1 **Nutrient availability and climate as the main determinants of the ratio**

2 **of biomass to NPP in woody and non-woody forest compartments**

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4 **Authors:** Marcos Fernández-Martínez [*ab], Sara Vicca [c], Ivan A. Janssens [c], Matteo

5 Campioli [c], Josep Peñuelas [ab].

6

7 **Addresses:**

8 [a] CSIC, Global Ecology Unit, CREAF-CSIC-UAB, Cerdanyola del Vallés 08193, Catalonia,

9 Spain

10 [b] CREAF, Cerdanyola del Vallès 08193, Catalonia, Spain.

11 [c] Centre of Excellence PLECO (Plant and Vegetation Ecology), Department of Biology,

12 University of Antwerp, 2610 Wilrijk, Belgium.

13

14 [*]**Corresponding author:**

15 Marcos Fernández-Martínez

16 Tel: +34 935 814 851

17 E-mail address: m.fernandez@creaf.uab.cat

18

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21

22 **Abstract**

23 Forest ecosystems accumulate large amounts of carbon in living tissues. The residence time of

24 this carbon in the ecosystem depends largely on the turnover time of these tissues, which can be

25 estimated as a surrogate of the ratio of biomass to net primary production (B:NPP). We used a

26 global forest database of 310 sites containing data for biomass stocks and NPP to investigate the

27 differences of B:NPPs among species and forest compartments and to determine B:NPPs main

28 exogenous (mainly climate and nutrient availability) and endogenous (leaf habit and stand age)

29 drivers. We used asymptotic exponential functions to adjust the B:NPPs of woody compartments

30 to a theoretical stationary state to allow comparisons between forests of different ages. The

31 B:NPPs of woody tissues (branches, stems, and coarse roots) were positively influenced by

32 stand age, conversely to fine roots and leaves, which were weakly dependent on the age of the

33 forest. The B:NPPs of woody tissues were positively correlated with nutrient availability, whereas

34 fine-root B:NPPs decreased with increasing nutrient availability. The foliar B:NPP of evergreen

35 forests was positively correlated with water deficit, and the fine-root B:NPP was correlated

36 positively with the seasonality of precipitation and with annual thermal amplitude but negatively

37 with water deficit. Our results support the influence of climate on the B:NPPs of non-woody

38 compartments and identify nutrient availability as the main influence on the B:NPPs of woody

39 tissues.

40

41 **Keywords:** turnover, residence time, nutrient availability, climate, stationary state, carbon

42 sequestration

1. Introduction

Forest ecosystems accumulate and sequester large amounts of carbon, both as living tissues and as soil organic matter (Dixon et al. 1994; Myneni et al. 2001; Pan et al. 2011). The expected duration of a carbon atom in an ecosystem, however, strongly depends on the compartment of the forest to which the atom was allocated (e.g. foliage, stems, roots; Luo et al. 2003; Zhang et al. 2010). To evaluate this duration, ecologists often use the term "turnover time" as the inverse of "turnover rate" as defined by Margalef (1974). The study of turnover times of compartments is of paramount importance not only to determine the duration of carbon sequestration in the living biomass of an ecosystem, and therefore to properly assess carbon sequestration, but also to provide a better understanding of carbon and nutrient cycling in forests.

The turnover time of carbon, also termed mean residence time, indicates the average time that a carbon atom remains in its initial ecosystem compartment under the assumption of stationarity: the condition for which input (biomass production) equal output (necromass production) (i.e. biomass does not accumulate in the system). This assumption, however, is rarely realised (except for foliage and fine roots), so the study of turnover times has usually been based on modelling (Dewar 1991; Kicklighter et al. 1999; Barrett 2002; Luo et al. 2003; Karlberg et al. 2006; Zhang et al. 2010) rather than on empirical data. In this sense, the ratio of biomass to net primary production (B:NPP) may serve as a useful surrogate of the turnover times under determined conditions (stationarity or pseudo-stationarity).

Extensive research has focused on the B:NPPs of foliage (Reich et al. 1992; Aerts 1995; Wright and Westoby 2003) and fine roots (Dahlman and Kucera 1965; Nadelhoffer 2000; Gill and Jackson 2000; Majdi et al. 2005), but very few studies have analysed other living compartments such as branches, stems, or coarse roots, and, to the best of our knowledge, no single study has yet synthesised the turnover times of all compartments in concert.

The factors controlling the variability of B:NPPs of different compartments in forests under various environmental conditions (e.g. climate and nutrient availability) and endogenous characteristics

69 (e.g. stand age and leaf habit) remain undetermined. Detecting the potential controls of B:NPPs

70 of different compartments may help to predict the fate of carbon in different types of forests.

71 Endogenous factors such as stand age and leaf habit or type, combined with exogenous factors

72 such as climate, nutrient availability, or management, can influence B:NPPs in different ways in

73 different forest compartments. Nutrient-rich forests tend to have lower B:NPPs than nutrient-poor

74 forests (Jordan and Herrera 1981) because of a higher biomass production, but this relationship

75 has only been tested for foliage and fine roots (Reich et al. 1992; Aerts 1995; Ryser 1996).

76 Nutrient-rich forests typically allocate a larger proportion of their photosynthates to aboveground

77 biomass compared to nutrient-poor forests (Litton et al. 2007; LeBauer and Treseder 2008; Vicca

78 et al. 2012; Fernández-Martínez et al. 2014a), and the ultimate effect of nutrient availability on

79 carbon sequestration in ecosystems thus depends on the concerted response of the turnover

80 times of the various plant organs and on the allocation strategy. Changes in carbon allocation

81 may also lead to differences in carbon stocks in aboveground versus belowground compartments,

82 depending on nutrient availability, and therefore to contrasting relationships between B:NPP and

83 nutrient richness for aboveground versus belowground compartments. If these mechanisms were

84 real, we would expect the relationship between B:NPP and higher nutrient availability to be

85 positive in aboveground compartments and negative in belowground compartments.

86 The aim of this study was to calculate the B:NPPs of five compartments (foliage, branches, stems,

87 coarse roots, and fine roots) of forest ecosystems around the world and to explore the

88 endogenous (stand age and leaf habit and type) and exogenous (climate and management)

89 factors that control them. We also particularly investigated the role of nutrient availability as a

90 likely control of B:NPP.

