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ORIGINAL ARTICLE

Nutrient availability and climate as the main determinants of the ratio of biomass to NPP in woody and non-woody forest compartments

Marcos Fernández-Martínez[1,2] · Sara Vicca[3] · Ivan A. Janssens[3] · Matteo Campioli[3] · Josep Peñuelas[1,2]

Abstract

Key message **Once the effect of stand age has been taken into account, nutrient availability and climate play a crucial role in determining the B:NPPs of woody and non-woody tissues.**

Abstract Forest ecosystems accumulate large amounts of carbon in living tissues. The residence time of this carbon in the ecosystem depends largely on the turnover time of these tissues, which can be estimated as a surrogate of the ratio of biomass to net primary production (B:NPP). We used a global forest database of 310 sites containing data for biomass stocks and NPP to investigate the differences of B:NPPs among species and forest compartments and to determine B:NPPs main exogenous (mainly climate and nutrient availability) and endogenous (leaf habit and stand age) drivers. We used asymptotic exponential functions to adjust the B:NPPs of woody compartments to a theoretical stationary state to allow comparisons between forests of different ages. The B:NPPs of woody tissues (branches, stems, and coarse roots) were positively influenced by stand age, conversely to fine roots and leaves, which were weakly dependent on the age of the forest. The B:NPPs of woody tissues were positively correlated with nutrient availability, whereas fine-root B:NPPs decreased with increasing nutrient availability. The foliar B:NPP of evergreen forests was positively correlated with water deficit, and the fine-root B:NPP was correlated positively with the seasonality of precipitation and with annual thermal amplitude but negatively with water deficit. Our results support the influence of climate on the B:NPPs of non-woody compartments and identify nutrient availability as the main influence on the B:NPPs of woody tissues.

Keywords Turnover · Residence time · Nutrient availability · Climate · Stationary state · Carbon sequestration

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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.

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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) equals 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 (e.g., stand age and leaf habit) remain undetermined. Detecting the potential controls of B:NPPs of different compartments may help to predict the fate of carbon in different types of forests.

Endogenous factors such as stand age and leaf habit or type, combined with exogenous factors such as climate, nutrient availability, or management, can influence B:NPPs in different ways in different forest compartments. Nutrient-rich forests tend to have lower B:NPPs than nutrient-poor forests (Jordano and Herrera 1981) because of a higher biomass production, but this relationship has only been tested for foliage and fine roots (Reich et al. 1992; Aerts 1995; Ryser 1996). Nutrient-rich forests typically allocate a larger proportion of their photosynthates to aboveground biomass compared to nutrient-poor forests (Litton et al. 2007; LeBauer and Treseder 2008; Vicca et al. 2012; Fernández-Martínez et al. 2014a), and the ultimate effect of nutrient availability on carbon sequestration in ecosystems thus depends on the concerted response of the turnover times of the various plant organs and on the allocation strategy. Changes in carbon allocation may also lead to differences in carbon stocks in aboveground versus belowground compartments, depending on nutrient availability, and therefore to contrasting relationships between B:NPP and nutrient richness for aboveground versus belowground compartments. If these mechanisms were real, we would expect the relationship between B:NPP and higher nutrient availability to be positive in aboveground compartments and negative in belowground compartments.

The aim of this study was to calculate the B:NPPs of five compartments (foliage, branches, stems, coarse roots, and fine roots) of forest ecosystems around the world and to explore the endogenous (stand age and leaf habit and type) and exogenous (climate and management) factors that control them. We also particularly investigated the role of nutrient availability as a likely control of B:NPP, hypothesising that higher nutrient availability would be correlated positively with higher B:NPP in aboveground compartments and negatively in belowground compartments.

Materials and methods

Data collection

Global forest database

We updated and analysed a global forest database (Luyssaert et al. 2007) containing data from 1990 to 2012 for NPP and stand biomass for five forest compartments [foliage, branches, stems, coarse roots, and fine roots (diameter $\leq$ 2 mm)] from 310 sites around the world comprising boreal, temperate, Mediterranean, and tropical biomes, albeit the tropical and Mediterranean forests were less well represented. Only 80 of the forests provided the necessary data to calculate B:NPP for at least one of the compartments and, therefore, these forests were the only ones used in the study of B:NPP. The database also included descriptive information of the forests, such as stand age, leaf type (needleleaved, broadleaved, or mixed forest), leaf habit (evergreen, deciduous, or mixed forest), type of management (managed or unmanaged forests), and nutrient availability (see Fernández-Martínez et al. 2014a; Vicca et al. 2012), which we used to calculate a proxy of nutrient richness (see section "Assessment of nutrient availability").

