalence of *Fagus sylvatica* or *Picea*
402 *abies* as the species of interest. Studies performed in forest stands with other dominating tree
403 species such as *Quercus* spp., *Pinus* spp. were far less abundant. Similarly, turnover studies
404 where ingrowth cores were used instead of employing the sequential coring method to measure
405 fine-root production, were far less abundant. Whereas in our study the data sets of *F. sylvatica*
406 derived mainly from Central Europe, the data sets of *P. abies* originated from Central as well as
407 from Northern Europe. Trees from Southern European countries were represented only by a

408 few data sets, and no conclusive turnover values can be suggested for this environment yet.
409 Overall, we propose that only the fine root turnover values in our study for the following species
410 may be recommended for further use in biogeochemical models with a reasonable degree of
411 accuracy: *F. sylvatica* and *P. abies*. We established turnover values of 1.11 y^{-1} for both *F.*
412 *sylvatica* and *P. abies*, using the Decision Matrix formula and the mean biomass data from
413 sequential coring.

414 The mean turnover values for temperate and boreal forests in our study were distinctly
415 higher compared to the values in the Gill and Jackson (2000), who compiled a data set of about
416 190 papers. Mean turnover values in our study, using maximum biomass data, were estimated
417 to be 0.81 y^{-1} for temperate forests at mean annual temperature (MAT) 7.9°C , and 1.25 y^{-1} for
418 boreal forest at MAT 3.3°C . Gill and Jackson (2000), however, estimated turnover values of
419 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.
420 Yuan and Chen (2010) found a similarly high turnover value for boreal forest (0.76 y^{-1}). In
421 contrast to our study, other reviews on turnover have shown significant but weak relations
422 between root turnover and MAT, e.g. Yuan and Chen (2010; $r^2 = 0.25$, $p = 0.001$) in boreal
423 forests, Finer et al. (2011; $r^2 = 0.15$, $p = 0.001$) and Gill and Jackson (2000; $r^2 = 0.07$, $p = 0.018$)
424 in a global datasets (see also Figure 5). Giving the low r^2 of these studies, one may assume
425 other environmental factors than MAT that act as large-scale drivers of root turnover in forests.

426

427 Turnover values applied in biogeochemical models

428

429 One of the aims of the present study was to deliver suitable fine-root turnover data of European
430 tree species, which may be used by modellers to construct ecosystem or biogeochemical
431 models. Such models are applied in many European countries to report the change of
432 belowground C in European forests as a reporting requirement for the Kyoto protocol
433 signatories. A brief overview of the models applied so far shows that a wide variety of root
434 turnover values are used, some resembling measured values, others less so. In one of the first
435 applications, the fine-root turnover value was set to 1.0 y^{-1} for deciduous broad-leaf and
436 deciduous needle-leaf trees and to 0.26 y^{-1} for evergreen needle-leaf trees (White et al. 2000,

437 using the Biome-BGC model). The distinct difference between deciduous trees and evergreen
438 needle-leaf trees mainly originated from the notion that fine-root turnover is equal to leaf
439 turnover, with 1.0 y^{-1} for deciduous leaves and 0.26 y^{-1} for evergreen needles/leaves. These
440 values are themselves derived from the mean age of foliage, which is one year for deciduous
441 trees and about four years for evergreens. A compilation of the various turnover values applied
442 in European modelling studies is shown in Table 6. Most recent studies applied a universal fine-
443 root turnover value of 0.7 y^{-1} to all forest tree species (Hickler et al. 2008, using the LPJ-GUESS
444 model). This assumption is based on Vogt et al. (1996) and on Li et al. (2003) (Thomas Hickler,
445 personal communication). Li et al. (2003) found a linear relationship between fine root
446 production and fine root biomass, with the turnover value 0.64 y^{-1} which was lower than the
447 original estimate of 0.73 y^{-1} from a previous analysis (Kurz et al. 1996). Using 'universal'
448 turnover values, however, should be discouraged if country-based C budgets have to be
449 reported within the frame to the Kyoto protocol and species-specific and biome based values of
450 root turnover are available.

451

452 **Conclusions**

453

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

462

463 **Acknowledgements** This study is a result of the activity of a Working Group of the COST
464 Action FP0803 "Belowground carbon turnover in European forests". We thank Astrid Meyer and
465 Thomas Hickler for helpful comments on the calculations and the models, and Beat Frey for

466 critical reading. We also would like to thank Carmen Biel, Karna Hansson, Peter Zeleznik,
467 Thomas Leski, Inger-Kappel Schmidt, Antonino di Iorio, Kyotaro Noguchi, and Yoni Ephrat, who
468 helped us in any way to write up this review.