91 **2. Materials and Methods**

92 *2.1. Data collection*

93 *2.1.1 Global forest database*

4

94   We updated and analysed a global forest database (Luyssaert et al. 2007) containing data from

95   1990 to 2012 for NPP and stand biomass for five forest compartments (foliage, branches, stems,

96   coarse roots, and fine roots [diameter ≤2 mm]) from 310 sites around the world comprising boreal,

97   temperate, Mediterranean, and tropical biomes, albeit the tropical and Mediterranean forests

98   were less well represented. Only 80 of the forests provided the necessary data to calculate

99   B:NPP for at least one of the compartments. The database also included descriptive information

100   of the forests, such as stand age, leaf type (needleleaved, broadleaved, or mixed forest), leaf

101   habit (evergreen, deciduous, or mixed forest), type of management (managed or unmanaged

102   forests), and nutrient availability (see Fernández-Martínez et al., 2014; Vicca et al., 2012), which

103   we used to calculate a proxy of *nutrient richness* (see section 2.2.3).

104   *2.1.2 Climatic data*

105   We extracted climatic data for our forests from the WorldClim database (Hijmans et al. 2005).

106   This database provides suitable climatic data with a high spatial resolution (30 arc seconds, ca. 1

107   km at the equator) and contains robust mean monthly climatic data derived from a lengthy time

108   series (1950 to 2000), including monthly temperature and precipitation and several other climatic

109   variables such as annual thermal amplitude and seasonality of precipitation.

110   The time series for evapotranspiration (MOD16A2) from MODIS (Moderate Resolution Imaging

111   Spectroradiometer) were downloaded for the period between 1 January 2000 and 27 December

112   2009 to obtain climatic proxies of potential and actual evapotranspiration (PET and AET,

113   respectively). We downloaded the data with a resolution of 9 km^2 (3 × 3 km) around the central

114   coordinates.

115   *2.2. Data analyses*

116   *2.2.1 B:NPPs*

117   We calculated B:NPP similar to previous studies (Dahlman and Kucera 1965; Margalef 1974;

118   Malhi et al. 1999; Gill and Jackson 2000), dividing stand biomass by mean NPP for each

119   compartment. The availability of NPP and biomass data was uneven for the compartments, so we

120   calculated B:NPP for foliage, branches, stems, and coarse and fine roots from 71, 44, 44, 70, and

121   80 forests, respectively.

122   Stand biomass was strongly age-dependent in non-stationary compartments such as branches,

123   stems, and coarse roots (**Figure S1**) (in contrast to foliage and fine roots). Previous studies have

124   suggested a strong relationship between NPP and stand age (Carey et al. 2001 and references

125   therein), but our data showed no clear trend with stand age (**Figure S2**). Nonetheless, comparing

126   the biomasses or B:NPPs of forests of differing average stand ages (and thus biomasses) would

127   be nonsensical for woody compartments. We avoided this problem and compared forests of

128   different ages by adjusting the biomasses and B:NPPs of branches, stems, and coarse roots to

129   their theoretical stationary state (at approximately 200 years of age, assumed to be when the

130   percent annual increase in biomass and B:NPP from most compartments was <0.5%). We thus

131   removed fast-growing species (e.g. *Acer* sp., *Alnus* sp., *Betula* sp., and *Populus* sp.) from the

132   analyses. We calculated the stationary B:NPP by first fitting our data to an asymptotic exponential

133   function, as conceptually suggested by Hougthon (2009). We then extracted the residuals of all

134   cases and summed them to the predicted biomass or B:NPP of the function for 200 y (i.e. raw

135   residuals + fitted B:NPP at 200 y). These adjusted values were used for regression models (see

136   section 2.2.4) and to obtain means. The fitted value at 200 y only changed the means of the

137   biomasses and B:NPPs, so our choice of age did not influence the significance of our results.

138   *2.2.2 Climatic predictors*

139   We used mean annual temperature (MAT) and precipitation (MAP) from the WorldClim database

140   and calculated the length of the warm period (sum of months >5 ºC) using mean monthly

141   temperatures. We also extracted two key climatic variables: annual thermal amplitude (mean

142   maximum minus mean minimum temperature for the year) and seasonality of precipitation

143   (measured as the coefficient of variation of precipitation among months).

144 We calculated the percentage water deficit from the MODIS evapotranspiration time series as

145 WD = (1 – [AET/PET])*100, (Fernández-Martínez et al. 2014b) as an indicator of the intensity of

146 water stress the forests must withstand. We thus used eight climatic predictor variables: MAT,

147 MAP, mean temperature and precipitation for the warm period, length of the warm period, annual

148 thermal amplitude, seasonality of precipitation, and WD.

149 *2.2.3 Assessment of nutrient availability*

150 The forest database contained information about the nutrient status of the forests for variables

151 such as soil type, texture, pH, nitrogen and phosphorous content, nitrogen mineralisation, C:N

152 ratio, and CEC; foliar nitrogen and phosphorous concentrations; nitrogen deposition; and the

153 history of the stand or explicit reports of the fertility of the forests (Vicca et al. 2012; Fernández-

154 Martínez et al. 2014a), but information for all variables was not available for each site. We coded

155 each variable into three levels of nutrient availability, high, medium, and low, following the

156 methodology and data reported by Fernández-Martínez et al. (2014a). We then transformed each

157 three-level factor into three dummy variables, each indicating high, medium, or low nutrient

158 availability. We next performed a factor analysis to reduce the number of dimensions of our data

159 set using only dummy variables indicating high and low nutrient availability. The first resulting

160 factor (F1: nutrient richness covariate) explained 16% of the variance of the data and was

161 correlated positively with nutrient-rich and negatively with nutrient-poor dummy variables.

162 *2.2.4 Statistical analyses*

163 We used stepwise forward regression models to correlate the B:NPPs (previously adjusted to the

164 stationary state of 200 y) with the climatic variables (see section 2.2.2), the nutrient richness

165 covariate (F1), management, and leaf type and habit. Predictor covariates were entered twice for

166 selection in the models, with and without transformation to natural logarithms, to identify possible

167 nonlinearities. The dependent variables usually required transformation to meet the assumptions

168 of normality and homoscedasticity of the residuals. We evaluated the contribution of each

169 predictor variable to B:NPP using the *PMVD* (Proportional Marginal Variance Decomposition,

170 (Grömping 2007)) metric of the R (R Core Team 2013) package *relaimpo* (Grömping 2006) as a

171 measure of the variance explained by each predictor. We excluded variables with high collinearity

172 from the models (variance inflation factor [VIF] >5). We also used the three levels of nutrient

173 availability (high, medium, and low) used by Vicca et al. (2012) and Fernández-Martínez et al.

174 (2014b) to compare means among groups. Differences among groups were tested using ANOVA

175 tables and the Tukey HSD test for multiple comparissons.

176 **3. Results**

177 *3.1. Adjusted B:NPPs across forest types*

178 A strong correlation between woody (branches, stems, and coarse roots) biomass and forest age

179 (**Figure S1**) produced a strong correlation between woody B:NPPs and stand age (**Figure 1**).