Climatic data

We extracted climatic data for our forests from the WorldClim database (Hijmans et al. 2005). This database provides suitable climatic data with a high spatial resolution (30 arc seconds, ca. 1 km at the equator) and contains robust mean monthly climatic data derived from a lengthy time series (1950–2000), including monthly temperature and precipitation and several other climatic variables such as annual thermal amplitude and seasonality of precipitation.

The time series for evapotranspiration (MOD16A2) from MODIS (Moderate resolution imaging spectroradiometer) were downloaded for the period between 1 January 2000 and 27 December 2009 to obtain climatic

proxies of potential and actual evapotranspiration (PET and AET, respectively). We downloaded the data with a resolution of 9 km^2 (3 × 3 km) around the central coordinates.

Data analyses

B:NPPs

We calculated B:NPP similar to previous studies (Dahlman and Kucera 1965; Margalef 1974; Malhi et al. 1999; Gill and Jackson 2000), dividing stand biomass by mean NPP for each compartment. The availability of NPP and biomass data was uneven for the compartments, so we calculated B:NPP for foliage, branches, stems, and coarse and fine roots from 71, 44, 44, 70, and 80 forests, respectively.

Stand biomass was strongly age-dependent in non-stationary compartments such as branches, stems, and coarse roots (Figure S1) (in contrast to foliage and fine roots). Previous studies have suggested a strong relationship between NPP and stand age (Carey et al. 2001; Michaletz et al. 2014), but our data showed no clear trend with stand age (Figure S2). Nonetheless, comparing the biomasses or B:NPPs of forests of differing average stand ages (and thus biomasses) would be nonsensical for woody compartments. We avoided this problem and compared forests of different ages by adjusting the biomasses and B:NPPs of branches, stems, and coarse roots to their theoretical stationary state (at approximately 200 years of age, assumed to be when the percent annual increase in biomass and B:NPP from most compartments was <0.5 %). We thus removed fast-growing species (e.g., *Acer* sp., *Alnus* sp., *Betula* sp., and *Populus* sp.) from the analyses. We calculated the stationary B:NPP by first fitting our data to an asymptotic exponential function, as conceptually suggested by Houghton (2009). We then extracted the residuals of all cases and summed them to the predicted biomass or B:NPP of the function for 200 years (i.e., raw residuals + fitted B:NPP at 200 years). These adjusted values were used for regression models (see section "Statistical analyses") and to obtain means. The fitted value at 200 years only changed the means of the biomasses and B:NPPs, so our choice of age did not influence the significance of our results.

Climatic predictors

We used mean annual temperature (MAT) and precipitation (MAP) from the WorldClim database and calculated the length of the warm period (sum of months >5 °C) using mean monthly temperatures. We also extracted two key climatic variables: annual thermal amplitude (mean maximum minus mean minimum temperature for the year) and seasonality of precipitation (measured as the coefficient of variation of precipitation among months).

We calculated the percentage water deficit from the MODIS evapotranspiration time series as WD = (1 − [AET/PET]) × 100, (Fernández-Martínez et al. 2014b) as an indicator of the intensity of water stress the forests must withstand. We thus used eight climatic predictor variables: MAT, MAP, mean temperature and precipitation for the warm period, length of the warm period, annual thermal amplitude, seasonality of precipitation, and WD.

Assessment of nutrient availability

The forest database contained information about the nutrient status of the forests for variables such as soil type, texture, pH, nitrogen and phosphorous content, nitrogen mineralisation, C:N ratio, and CEC; foliar nitrogen and phosphorous concentrations; nitrogen deposition; and the history of the stand or explicit reports of the fertility of the forests (Vicca et al. 2012; Fernández-Martínez et al. 2014a), but information for all variables was not available for each site. We coded each variable into three levels of nutrient availability, high, medium, and low, following the methodology and data reported by Fernández-Martínez et al. (2014a). We then transformed each three-level factor into three dummy variables, each indicating high, medium, or low nutrient availability. We next performed a factor analysis to reduce the number of dimensions of our dataset using only dummy variables indicating high and low nutrient availability. The first resulting factor (F1: nutrient richness covariate) explained 16 % of the variance of the data and was correlated positively with nutrient-rich and negatively with nutrient-poor dummy variables.