469

470 **References**

- 471 Ahlström K, Persson H, Börjesson I (1988) Fertilization in a mature Scots pine (*Pinus sylvestris*
472 L.) stand - effects on fine roots. *Plant Soil* 106:179-190.
- 473 Bakker MR (1999) The effect of lime and gypsum applications on a sessile oak (*Quercus*
474 *petraea* (M.) Liebl.) stand at La Croix Scaille (French Ardennes) II. Fine root dynamics. *Plant*
475 *Soil* 206:109-121
- 476 Børja I, De Wit HA, Steffenrem A, Majdi H (2008) Stand age and fine root biomass, distribution
477 and morphology in a Norway spruce chronosequence in southeast Norway. *Tree Physiol*
478 28:773-784
- 479 Brunner I, Godbold DL (2007) Tree roots in a changing world. *J For Res* 12:78-82
- 480 Brunner I, Graf Pannatier E, Frey B, Rigling A, Landolt W, Zimmermann S, Dobbertin M (2009)
481 Morphological and physiological responses of Scots pine fine roots to water supply in a dry
482 climatic region in Switzerland. *Tree Physiol* 29:541-550
- 483 Chertov OG, Komarov AS, Nadporozhskaya M, Bykhovets SS, Zudin SL (2001) ROMUL - a
484 model of forest soil organic matter dynamics as a substantial tool for forest ecosystem
485 modeling. *Ecol Model* 138:289-308
- 486 Cienciala E, Tatarinov FA (2006) Application of BIOME-BGC model to managed forests. 2.
487 Comparison with long-term observations of stand production for major tree species. *For Ecol*
488 *Manag* 237:252-266
- 489 Dannoura M, Kominami Y, Oguma H, Kanazawa Y (2008) The development of an optical
490 scanner method for observation of plant root dynamics. *Plant Root* 2:14-18
- 491 Eldhuset TD, Lange H, de Wit HA (2006) Fine root biomass, necromass and chemistry during
492 seven years of elevated aluminium concentrations in the soil solution of a middle-aged *Picea*
493 *abies* stand. *Sci Total Environ* 369:344-356
- 494 Endrulat T, Saurer M, Buchmann N, Brunner I (2010) Incorporation and remobilization of ¹³C
495 within the fine-root systems of individual *Abies alba* trees in a temperate coniferous stand.
496 *Tree Physiol* 30:1515-1527

- 497 Fairley RI, Alexander IJ (1985) Methods of calculating fine root production in forests. In: Fitter
498 AH, Atkinson D, Read DJ. (eds) Ecological interactions in soil: plants, microbes and animals.
499 Blackwell. Oxford, pp 37-42
- 500 Finer L, Ohashi M, Noguchi K, Hirano Y (2011) Fine root production and turnover in forest
501 ecosystems in relation to stand and environmental characteristics. For Ecol Manag
502 262:2008-2023
- 503 Fritz HW (1999) Feinwurzel-Verteilung, -Vitalität, -Produktion und -Umsatz von Fichten (*Picea*
504 *abies* (L.) Karst.) auf unterschiedlich versauerten Standorten. Ber Forsch Zent Waldökosyst,
505 Reihe A, 165:1-138
- 506 Gaudinski JB, Tom MS, Riley WJ, Dawson TE, Joslin JD, Majdi H (2010) Measuring and
507 modeling the spectrum of fine-root turnover times in three forests using isotopes,
508 minirhizotrons, and the Radix model. Glob Biogeochem Cycles 24:GB3029
- 509 Gaudinski JB, Trumbore SE, Davidson EA, Cook AC, Makrewitz D, Richter DD (2001) The age
510 of fine-root carbon in three forests of the eastern United States measured by radiocarbon.
511 Oecologia 129:420-429
- 512 Genenger M, Zimmermann S, Hallenbarter D, Landolt W, Frossard E, Brunner I (2003) Fine
513 root growth and element concentrations of Norway spruce as affected by wood ash and
514 liquid fertilisation. Plant Soil 255:253-264
- 515 Gill RA, Jackson R (2000) Global patterns of root turnover for terrestrial ecosystems. New
516 Phytol 147:13-31
- 517 Hendricks JJ, Hendrick RL, Wilson CA, Mitchell RJ, Pecot SD, Guo D (2006) Assessing the
518 patterns and controls of fine root dynamics: an empirical test and methodological review. J
519 Ecol 94:40-57
- 520 Hertel D (1999) Das Feinwurzelsystem von Rein- und Mischbeständen der Rotbuche: Struktur,
521 Dynamik und interspezifische Konkurrenz. Diss Bot 317:1-185
- 522 Hickler T, Smith B, Prentice C, Mjöfors K, Miller P, Arnetz A, Sykes MT (2008) CO₂ fertilization
523 in temperate FACE experiments not representative of boreal and tropical forests. Glob
524 Change Biol 14:1531-1542