180 The asymptotic exponential functions indicated that branches reached a stable B:NPP of 45 y

181 when trees were about 150 years old (**Figure 1a**). Stationary B:NPPs for stems and coarse roots

182 reached 115 and 104 y, respectively, at an age of approximately 200 y (**Figure 1b and c**). The

183 fitted functions between B:NPP and stand age presented a pseudo-R^2 of 0.31, 0.81, and 0.73 in

184 branches, stems, and coarse roots, respectively (**Figure 1**). B:NPP and stand age were not

185 significantly correlated for fine roots or evergreen foliage (**Figure 2**).

186 Stationary B:NPP did not significantly differ among biomes or leaf habits in woody compartments

187 (ANOVA, $P > 0.05$) but differed significantly between leaf types for foliage and fine roots (ANOVA,

188 $P < 0.01$; **Table 1**). Biome-averaged differences among woody fractions (branches, stems, and

189 coarse roots), however, were large. The B:NPPs at the 20 and 80 percentiles were 21-80 y for

190 branches, 71-171 y for stems, and 63-176 y for coarse roots. Differences among woody

191 compartments were statistically significant for some species **(Table 1)**. For example, *Fagus*

192 *sylvatica* had a longer B:NPP in the stem (122 ± 19) and coarse-root (83.9 ± 18) fractions than in

193 the branch fraction (22 ± 3, $P < 0.05$). This trend was also consistent for *Picea abies* and

194 *Pseudotsuga menziesii* ($P < 0.05$ and $P < 0.01$, respectively). The B:NPPs of fine roots and

195 leaves ranged between 1 and 5 y, with lower B:NPPs in deciduous than evergreen forests for
196 both fine roots and leaves ($P < 0.01$, Table 1).

197 *3.2. Controls of the B:NPPs*

198 Our results indicated that the various forest compartments were correlated with different
199 endogenous and exogenous factors **(Table 2)**. Age-adjusted B:NPP was controlled by nutrients
200 in the compartments that accumulate biomass over long periods (branches, stems, and coarse
201 roots). Nutrient richness explained 20, 35, 9, and 6% of the variance in the B:NPPs of branches,
202 stems, and coarse and fine roots, respectively. Foliage B:NPP was not correlated with nutrient
203 availability ($P > 0.05$, **Table 2**). Nutrient-rich forests had longer B:NPPs than nutrient-poor forests
204 in woody compartments (Tukey's test, $P < 0.05$; **Table S2, Figure 3a, b, and c**). The response of
205 the B:NPPs of woody fractions to nutrient availability, however, differed from the response of the
206 fine-root fraction (**Table 2, Figure 4**), which behaved oppositely (**Table S2, Figure 3d**). Forests
207 with higher nutrient availability had longer B:NPPs in woody tissues (branches, stems, and
208 coarse roots, **Figure 4a**) in comparison to nutrient-poor forests ($P < 0.05$), but forests with
209 nutrient limitations had longer B:NPPs in fine roots than nutrient-rich forests ($P = 0.002$; **Figure**
210 **4b**). Nutrient availability was not aligned with old or young forests (ANOVA, $P > 0.1$). Our results
211 should therefore not be biased because of age differences between nutrient-rich and nutrient
212 poor forests. Despite the possible combined effect that nutrient availability and management can
213 have on biomass production (Campioli et al. 2015), B:NPP did not differ significantly between
214 managed and unmanaged forests in any compartment.

215 Carbon stocks in the biomasses of branches and stems increased with nutrient availability (**Table**
216 **S2, Figure 5**; $P < 0.05$). Fine roots had the opposite trend, but the results were not statistically
217 significant. Production (NPP) varied little (**Table S2, Figure 5**) among nutrient classes. The
218 differences in B:NPP with nutrient availability were thus due to differences in stand biomass
219 rather than to differences in NPP.

9

220 Leaf habit was responsible for the largest differences in foliage B:NPP **(Table S2)**. Foliage B:NPP

221 averaged approximately 1 y in deciduous forests and 4.3 ± 0.4 y in evergreen forests **(Table S2)**.

222 Branch B:NPP was longer in evergreen than deciduous forests **(Table 2)**. Evergreen foliage

223 B:NPPs were positively correlated with water deficit, and fine-root B:NPPs were higher in forests

224 with low water stress (**Table 2**). The seasonality of precipitation, however, was the most

225 (positively) correlated variable with fine-root B:NPP, explaining 58% of its variance. High values

226 of annual thermal amplitude were also correlated with high fine-root B:NPPs. Evergreen foliage

227 and fine-root B:NPPs were marginally positively correlated with stand age (**Figure 2**, **Table 2**).

228 **4. Discussion**

229 Our results identified large differences in B:NPPs among forest compartments but only small

230 differences among tree species (**Tables 1 and S2, Figure 3**). The slow-growing species in this

231 study may thus have similar structural and functional properties, which allowed us to compare the

232 role of exogenous controls of B:NPP spatial variability. The B:NPPs were mostly driven by

233 climate in non-woody tissues but by age and nutrient availability in woody tissues.

234 *4.1. The role of climate in non-woody compartments*

235 Climate played a significant role in determining the B:NPPs of non-woody compartments such as

236 foliage and fine roots but not of branches, stems, and coarse roots. The negative correlation

237 between foliar B:NPPs and water deficit may indicate that forests under high water stress are

238 unable to sustain as much leaf biomass as forests with good hydric conditions, as previous

239 studies have reported (Fernández-Martínez et al. 2014b).

240 Fine-root B:NPPs were strongly correlated with intra-annual climatic variability (thermal amplitude

241 and especially the seasonality of precipitation). This relationship supports previous findings,

242 suggesting that the B:NPPs of fine roots decrease with climatic seasonality (Gill and Jackson

243 2000). Climatic seasonality may lead to periods of extreme weather (e.g. drought or cold) during

244 the year that may kill fine roots, thus decreasing their life span. This negative effect of seasonality

245 may also indicate that warmer forests (with less seasonality) need a higher fine-root NPP to

246 sustain the same pools of fine-root biomass (Gill and Jackson 2000) due to the higher metabolic

247 rates.

248 In contrast to foliage and fine roots, the B:NPPs of woody tissues were not correlated with climate,

249 perhaps because woody tissues are organs that accumulate much biomass in a very recalcitrant

250 form and are therefore relatively insensitive to meteorological conditions. Also, the turnover of

251 woody tissues is primarily associated with tree mortality and is therefore less sensitive to normal

252 meteorological conditions (without considering events of extreme weather causing disturbances

253 such as windthrows, storms, or heat waves causing mass mortality).

