1   **Fine-root turnover of European forest trees revisited: an analysis of data**

2   **from sequential coring and ingrowth cores**

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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.

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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 (^{13}C, ^{14}C) 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 (McClaugherty 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 (Finér

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**

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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    $P_{a\,(MM)} = B_{max} - B_{min}$ [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    $P_{a\,(DM)} = \sum P$ [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    $P = \Delta B + \Delta N$ a) if biomass and necromass have increased   [3]

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

176                      $|\Delta N|$

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

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

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

180   I∆NI

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

200

201   As an alternative, the turnover T_{Bmean} 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     $B_{mean} = \sum B / n$ (n = number of samples per year)   [7]

206

207    $T_{Bmean} = P_a / B_{mean}$ [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

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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

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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_{Bmean}

277   = 1.3 T_{Bmax}; 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 $T_{Bmax} = 0.228 \; e^{0.036 \; MAT}$, 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**

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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.

321 2003). The Maximum-Minimum method is therefore only suitable for ecosystems with strong

322 annual fluctuation of fine root biomass where turnover is not expected to exceed 1. In a forest

323 ecosystem where root production and root death occur continuously and on a similar level all

324 year round ('steady state'), no differences between maximum and minimum biomass will be

325 observed. Such an observation will result in a zero estimate of root production and

326 subsequently a zero estimate of root turnover (compare also Kurz and Kimmins 1987). For

327 example, this may be the case in tropical rainforests, which lack pronounced seasonality.

328   Moving on to the Decision Matrix method, the weak point of this method is - as with all

329 methods using dead roots - the difficulty of accurately quantifying root necromass. The

330 potentially rapid disappearance of root necromass may lead to underestimates (Hendricks et al.

331 2006). Nevertheless, we propose that if necromass observations are available or can be

332 obtained, the Decision Matrix should be favoured over the Minimum-Maximum formula. The

333 former considers both living and dead fine roots, the calculation is thus based on more

334 information, reducing the scope for significant errors. However, distinguishing between biomass

335 and necromass is often difficult, as is recognising the difference between partially decomposed

336 fine-root and foliage litter. An important source of variation between estimates from different

337 sources is the arbitrarily imposed root fragment size limit. Whereas Hertel (1999) used for his

338 calculation fine-root litter fragments >0.25 mm length, other authors set the minimum fragments

339 length either at >1 mm (Fritz 1999; Wu 2000) or >5 mm length (Richter 2007), thus varying the

340 amount of necromass recovered from the soil. Comprehensive comparisons of the two methods

341 have also been carried out by other authors (Vogt et al. 1998; Hendricks et al. 2006).

342   Even though root coring methods – whether sequential or ingrowth – do deliver

343 dependable and comparable measurements of fine root turnover, the application of the

344 minirhizotron technique to estimate fine-root production and turnover is still favoured over the

345 sequential coring or the ingrowth core method in certain situations (Hendricks et al. 2006).

346 Turnover estimates obtained by minirhizotron studies can be higher than 1 and the method

347 allows for repeated observation of the same roots. The latest variation of the minirhizotron

348 technique involves using a series of buried flatbed scanners. This adaptation offers the

349 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

469

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631

632

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

634

635

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

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

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	

664   b) Calculation of the annual production P_a

665

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

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

674

Method	Formula	Calculation		Turnover T (y^{-1})
		Using B_{mean}	Using B_{max}	
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

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)

Country -Site	Mean annual temp. (°C)	Soil layers	Depth (cm)	Diam. (mm)	Age (y)	Biomass (B) Mean (g m^{-2})	Max. (g m^{-2})	Decision Matrix Production (g m^{-2} y^{-1})	Turnover B_{mean} (y^{-1})	B_{max} (y^{-1})	Maximum-Minimum Production (g m^{-2} y^{-1})	Turnover B_{mean} (y^{-1})	B_{max} (y^{-1})	References
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)