- 525 Hickler T, Prentice IC, Smith B, Sykes MT, Zaehle S (2006) Implementing plant hydraulic
526 architecture within the LPJ dynamic global vegetation model. *Glob Ecol Biogeogr* 15:567-
527 577
- 528 Hickler T, Smith B, Sykes MT, Davis M, Sugita S, Walker K (2004) Using a generalized
529 vegetation model to simulate vegetation dynamics in northeastern USA. *Ecology* 85:519-530
- 530 Hirano Y, Noguchi K, Ohashi M, Hishi T, Makita N, Fujii S, Finér L (2009) A new method for
531 placing and lifting root meshes for estimating fine root production in forest ecosystems. *Plant*
532 *Root* 3:26-31
- 533 Johnson MG, Tingey DT, Phillips DL, Storm MJ (2001) Advancing fine root research with
534 minirhizotrons. *Environ Exp Bot* 45:263-289
- 535 Jourdan C, Silva EV, Goncalves JLM, Ranger J, Moreira RM, Laclau JP (2008) Fine root
536 production and turnover in Brazilian *Eucalyptus* plantations under contrasting nitrogen
537 fertilization regimes. *For Ecol Manag* 256:396-404
- 538 Konôpka B, Yuste JC, Janssens IA, Ceulemans R (2005) Comparison of fine root dynamics in
539 Scots pine and Pedunculate oak in sandy soil. *Plant Soil* 276:33-45
- 540 Konôpka B (2009) Differences in fine root traits between Norway spruce (*Picea abies* (L.)
541 Karst.) and European beech (*Fagus sylvatica* L.) - A case study in the Kysucké Beskydy
542 Mts. *J For Sci* 55:556-566
- 543 Kurz WA, Kimmins JP (1987) Analysis of some sources of error in methods used to determine
544 fine root production in forest ecosystems: a simulation approach. *Can J For Res* 17:909-912
- 545 Li Z, Kurz WA, Apps MJ, Beukema SJ (2003) Belowground biomass dynamics in the carbon
546 budget model of the Canadian forest sector: recent improvements and implications for the
547 estimation of NPP and NEP. *Can J For Res* 33:106-126
- 548 López B, Sabaté S, Gracia CA (2001) Annual and seasonal changes in fine root biomass of a
549 *Quercus ilex* L. forest. *Plant Soil* 230:125-13
- 550 Lukac M, Godbold DL (2010) Fine root biomass and turnover in southern taiga estimated by
551 root inclusion nets. *Plant Soil* 331:505-513

- 552 Lukac M, Calfapietra C, Godbold DL (2003) Production, turnover and mycorrhizal colonization
553 of root systems of three *Populus* species grown under elevated CO₂ (POPFACE). *Glob*
554 *Change Biol* 9:838-848
- 555 Majdi H, Andersson P (2005) Fine root production and turnover in a Norway spruce stand in
556 northern Sweden: effects of nitrogen and water manipulation. *Ecosystems* 8:191-199
- 557 Majdi H, Pregitzer K, Morén AS, Nylund JE, Ågren GI (2005) Measuring fine root turnover in
558 forest ecosystems. *Plant Soil* 276:1-8
- 559 Makkonen K, Helmisaari HS (1999) Assessing fine-root biomass and production in a Scots pine
560 stand - comparison of soil core and root ingrowth core methods. *Plant Soil* 210:43-50
- 561 Makkonen K, Helmisaari HS (2001) Fine root biomass and production in Scots pine stands in
562 relation to stand age. *Tree Physiol* 21:193-198
- 563 Matamala R, Gonzalez-Meler MA, Jastrow JD, Norby RJ, Schlesinger WH (2003) Impacts of
564 fine root turnover on forest NPP and soil C sequestration potential. *Science* 302:1385-1387
- 565 McClaugherty CA, Aber JD, Melillo JM (1982) The role of fine roots in the organic-matter and
566 nitrogen budgets of two forested ecosystems. *Ecology* 63:1481-1490
- 567 Miguel Pérez C (2010) Respuestas ecofisiológicas y estructurales a la recurrencia, duracion e
568 intensidad de la sequia en plantaciones y bosques mixtos de *Quercus ilex*, *Quercus*
569 *pubescens* y *Quercus cerrioides*. Dissertation, Institut de Recerca i Tecnologia
570 Agroalimentaries IRTA, Universitat Autònoma de Barcelona UAB
- 571 Osawa A, Aizawa R (2012) A new approach to estimate fine root production, mortality, and
572 decomposition using litter bag experiments and soil core techniques. *Plant Soil* (in press).
573 DOI: 10.1007/s11104-011-1096-6
- 574 Ostonen I, Lohmus K, Pajuste K (2005) Fine root biomass, production and its proportion of NPP
575 in a fertile middle-aged Norway spruce forest: Comparison of soil core and ingrowth core
576 methods. *For Ecol Manag* 21:264-277
- 577 Persson H (1980a) Fine-root production, mortality and decomposition in forest ecosystems.
578 *Vegetatio* 41:101-109
- 579 Persson H (1980b) Fine-root dynamics in a Scots pine stand, with and without near optimum
580 nutrient and water regimes. *Acta Phytogeogr Suec* 68:101-110.