254 *4.2. The role of nutrient availability in woody and non-woody compartments*

255 The positive effect of nutrient availability on woody B:NPPs was driven by the larger carbon pools

256 in nutrient-rich than in nutrient-poor forests, not by an increase in biomass production (NPP),

257 which remained fairly constant among the classes of nutrient availability (**Table S2**). We can thus

258 infer that either necromass production is higher in nutrient-poor forests or that nutrient-rich forests

259 can sustain more living biomass than nutrient-poor forests. This finding also supports the

260 hypothesis that nutrient-rich forests allocate larger proportions of photosynthates to wood than

261 nutrient-poor forests (Vicca et al. 2012). Woody compartments have longer B:NPPs than non-

262 woody organs (**Tables 1 and S2, Figure 3**), so our findings also suggest that nutrient-rich forests

263 are more likely to act as carbon sinks than nutrient-poor forests (Fernández-Martínez et al.

264 2014a). Nutrient-rich forests thus accumulate more biomass, and the carbon is more likely to

265 reside longer in the living biomass.

266 In contrast to woody compartments, fine-root B:NPPs are shorter in nutrient-rich forests,

267 supporting previous research suggesting that nutrient-poor forests increase the life-span of fine

268 roots to increase nutrient-use efficiencies and thus to avoid nutrient losses (Reich et al. 1992;

269 Aerts 1995; Ryser 1996). Foliar B:NPPs were not significantly correlated with nutrient richness,

270 which may be linked to the hypothesised higher resorptive capacity of leaves than of fine roots

271 (Freschet et al. 2010).

11

272 *4.3. Methodological considerations*

273 The non-stationarity of woody compartments that we have attempted to resolve by removing the

274 effect of stand age from our estimates of B:NPP suggests that our results should be interpreted

275 with caution. Turnover times in leaves and fine roots could theoretically be calculated as the pool-

276 to-flux ratio, because biomass in these compartments reaches a steady state at relatively young

277 ages (Ryan et al. 1997; Chen et al. 2007). This methodology (simple B:NPP calculation) to

278 evaluate turnover times, however, may certainly underestimate the real average time that an

279 amount of carbon will reside in compartments where biomass increases with time (i.e. branches,

280 stems, and coarse roots), leading to a strong association between turnover time and age (**Figure**

281 **1**). Biomass in woody compartments, however, tends to a steady state with age (Hougthon 2009;

282 Fernández-Martínez et al. 2014b), so the pool-to-flux ratio might provide reliable estimates in old-

283 growth forests that have already reached a stationary state when the inputs equal the outputs

284 (NPP – necromass production = 0). The alternative to studying only old-growth forests is to adjust

285 the pool-to-flux ratio to a theoretical stationary state of the stands following an asymptotic function

286 describing the increase in pool-to-flux ratio with age, which is the methodology we have chosen.

287 By adjusting B:NPPs to the stationary state, we can provide surrogates of turnover times that

288 should be useful to forest managers and the modelling community.

289 **5. Conclusions**

290 We detected large differences in B:NPPs among forest compartments but only small differences

291 among tree species (**Tables 1 and S2, Figure 3**). Once the effect of stand age was removed for

292 compartments without stationary behaviour (**Figure. 1**), nutrient availability (**Figure 4**) and

293 climate (mostly water deficit and seasonality) were identified as playing crucial roles in

294 determining the B:NPPs of woody and non-woody tissues, respectively (**Table 2**).

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Figure captions

Figure 1: Relationships of the B:NPPs of a) branches, b) stems, and c) coarse-roots with stand age. Data were fitted using an asymptotic exponential function.

Figure 2: Relationships of the B:NPPs of a) foliage and b) fine roots with stand age.

Figure 3: B:NPPs of a) branches, b) stems, c) coarse roots, and d) fine roots for different levels of nutrient availability. The branch, stem, and coarse-root B:NPPs have been adjusted to the stationary state (200 y) using the equations in **Figure 1**. Exact values can also be found in **Table S2**. Different letters above the bars indicate significant differences using Tukey's HSD test for multiple comparisons at the 0.05 level.

Figure 4: Relationships of the B:NPPs of (a) stems and (b) fine roots with nutrient richness.

Figure 5. Stand biomass and NPP of branches, stems, coarse-roots and fine-roots for different levels of nutrient availability. The biomasses for branches, stems, and coarse roots have been adjusted to the stationary state (200 y) using an asymptotic exponential function (see Materials and Methods for further information). Exact values can also be found in **Table S2**. Different letters above the bars indicate significant differences using Tukey's HSD test for multiple comparisons at the 0.05 level.

398   **Table 1:** B:NPPs (mean years ± standard error) of leaves, branches, stems, and coarse and fine

399   roots across species and biomes adjusted to the stationary state (200 y) (except for foliage and

400   fine roots). The number of forests is shown in parentheses. Different letters within a column

401   indicate significant differences among groups ($P < 0.05$) using Tukey's HSD test for multiple

402   comparisons.

Species	Foliage	Branches	Stems	Coarse roots	Fine roots
Cocos nucifera	2.5 (1)				
Fagus sylvatica	1.1 ± 0.1 (12)	21.6 ± 3.0 (5)	121.9 ± 19.2 (5)	83.9 ± 17.6 (8)	1.1 ± 0.04 (8)
Larix gmelinii		20.9 (1)	100.2 (1)	37.0 (1)	
Picea abies	4.4 ± 0.4 (11)	31.3 ± 16.6 (5)	134.1 ± 31.1 (5)	86.1 ± 7.4 (7)	1.4 ± 0.4 (7)
Picea mariana	9.5 (2)			186.7 (2)	5.5 (1)
Pinus banksiana	2.0 (1)			277.9 (1)	3.4 (1)
Pinus ponderosa	4.1 ± 0.5 (13)	99.7 ± 35.2 (12)	118.5 ± 17.9 (12)	132.5 (2)	2.0 (2)
Pinus radiata	5.3 (1)		167.5 (1)	155.5 (1)	0.7 (1)
Pinus strobus				163.3 ± 18.1 (4)	
Pinus sylvestris	4.4 ± 1.1 (6)	134.7 ± 99.0 (3)	93.8 ± 23.1 (3)	124.2 ± 63.5 (3)	2.1 ± 0.6 (3)
Pinus taeda				167.4 (1)	
Pseudotsuga menziesii	3.5 ± 0.5 (12)	35.8 ± 5.6 (12)	94.0 ± 14.1 (12)	85.0 ± 15.6 (12)	6.1 ± 0.6 (11)