Statistical analyses

We used stepwise forward regression models to correlate the B:NPPs (previously adjusted to the stationary state of 200 years) with the climatic variables (see section "Climatic predictors"), the nutrient richness covariate (F1), management, and leaf type and habit. Predictor covariates were entered twice for selection in the models, with and without transformation to natural logarithms, to identify possible nonlinearities. The dependent variables usually required transformation to meet the assumptions of normality and homoscedasticity of the residuals. We evaluated the contribution of each predictor variable to B:NPP using the *PMVD* [Proportional Marginal Variance Decomposition, (Grömping 2007)] metric of the R (R Core Team 2013) package *relaimpo* (Grömping 2006) as a measure of the variance explained by each predictor. We excluded variables with high collinearity from the models (variance inflation factor [VIF] >5). We also used the three levels of nutrient availability (high, medium, and low) used by Vicca et al. (2012) and Fernández-Martínez et al. (2014a)

to compare means among groups. Differences among groups were tested using ANOVA tables and the Tukey's HSD test for multiple comparissons.

Results

Adjusted B:NPPs across forest types

A strong correlation between woody (branches, stems, and coarse roots) biomass and forest age (Figure S1) produced a strong correlation between woody B:NPPs and stand age (Fig. 1). The asymptotic exponential functions indicated that branches reached a stable B:NPP of 45 years when trees were about 150 years old (Fig. 1a). Stationary B:NPPs for stems and coarse roots reached 115 and 104 years, respectively, at an age of approximately 200 y (Fig. 1b, c). The fitted functions between B:NPP and stand age presented a pseudo-R^2 of 0.31, 0.81, and 0.73 in branches, stems, and coarse roots, respectively (Fig. 1). B:NPP and stand age were not significantly correlated for fine roots or evergreen foliage (Fig. 2).

Stationary B:NPP did not significantly differ among biomes or leaf habits in woody compartments (ANOVA, $P > 0.05$) but differed significantly between leaf types for foliage and fine roots (ANOVA, $P < 0.01$; Table 1). Biome-averaged differences among woody fractions (branches, stems, and coarse roots), however, were large. The B:NPPs at the 20 and 80 percentiles were 21–80 years for branches, 71–171 years for stems, and 63–176 years for coarse roots. Differences among woody compartments were statistically significant for some species (Table 1). For example, *Fagus sylvatica* had a longer B:NPP in the stem (122 ± 19) and coarse-root (83.9 ± 18) fractions than in the branch fraction (22 ± 3, $P < 0.05$). This trend was also consistent for *Picea abies* and *Pseudotsuga menziesii* ($P < 0.05$ and $P < 0.01$, respectively). The B:NPPs of fine roots and leaves ranged between 1 and 5 years, with lower B:NPPs in deciduous than evergreen forests for both fine roots and leaves ($P < 0.01$, Table 1).

Controls of the B:NPPs

Our results indicated that the various forest compartments were correlated with different endogenous and exogenous factors (Table 2). Age-adjusted B:NPP was correlated with nutrients in the compartments that accumulate biomass over long periods (branches, stems, and coarse roots). Nutrient
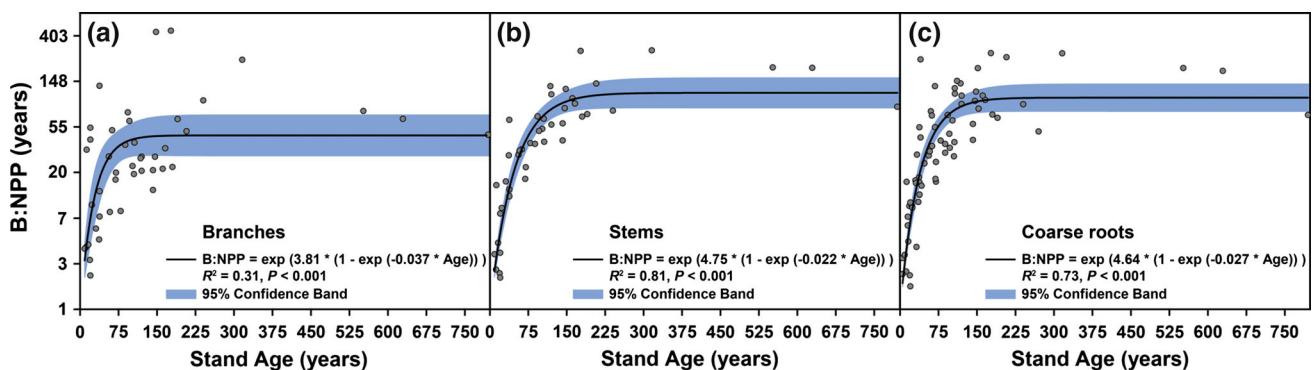