- 581 Persson H, Ahlström K (1994) The effects of alkalizing compounds on fine-root growth in a
582 Norway spruce stand in southwest Sweden. *J Environ Sci Health A* 29:803-820
- 583 Persson HÅ, Stadenberg I (2010) Fine-root dynamics in a Norway spruce forest (*Picea abies*
584 (L.) Karst) in Eastern Sweden. *Plant Soil* 330:329-344
- 585 Pietsch SA, Hasenauer H, Thornton PE (2005) BGC-model parameters for tree species growing
586 in central European forests. *For Ecol Manag* 211:264-295
- 587 Publicover DA, Vogt KA (1993) A comparison of methods for estimating forest fine root
588 production with respect to sources of error. *Can J For Res* 23:1179-1186
- 589 Richter A (2007) Fine root growth and vitality of European beech in acid forest soils with a low
590 base saturation. Dissertation, ETH Zürich
- 591 Sah SP, Jungner H, Oinonen M, Kukkola M, Helmisaari H-S (2011) Does the age of fine root
592 carbon indicate the age of fine roots in boreal forests? *Biogeochemistry* 104:91-102.
- 593 Santantonio D, Grace JC (1987) Estimating fine-root production and turnover from biomass and
594 decomposition data: a compartment-flow model. *Can J For Res* 17:900-908.
- 595 Silver WL, Thompson AW, McGroddy ME, Varner RK, Dias JD, Silva H, Crill PM, Keller M
596 (2005) Fine root dynamics and trace gas fluxes in two lowland tropical forest soils. *Glob*
597 *Change Biol* 11:290-306
- 598 Sitch S, Smith B, Prentice IC, Arneth A, Bondeau A, Cramer W, Kaplan J, Levis S, Lucht W,
599 Sykes M, Thonicke K, Venevsky S (2003) Evaluation of ecosystem dynamics, plant
600 geography and terrestrial carbon cycling in the LPJ Dynamic Global Vegetation Model. *Glob*
601 *Change Biol* 9:161-185
- 602 Smith B, Prentice IC, Sykes MT (2001) Representation of vegetation dynamics in the modelling
603 of terrestrial ecosystems: comparing two contrasting approaches within European climate
604 space. *Glob Ecol Biogeogr* 10:621-637
- 605 Stober C, George E, Persson H (2000) Root growth and response to nitrogen. In: Schulze ED
606 (ed) *Carbon and nitrogen cycling in European forest ecosystems*. Springer, Berlin, pp 99-121
- 607 Strand AE, Pritchard SG, McCormack ML, Davis MA, Oren R (2008) Irreconcilable differences:
608 fine-root life spans and soil carbon persistence. *Science* 319:456-458

- 609 Tatarinov FA, Cienciala E (2006) Application of BIOME-BGC model to managed forests 1.
610 Sensitivity analysis. For Ecol Manag 237:267-279
- 611 Tierney G, Fahey T (2002) Fine root turnover in a northern hardwood forest: a direct
612 comparison of the radiocarbon and minirhizotron methods. Can J For Res 32:1692-1697
- 613 Trumbore SE, Gaudinski JB (2003) The secret lives of roots. Science 302:1344-1345
- 614 Vogt KA, Vogt DJ, Palmiotto PA, Boon P, O'Hara J, Asbjornson H (1996) Review of root
615 dynamics in forest ecosystems grouped by climate, climatic forest type and species. Plant
616 Soil 187:159-219
- 617 Vogt KA, Persson H (1991) Measuring growth and development of roots. In: Lassoie JP,
618 Hinkley TM (eds) Techniques and approaches in forest tree ecophysiology. CRC Press,
619 Boca Raton, pp 477-501
- 620 Vogt KA, Vogt DJ, Bloomfield J (1998) Analysis of some direct and indirect methods for
621 estimating root biomass and production of forest at ecosystem level. Plant Soil 200:71-89
- 622 White MA, Thornton PE, Running SW, Nemai RR (2000) Parametrization and sensitivity
623 analysis of the BIOME-BGC terrestrial ecosystem Model: Net primary production controls.
624 Earth Interact 4:1-85
- 625 Wu K (2000) Fine root production and turnover and its contribution to nutrient cycling in two
626 beech (*Fagus sylvatica* L.) forest ecosystems. Ber Forsch Zent Waldökosyst, Reihe A,
627 170:1-130
- 628 Yuan ZH, Chen HYH (2010) Fine root biomass, production, turnover rates, and nutrient
629 contents in boreal forest ecosystems in relation to species, climate, fertility, and stand age:
630 Literature review and meta-analyses. Crit Rev Plant Sci 29:204-221
631
632

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

634

635

636

Biomass increase

Biomass decrease

637

638

Necromass increase

 $P = \Delta B + \Delta N$ $P = \Delta B + \Delta N^1$ or $P = 0^2$

639

Necromass decrease

 $P = \Delta B$ $P = 0$

640

641

¹ if $|\Delta B| < |\Delta N|$

642

² if $|\Delta B| > |\Delta N|$

643

644

645 **Table 2** Worked sample with a data set from sequential coring (data from Ostonen et al.
646 2005). Formulas are according to the Material and Methods section

647

648 a) Calculation of the production P using the Decision Matrix

649

650	Sampling date	Biomass (g m ⁻²)	Necromass (g m ⁻²)	Formula	Calculation	Production P (g m ⁻² t ⁻¹)
651						
652						
653	June 1996	127	130			
654	July 1996	161	178	[3]	(161-127)+(178-130)	82
655	Aug. 1996	166	114	[4]	166-161	5
656	Sept. 1996	165	174	[3]	(165-166)+(174-114)	59
657	Oct. 1996	199	198	[3]	(199-165)+(198-174)	58
658	Nov. 1996	64	159	[5]	0	0
659	June 1997	110	125	[4]	110-64	46
660						
661	Mean [7]:	141				Sum [2]: 250
662						

663

664 b) Calculation of the annual production P_a

665

666	Method	Formula	Calculation	Annual production P _a (g m ⁻² y ⁻¹)
667				
668				
669	Decision Matrix	[2]	82+5+59+58+0+46	250
670	Maximum-Minimum	[1]	199-64	135
671				

672

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

674

675	Method	Formula	Calculation		Turnover T (y ⁻¹)
676			Using B _{mean}	Using B _{max}	
677					
678	Decision Matrix	[6]	250 / 141	-	1.77
679	Decision Matrix	[8]	-	250 / 199	1.26
680	Maximum-Minimum	[6]	135 / 141	-	0.95
681	Maximum-Minimum	[8]	-	135 / 199	0.68
682					