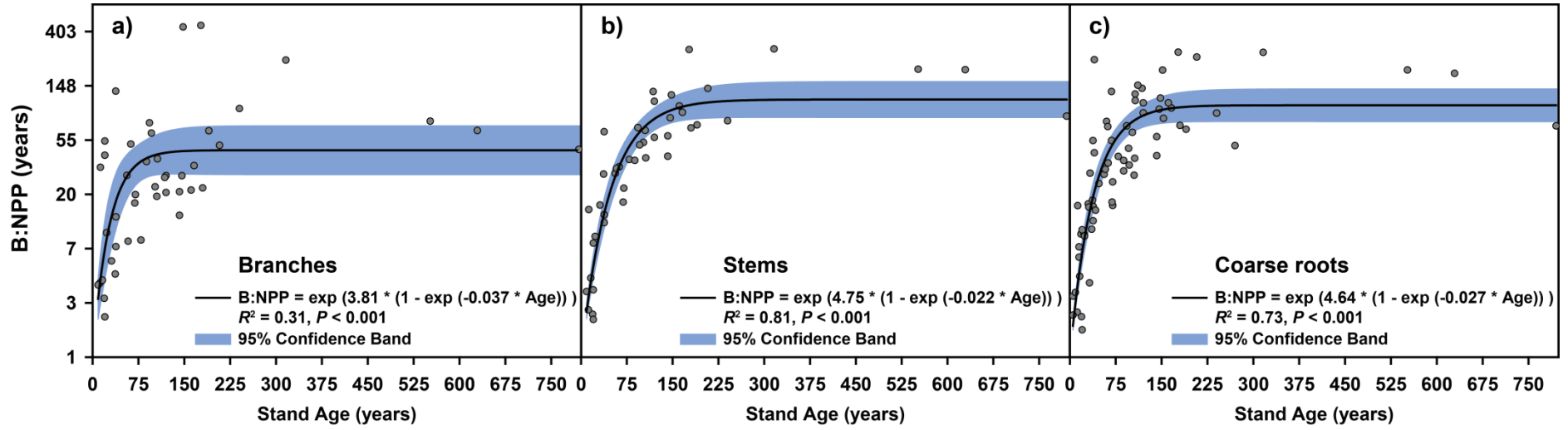| Biome					
Boreal evergreen	5.4 ± 1.1[a] (9)	134.7 ± 99.9[a] (3)	93.8 ± 23.1[a] (3)	172.8 ± 36.9[a] (6)	3.0 ± 0.7[ab] (5)
Boreal deciduous	1.0[b] (2)	20.9[a] (1)	100.2[a] (1)	37.0[a] (1)	2.2[ab] (1)
Temperate evergreen	4.1 ± 0.3[a] (42)	99.5 ± 22.8[a] (32)	139.7 ± 20.3[a] (32)	132.5 ± 15.8[a] (31)	3.7 ± 0.6[a] (24)
Temperate deciduous	1.1 ± 0.1[b] (15)	30.2 ± 7.7[a] (7)	113.4 ± 14.7[a] (7)	184.4 ± 89.8[a] (12)	1.4 ± 0.2[b] (12)

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Table 2: Summary of the models for the B:NPPs of evergreen foliage, branches, stems, and coarse and fine roots using stepwise forward regressions. For these analyses, the B:NPPs of woody compartments were adjusted to 200 y using an asymptotic exponential function (see Materials and Methods). Values indicate β ± standard error, and the proportion of variance explained (in %) is shown in parentheses. For branches, stems, and coarse roots, the reported variance explained by stand age (*) is the R^2 from the asymptotic exponential functions in **Figure 1** and is not accounted for in the R^2 of the stepwise models. All coefficients were significant at the 0.05 level except those marked with [†], indicating significance at the 0.1 level, or by n.s., indicating that the term was not significant. PS, precipitation seasonality; ThA, annual thermal amplitude; WD, water deficit. Ln indicates natural-log transformation. For leaf habit, D indicates deciduous and E indicates evergreens.

Stepwise regression	Ln foliage	Ln branches	Ln stems	Ln coarse roots	Ln fine roots
Leaf habit		D < E (11)			
Nutrient richness (F1)		0.48 ± 0.15 (20)	0.59 ± 0.15 (35)	0.36 ± 0.14 (9)	-0.18 ± 0.09 (6)
PS					0.69 ± 0.08 (58)
Ln ThA				0.26 ± 0.14 (5)[†]	0.25 ± 0.10 (5)
Ln WD	0.30 ± 0.13 (8)				-0.23 ± 0.09 (4)
Ln Age	0.28 ± 0.13 (7)	(31)*	(81)*	(73)*	0.19 ± 0.08 (5)
R^2	15	31	35	14	78

Figure 1

Figure 2

Figure 3

a) Branches   b) Stems   c) Coarse roots   d) Fine roots

Figure 4

a) Stems

$R^2 = 0.36$; $P < 0.001$

b) Fine roots

$R^2 = 0.21$; $P = 0.002$

Ln B:NPP (years)