711 **Table 3**   (continued)
712
713 *Picea abies:*

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 *Pinus sylvestris:*

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 *Populus spp.:*

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 *Quercus ilex / Q. cerrioides:*

733	ES-Bages	14.4		0-50	<5	10	858	1336	-	-	-	812	0.95	0.61	Miguel Pérez (2010)

734 *Quercus petraea:*

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
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

Country -Site	Mean annual temp. (°C)	Depth (cm)	Year after install. (y)	Diam. (mm)	Age (y)	Biomass (B) Mean (g m^{-2})	Max. (g m^{-2})	Decision Matrix Production (g m^{-2} y^{-1})	Turnover B_{mean} (y^{-1})	B_{max} (y^{-1})	Maximum-Minimum Production (g m^{-2} y^{-1})	Turnover B_{mean} (y^{-1})	B_{max} (y^{-1})	References
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)

758 **Table 5** Summary of biomass, annual production, and turnover values (±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})
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)

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

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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)

815   [1] and Tatarinov and Ciencela (2006)

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)

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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

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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 (△), temperate (●), and tropical (◊). 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
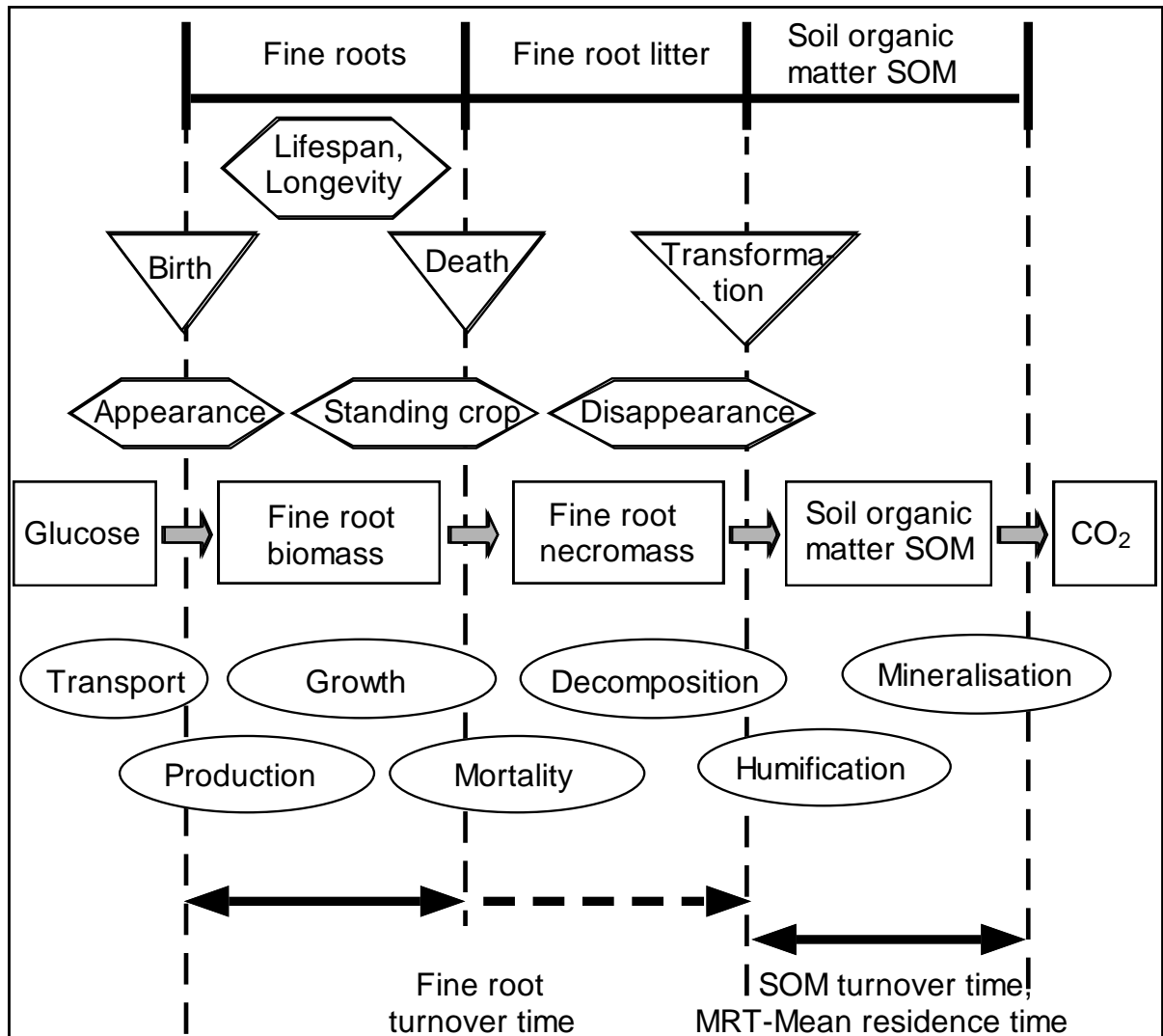
841   maximum biomass data)