683

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

687

688	Country	Mean	Soil	Depth	Diam.	Age	Biomass (B)		Decision Matrix		Maximum-Minimum		References		
689	-Site	annual	layers				Mean	Max.	Production	Turnover	Production	Turnover			
690		temp.							B_{mean}	B_{max}		B_{mean}		B_{max}	
691		(°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)
692	<hr/>														
693	<i>Eucalyptus grandis:</i>														
694	Brasil	19.0		0-30	<2	8	89	120	153	1.71	1.28	48	0.54	0.40	Jourdan et al. (2008)
695	<i>Fagus sylvatica:</i>														
696	CH-Entl.	6.7	A,B	0-25	<2	a	422	580	395	0.94	0.68	290	0.69	0.50	Richter (2007)
697	CH-Krau.	8.2	A,B	0-25	<2	a	480	710	476	0.99	0.67	356	0.74	0.50	Richter (2007)
698	CH-Nied.	8.7	A,B	0-25	<2	a	413	501	281	0.68	0.56	217	0.53	0.43	Richter (2007)
699	CH-Walt.	7.4	A,B	0-25	<2	a	348	441	193	0.55	0.44	171	0.49	0.39	Richter (2007)
700	CH-Vord.	8.8	A,B	0-25	<2	a	807	957	597	0.74	0.62	356	0.44	0.37	Richter (2007)
701	CH-Zofi.	8.2	A,B	0-25	<2	a	517	600	144	0.28	0.24	142	0.27	0.24	Richter (2007)
702	DE-Gött.	8.7	A	0-15	<2	a	177	219	41	0.23	0.19	75	0.42	0.34	Hertel (1999)
703	DE-Lüne.	8.1	O,A	0-5	<2	a	279	312	458	1.64	1.47	97	0.35	0.31	Hertel (1999)
704	DE-Soll.	6.9	O,A	0-5	<2	a	134	149	226	1.68	1.51	45	0.33	0.30	Hertel (1999)
705	DE-Zieg.	8.6	O,A	0-10	<2	a	70	100	203	2.92	2.04	46	0.66	0.46	Hertel (1999)
706	DE-Gött.	7.0	A,B	0-20	<2	a	195	282	218	1.12	0.77	157	0.81	0.56	Wu (2000)
707	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)
708	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)

709

710

711 **Table 3** (continued)

712	<hr/>														
713	<i>Picea abies:</i>														
714	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)
715	DE-Barb.	8.0	O,A	0-40	<2	a	182	235	116	0.63	0.49	124	0.68	0.53	Fritz (1999)
716	DE-Eber.	7.8	A,M	0-40	<2	a	150	188	83	0.56	0.44	90	0.60	0.48	Fritz (1999)
717	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)
718	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)
719	EE-Roel.	5.4		0-40	<2	a	142	199	251	1.77	1.26	135	0.95	0.68	Ostonen et al. (2005)
720	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)
721	NO-Nordm.	3.8		0-40	<2	50	462	603	298	0.65	0.49	282	0.61	0.47	Eldhuset et al. (2006)
722	NO-Nordm.	3.8		0-60	<2	60	56	62	63	1.13	1.02	17	0.31	0.27	Børja et al. (2008)
723	NO-Nordm.	3.8		0-60	<2	120	50	63	70	1.40	1.11	22	0.48	0.35	Børja et al. (2008)
724	SE-Forsm.	5.5		0-40	<2	a	304	410	241	0.79	0.59	186	0.61	0.45	Persson and Stadenb. (2010)
725	<i>Pinus sylvestris:</i>														
726	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)
727	SE-Ivan	5.2	F,H	-	<2	a	120	153	242	2.03	1.58	69	0.58	0.45	Persson (1980a)
728	<i>Populus spp.:</i>														
729	IT-P. alba	14.4			<2	2	110	143	55	0.50	0.39	56	0.51	0.40	Lukac et al. (2003)
730	IT-P. nigra	14.4			<2	2	109	158	84	0.77	0.53	84	0.77	0.53	Lukac et al. (2003)
731	IT-P. eura.	14.4			<2	2	146	187	55	0.37	0.29	89	0.61	0.48	Lukac et al. (2003)
732	<i>Quercus ilex / Q. cerroides:</i>														
733	ES-Bages	14.4		0-50	<5	10	858	1336	-	-	-	812	0.95	0.61	Miguel Pérez (2010)
734	<i>Quercus petraea:</i>														
735	FR-La Croix	8.0		0-55	<2	a	310	346	53	0.17	0.15	63	0.29	0.18	Bakker (1999)
736	<hr/>														
737															

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

741

742	Country	Mean	Depth	Year	Diam.	Age	Biomass (B)		Decision Matrix		Maximum-Minimum		References		
743	-Site	annual		after			Mean	Max.	Production	Turnover	Production	Turnover			
744		temp.		install.					B_{mean}	B_{max}		B_{mean}	B_{max}		
745		(°C)	(cm)	(y)	(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)	
746	<hr/>														
747	<i>Fagus sylvatica:</i>														
748	DE-Gött.	7.0	0-20	2	<2	a	42	107	107	2.58	1.00	107	2.58	1.00	Wu (2000)
749	DE-Soll.	6.4	0-20	2	<2	a	48	123	123	2.57	1.00	123	2.57	1.00	Wu (2000)
750	<i>Picea abies:</i>														
751	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)
752	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)
753	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)
754	<i>Pinus sylvestris:</i>														
755	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)
756	SE-Ivan.	5.2	-	2	<2	a	65	136	126	1.96	0.93	115	1.78	0.84	Persson (1980a)
757	<hr/>														