Ln Nutrient Richness (F1)
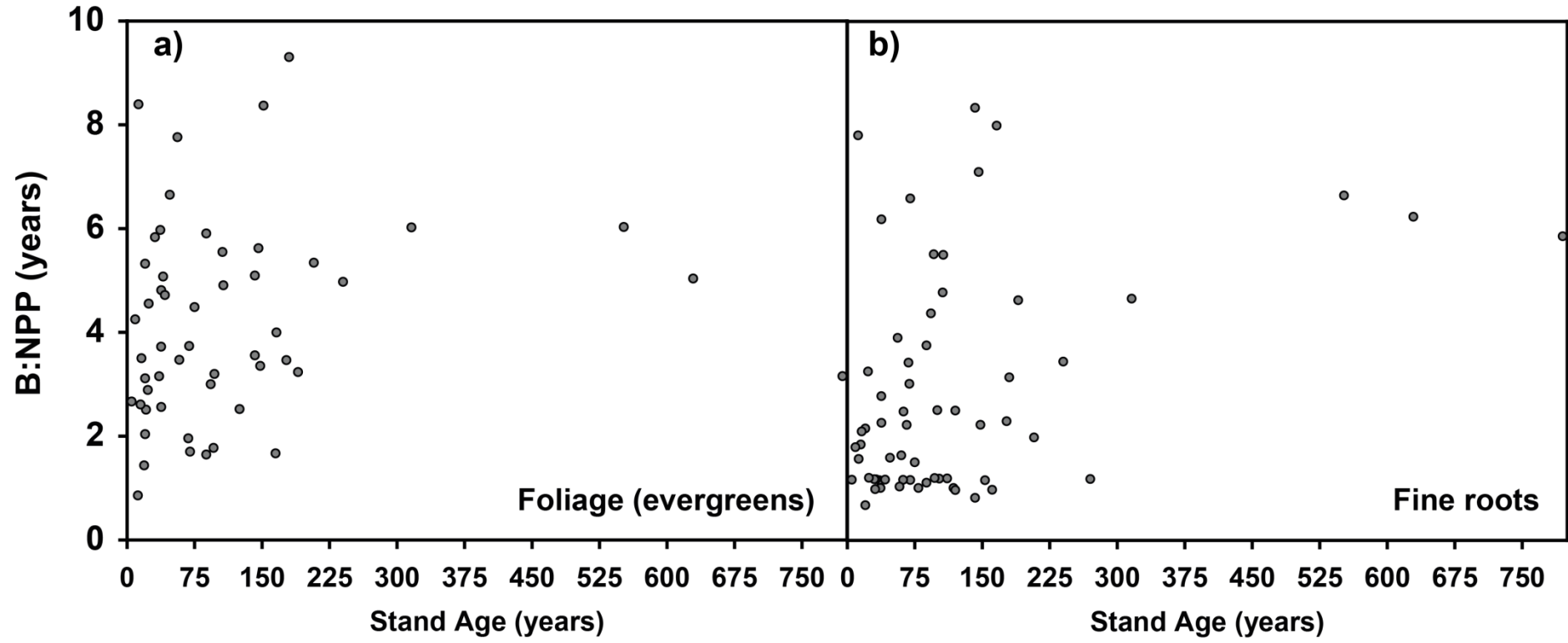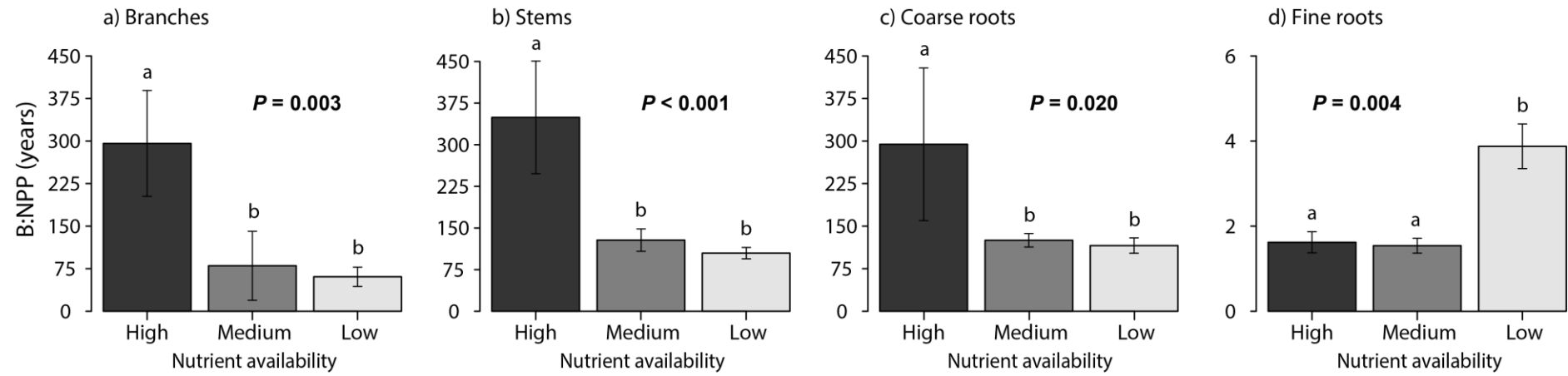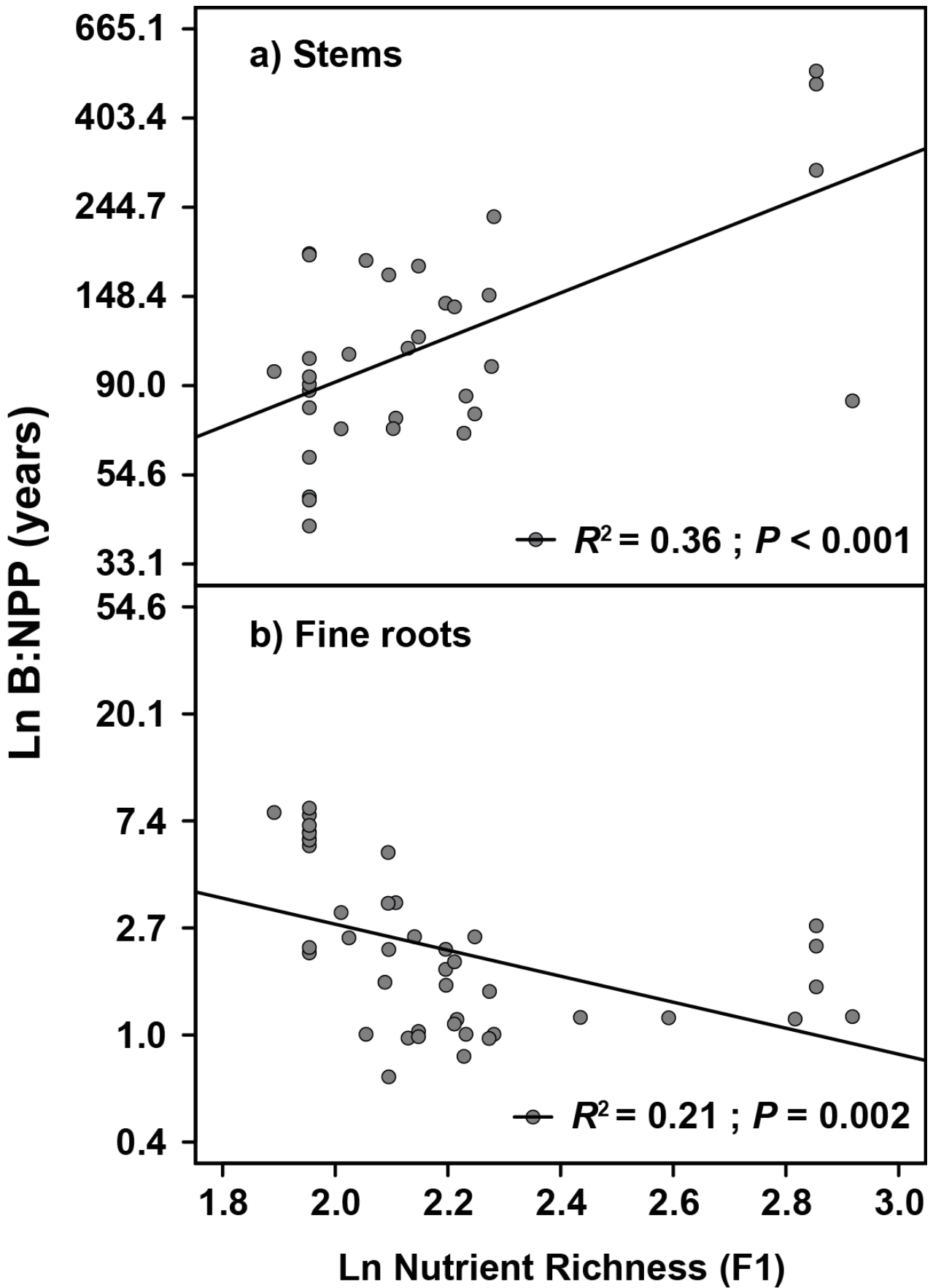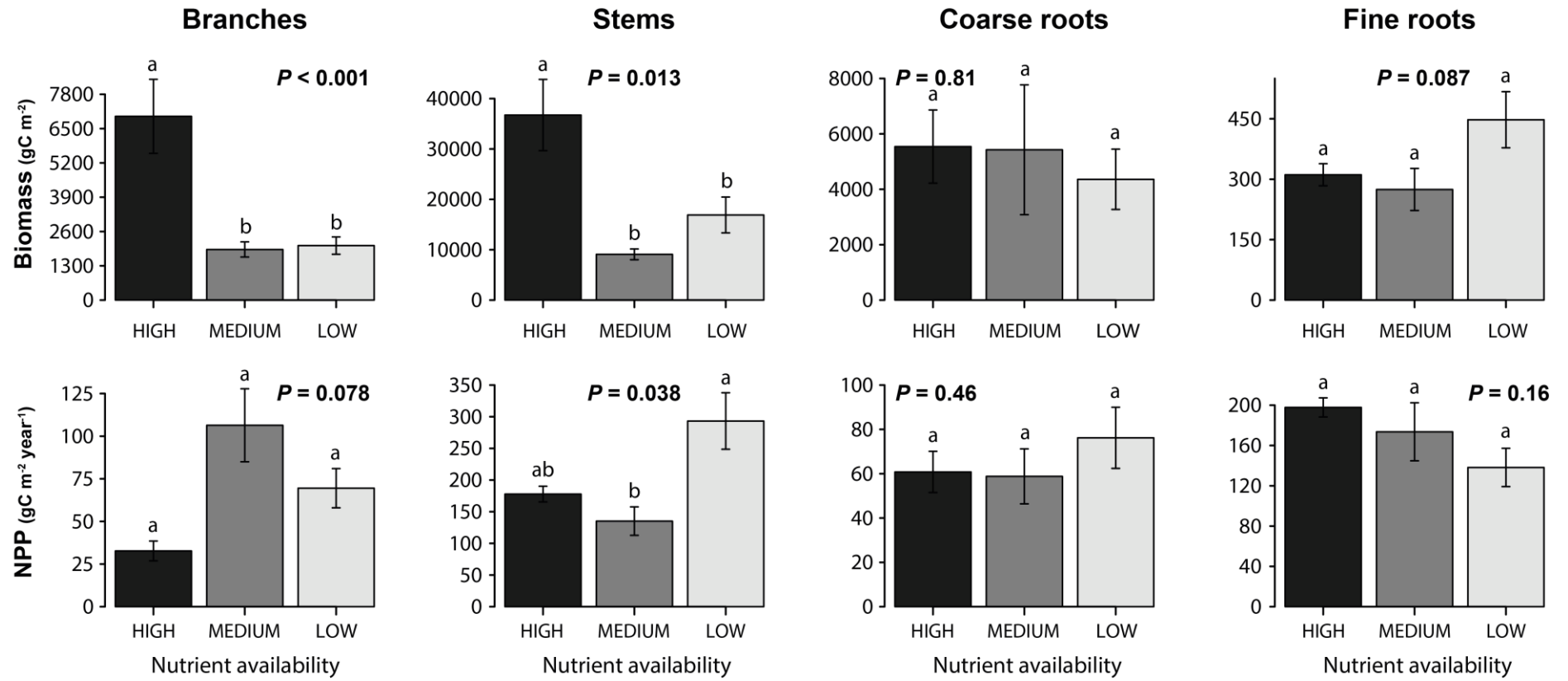
Supplementary material