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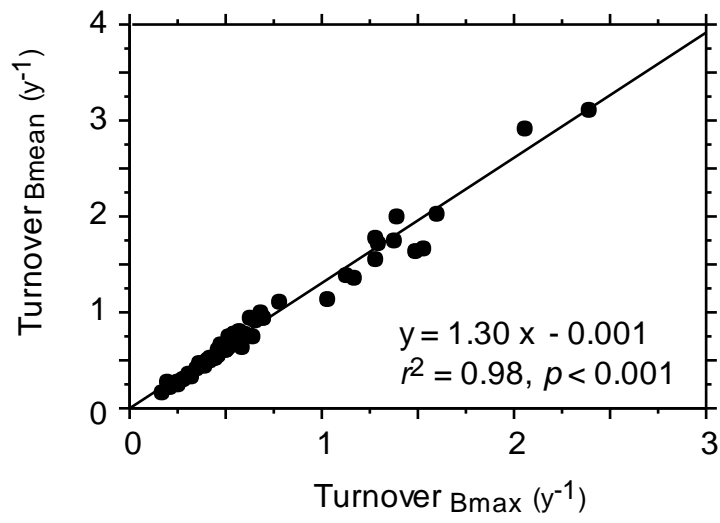
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853   Figure 1.

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The plot shows a scatter with regression:

$$y = 1.30\,x - 0.001$$
$$r^2 = 0.98,\ p < 0.001$$

X-axis: Turnover $_{Bmax}$ (y^{-1})

Y-axis: Turnover $_{Bmean}$ (y^{-1})

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874   Figure 2.

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The plot shows Turnover$_{whole\ profile}$ (y^{-1}) on the y-axis versus Turnover$_{layer-per-layer}$ (y^{-1}) on the x-axis, with fitted line:

$$y = 0.88\ x - 0.18$$
$$r^2 = 0.92,\ p < 0.001$$
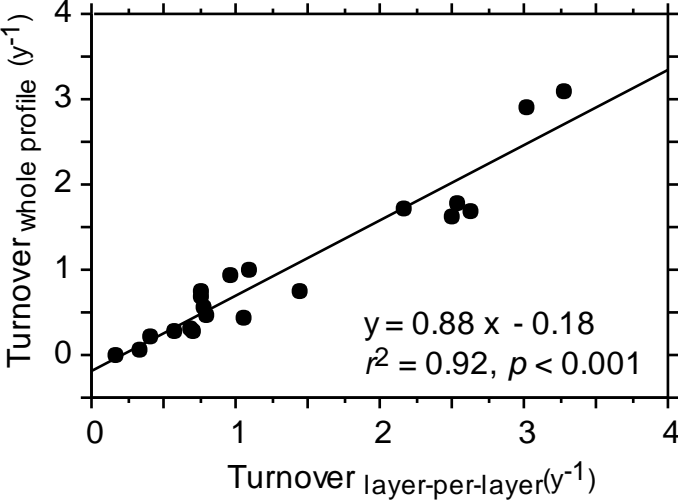
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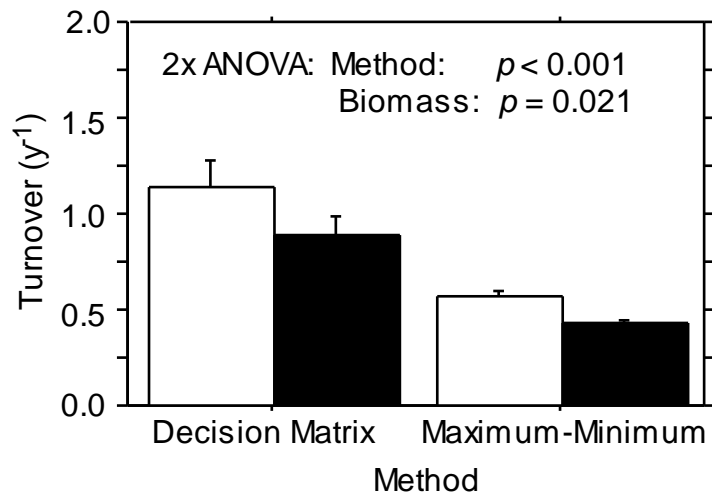888

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891   Figure 3.

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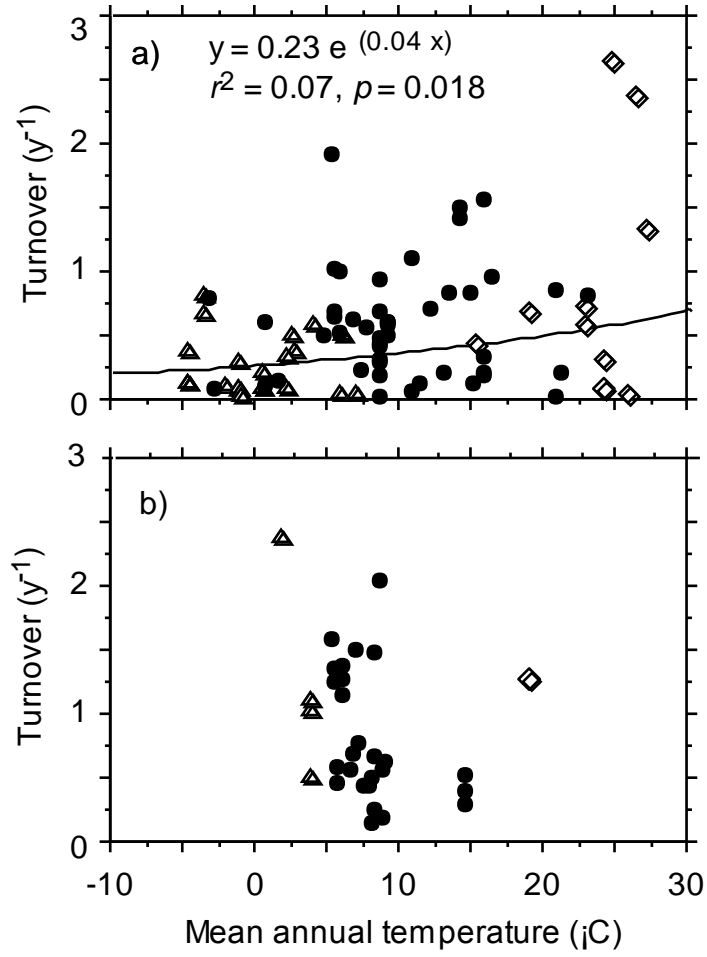
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909   Figure 4.

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923   Figure 5.

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