758 **Table 5** Summary of biomass, annual production, and turnover values (\pm SE) of fine roots of
 759 common European tree species. The annual production is calculated with the 'Decision Matrix' or the
 760 'Maximum-Minimum' formula, and the turnover is calculated by dividing the annual production by the
 761 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)	
762	<hr/>								
763	<u>Sequential coring method</u>								
764	<i>Fagus sylvatica</i> (n=13)								
765	327	411	278	1.11	0.86	163	0.53	0.41	
766	(\pm 57)	(\pm 71)	(\pm 44)	(\pm 0.21)	(\pm 0.16)	(\pm 31)	(\pm 0.06)	(\pm 0.03)	
767	<i>Picea abies</i> (n=11)								
768	184	240	177	1.11	0.88	110	0.57	0.44	
769	(\pm 37)	(\pm 49)	(\pm 30)	(\pm 0.14)	(\pm 0.11)	(\pm 24)	(\pm 0.05)	(\pm 0.04)	
770	<i>Pinus sylvestris</i> (n=2)								
771	199	258	552	2.57	1.98	125	0.62	0.48	
772	(\pm 80)	(\pm 105)	(\pm 310)	(\pm 0.54)	(\pm 0.40)	(\pm 56)	(\pm 0.04)	(\pm 0.02)	
773	<u>Ingrowth cores method</u>								
774	<i>Fagus sylvatica</i> (n=2)								
775	45	115	115	2.58	1.00	115	2.58	1.00	
776	(\pm 3)	(\pm 8)	(\pm 8)	(\pm 0.01)	(\pm 0.00)	(\pm 8)	(\pm 0.01)	(\pm 0.00)	
777	<i>Picea abies</i> (n=3)								
778	67	102	73	1.15	0.72	63	0.98	0.62	
779	(\pm 8)	(\pm 2)	(\pm 8)	(\pm 0.28)	(\pm 0.09)	(\pm 7)	(\pm 0.21)	(\pm 0.07)	
780	<i>Pinus sylvestris</i> (n=2)								
781	55	99	82	1.40	0.76	76	1.31	0.72	
782	(\pm 11)	(\pm 37)	(\pm 45)	(\pm 0.56)	(\pm 0.17)	(\pm 39)	(\pm 0.47)	(\pm 0.12)	
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791 **Table 6** Fine-root turnover values of European trees used in biogeochemical models

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794	Tree type	Tree species	Turnover (y^{-1})	Model	Reference
795	Broad- / Deciduous	needle-leaved	1.0	Biome-BGC	White et al. (2000)
796	Broad-leaved	summergreen	1.0	LPJ-GUESS	Smith et al. (2001)
797	Broad-leaved		1.0	LPJ-GUESS	Hickler et al. (2004)
798	Broad-leaved		0.7	LPJ-GUESS	Hickler et al. (2006, 2008)
799		<i>Fagus sylvatica</i>	1.023	Biome-BGC	Ciencela and Tatarinov (2006) ¹
800		<i>Fagus sylvatica</i>	1.0	Biome-BGC	Pietsch et al. (2005)
801		<i>Quercus robur</i>	1.023	Biome-BGC	Ciencela and Tatarinov (2006) ¹
802		<i>Quercus robur</i>	1.0	Biome-BGC	Pietsch et al. (2005)
803		<i>Quercus petraea</i>	1.023	Biome-BGC	Ciencela and Tatarinov (2006) ¹
804		<i>Quercus petraea</i>	1.0	Biome-BGC	Pietsch et al. (2005)
805		<i>Larix decidua</i>	1.0	Biome-BGC	Pietsch et al. (2005)
806	Evergreen	needle-leaved	0.26	Biome-BGC	White et al. (2000)
807	Needle- / Broad-leaved	evergreen	0.5	LPJ-GUESS	Smith et al. (2001)
808	Needle-leaved		0.5	LPJ-GUESS	Hickler et al. (2004)
809	Needle-leaved		0.7	LPJ-GUESS	Hickler et al. (2006, 2008)
810		<i>Picea abies</i>	0.811	Biome-BGC	Ciencela and Tatarinov (2006) ¹
811		<i>Picea abies</i>	0.195	Biome-BGC	Pietsch et al. (2005)
812		<i>Pinus sylvestris</i>	0.18	Biome-BGC	Pietsch et al. (2005)
813		<i>Pinus cembra</i>	0.18	Biome-BGC	Pietsch et al. (2005)

814
815 ¹ and Tatarinov and Ciencela (2006)

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817

818 **Figure Captions**

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

822

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

826

827 **Fig 3** Relationship between turnover values calculated per whole soils profiles or per individual soil
828 layers (summed *versus* individual layers). Turnover values were calculated the whole data set of
829 sequential coring and using the Decision Matrix method and maximum biomass data (data from Hertel
830 1999; Richter 2007; Makkonen and Helmisaari 1999; Bakker 1999; Ostonen et al. 2005; Jourdan et al.
831 2008). Mean soil depth is 44 cm, and the average number of individual soil layers is 4