Figure captions

Table S1: B:NPPs (mean years ± standard error) of leaves, branches, stems, and coarse and fine roots across species and biomes. The B:NPPs were not adjusted to the stationary state. The number of forests is shown in parentheses.

| Species	Foliage	Branches	Stems	Coarse roots	Fine roots
Cocos nucifera	2.5 (1)				
Fagus sylvatica	1.1 ± 0.1 (12)	20.3 ± 3.1 (5)	87.4 ± 18.1 (5)	66.4 ± 17.2 (8)	1.1 ± 0.04 (8)
Larix gmelinii		19.3 (1)	65.2 (1)	28.6 (1)	
Picea abies	4.4 ± 0.4 (11)	26.0 ± 17.9 (5)	42.9 ± 11.1 (5)	35.5 ± 10.8 (7)	1.4 ± 0.4 (7)
Picea mariana	9.5 (2)			162.8 (2)	5.5 (1)
Pinus banksiana	2.0 (1)			133.3 (1)	3.4 (1)
Pinus ponderosa	4.1 ± 0.5 (13)	84.7 ± 37.0 (12)	62.4 ± 23.2 (12)	62.3 (2)	2.0 (2)
Pinus radiata	5.3 (1)		8.2 (1)	10.4 (1)	0.7 (1)
Pinus strobus				24.1 ± 11.5 (4)	
Pinus sylvestris	4.4 ± 1.1 (6)	41.9 ± 9.7 (3)	71.0 ± 39.8 (3)	118.0 ± 67.9 (3)	2.1 ± 0.6 (3)
Pinus taeda				7.6 (1)	
Pseudotsuga menziesii	3.5 ± 0.5 (12)	26.8 ± 7.2 (12)	62.8 ± 20.9 (12)	62.6 ± 20.2 (12)	6.1 ± 0.6 (11)
Biomes					
Boreal Evergreen	5.4 ± 1.1 (9)	41.9 ± 9.7 (3)	71.0 ± 39.8 (3)	132.1 ± 35.2 (6)	3.0 ± 0.7 (5)
Boreal Deciduous	1.0 (2)	19.3 (1)	65.2 (1)	28.6 (1)	2.2 (1)
Temperate Evergreen	4.1 ± 0.3 (41)	66.3 ± 19.4 (32)	64.5 ± 13.8 (32)	56.2 ± 11.8 (31)	3.7 ± 0.6 (24)
Temperate Deciduous	1.1 ± 0.1 (15)	25.8 ± 4.8 (7)	75.4 ± 15.0 (7)	81.1 ± 18.6 (12)	1.4 ± 0.2 (12)

Table S2: B:NPPs, biomasses, and net primary productions (NPPs) of foliage, branches, stems, and coarse and fine roots grouped by leaf type (foliage) and nutrient availability. The B:NPPs and mean biomasses of branches, stems, and coarse roots were adjusted to the theoretical stationary state (200 y, see **Figure 1**). N indicates the number of forests. Different letters within a column and compartment indicate differences between groups using Tukey's test for multiple comparisons at the 0.05 level.

Compartment		B:NPP (years)	Biomass ($gC\ m^{-2}$)	NPP ($gC\ m^{-2}\ y^{-1}$)		N
	Leaf habit					
Foliage	Evergreen	4.3 ± 0.4^a	499.8 ± 90.9^a	129.6	$\pm 22.7^a$	53
	Deciduous	1.1 ± 0.1^b	198.2 ± 22.3^b	180.4	$\pm 16.7^b$	18
	Nutrient availability					
Branches	High	295.8 ± 49.9^a	6965.1 ± 1402.9^a	32.7	$\pm 5.8^a$	4
	Medium	80.2 ± 42.9^b	1918.6 ± 287.6^b	106.4	$\pm 21.4^a$	7
	Low	60.8 ± 21.3^b	2065.9 ± 328.3^b	69.5	$\pm 11.5^a$	22
Stems	High	349.3 ± 54.3^a	36740.9 ± 7075.4^a	177.8	$\pm 12.4^{ab}$	4
	Medium	128.2 ± 14.2^b	9085.9 ± 1063.6^b	135.1	$\pm 22.5^b$	7
	Low	104.7 ± 12.8^b	16902.2 ± 3555.6^b	293.2	$\pm 44.6^a$	24
Coarse roots	High	294.4 ± 101.7^a	5541.7 ± 1319.9^a	60.8	$\pm 9.3^a$	8
	Medium	125.1 ± 13.1^b	5426.4 ± 2343.3^a	58.8	$\pm 12.4^a$	17
	Low	115.8 ± 18.5^b	4360.6 ± 1088.1^a	76.2	$\pm 13.8^a$	26
Fine roots	High	1.6 ± 0.2^a	311.1 ± 27.4^a	197.8	$\pm 9.5^a$	7
	Medium	1.5 ± 0.2^a	274.6 ± 52.2^a	173.6	$\pm 28.8^a$	11
	Low	3.9 ± 0.7^b	447.6 ± 69.6^a	138.2	$\pm 19.0^a$	25

444 **Figure S1.** Relationships between biomass and stand age for branches, stems, and coarse roots. Data were fitted using an asymptotic

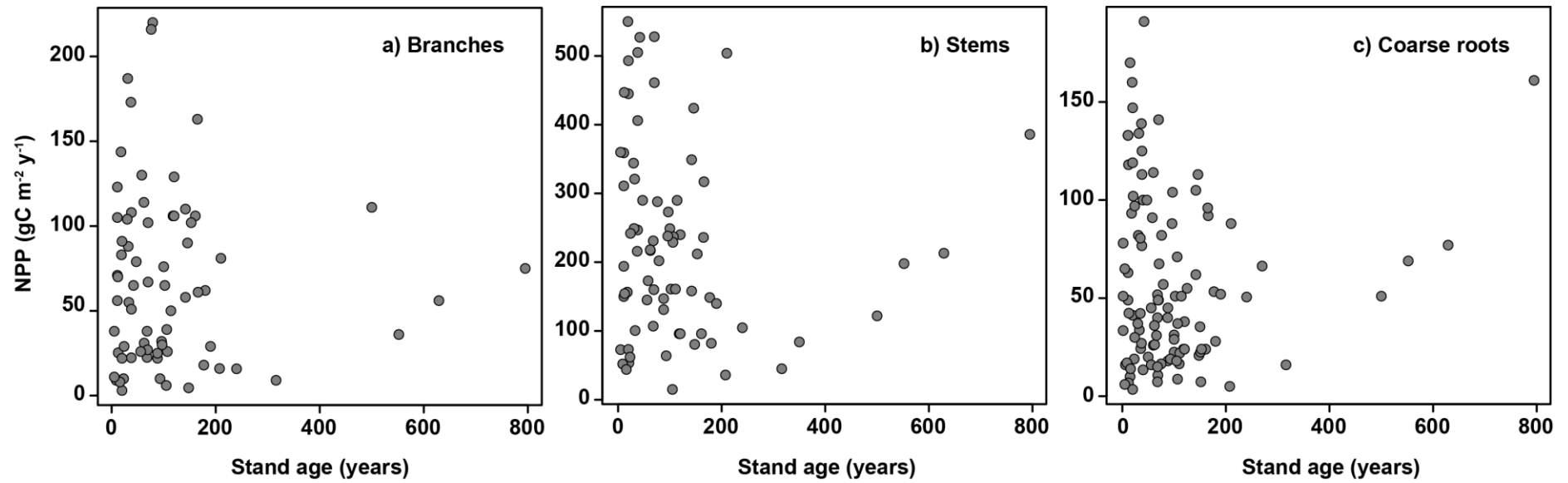445 exponential function.

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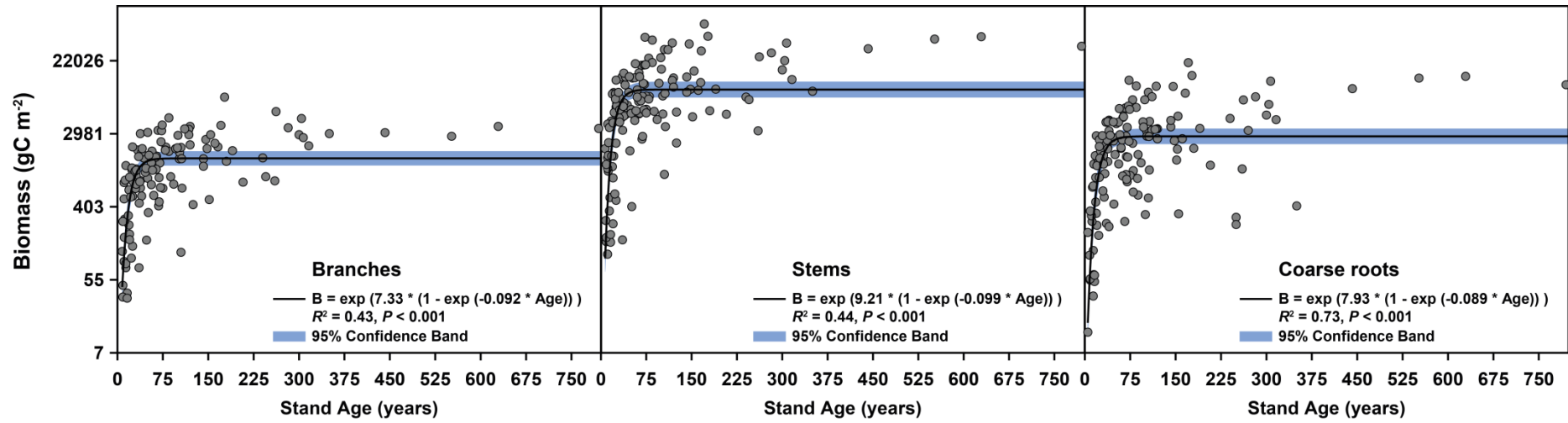
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450 **Figure S2.** Relationships between net primary production (NPP) and stand age for a) branches, b) stems, and c) coarse roots. Any of the

451 fractions presented significant relationships.

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