832

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

836

837 **Fig 5** Relationship between turnover and mean annual temperature, and divided into the three
838 vegetation zones boreal/alpine (Δ), temperate (\bullet), and tropical (\diamond). a) Data from a global study
839 (redrawn from Appendix 1 of Gill and Jackson 2000). b) Present study (turnover values were
840 calculated from the whole data of sequential coring and using the Decision Matrix method and
841 maximum biomass data)

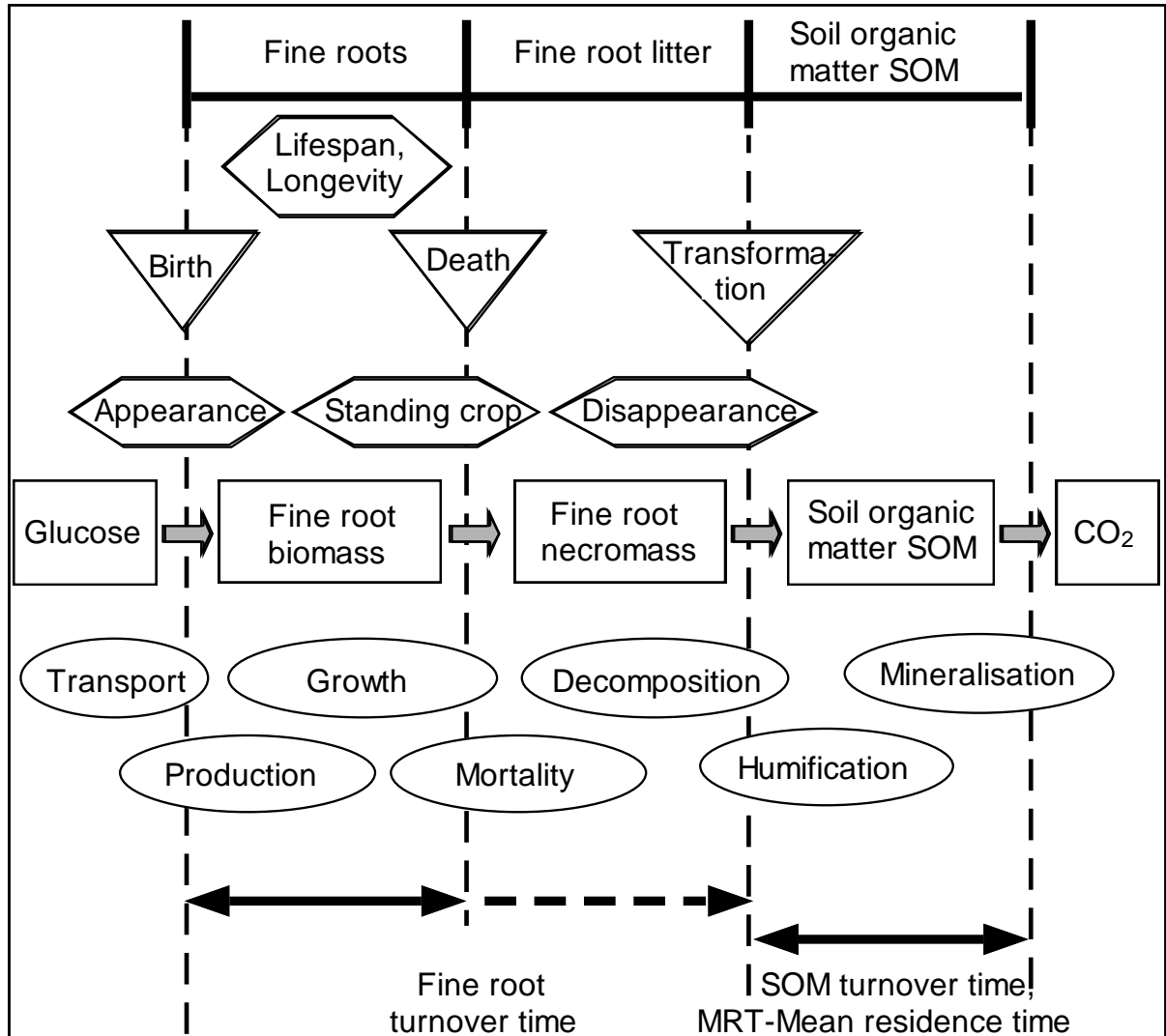
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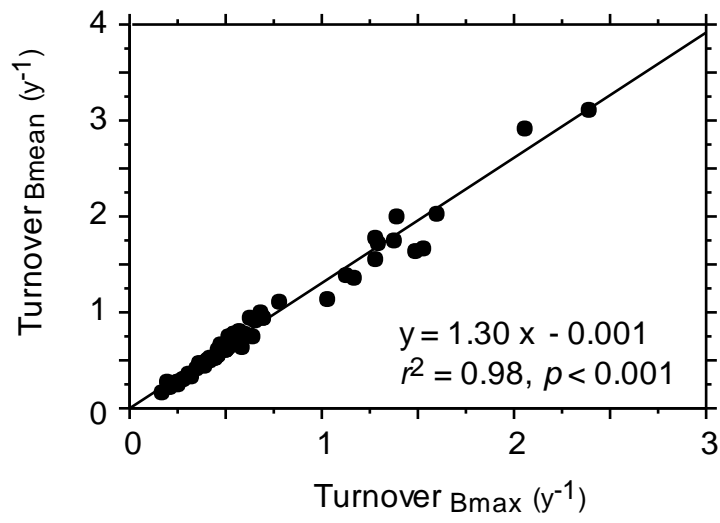
853 Figure 1.

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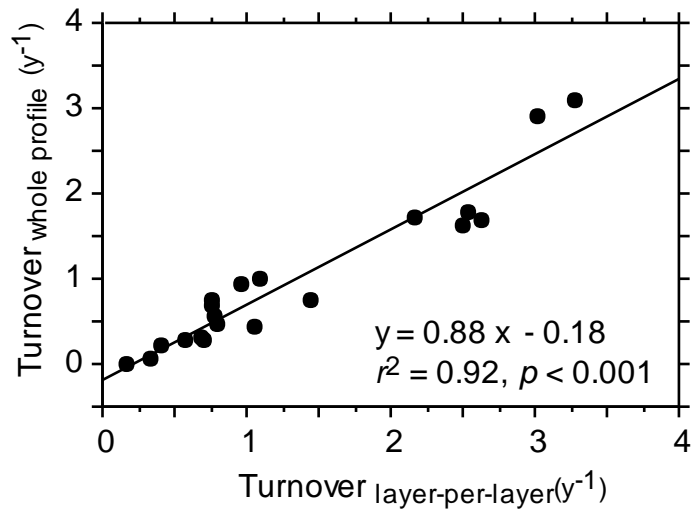
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874 Figure 2.

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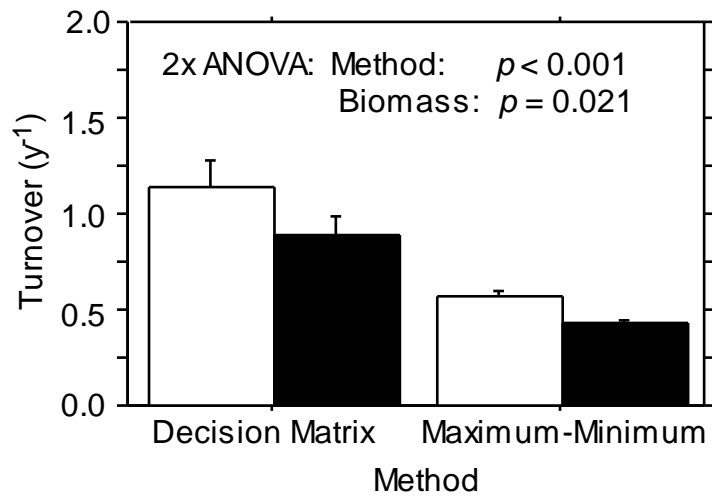
891 Figure 3.

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909 Figure 4.

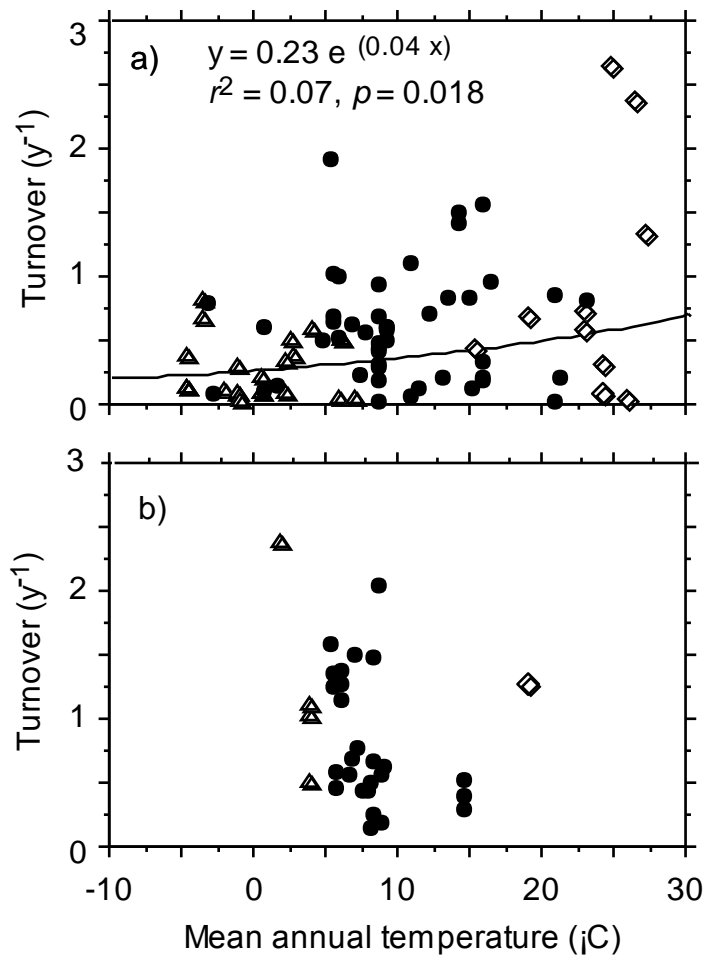
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923 Figure 5.

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