Fig. 1 Relationships of the B:NPPs of **a** branches, **b** stems, and **c** coarse roots with stand age. Data were fitted using an asymptotic exponential function

Fig. 2 Relationships of the B:NPPs of **a** foliage and **b** fine roots with stand age
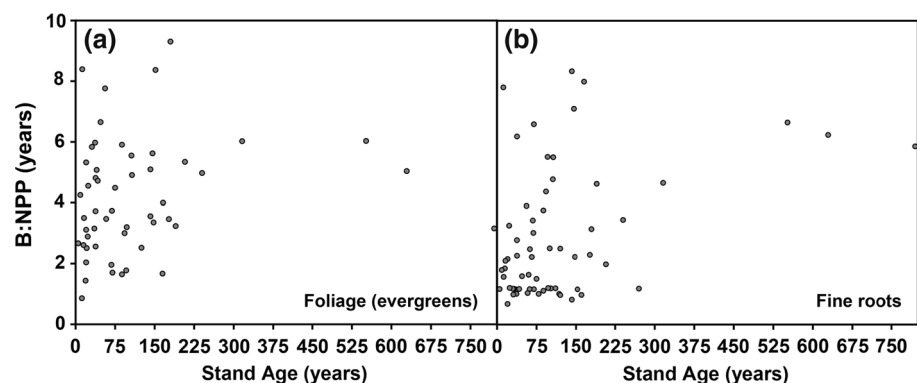
Table 1 B:NPPs (mean years ± standard error) of foliage, branches, stems, and coarse and fine roots across species and biomes adjusted to the stationary state (200 years) (except for foliage and fine roots)

	Foliage		Branches		Stems		Coarse roots		Fine roots	
Species										
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)

The number of forests is shown in parentheses. Different letters within a column indicate significant differences among groups ($P < 0.05$) using Tukey's HSD test for multiple comparisons

Table 2 Summary of the models for the B:NPPs of evergreen foliage, branches, stems, and coarse and fine roots using stepwise forward regressions

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	

For these analyses, the B:NPPs of woody compartments were adjusted to 200 years 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

Ln indicates natural-log transformation. For leaf habit, *D* indicates deciduous and *E* indicates evergreens. *PS* indicates precipitation seasonality, *ThA* is annual thermal amplitude and *WD* is water deficit

(*) is the R^2 from the asymptotic exponential functions in Fig. 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

richness explained 20, 35, 9, and 6 % of the variance in the B:NPPs of branches, stems, and coarse and fine roots, respectively. Foliage B:NPP was not correlated with nutrient availability ($P > 0.05$, Table 2). Nutrient-rich forests had longer B:NPPs than nutrient-poor forests in woody compartments (Tukey's test, $P < 0.05$; Table S2, Fig. 3a–c). The response of the B:NPPs of woody fractions to nutrient availability, however, differed from the response of the fine-root fraction (Table 2, Fig. 4), which behaved

oppositely (Table S2, Fig. 3d). Forests with higher nutrient availability had longer B:NPPs in woody tissues (branches, stems, and coarse roots, Fig. 4a) in comparison to nutrient-poor forests ($P < 0.05$), but forests with nutrient limitations had longer B:NPPs in fine roots than nutrient-rich forests ($P = 0.002$; Fig. 4b). Nutrient availability was not aligned with old or young forests (ANOVA, $P > 0.1$). Our results should therefore not be biased because of age differences between nutrient-rich and nutrient-poor forests. Despite the
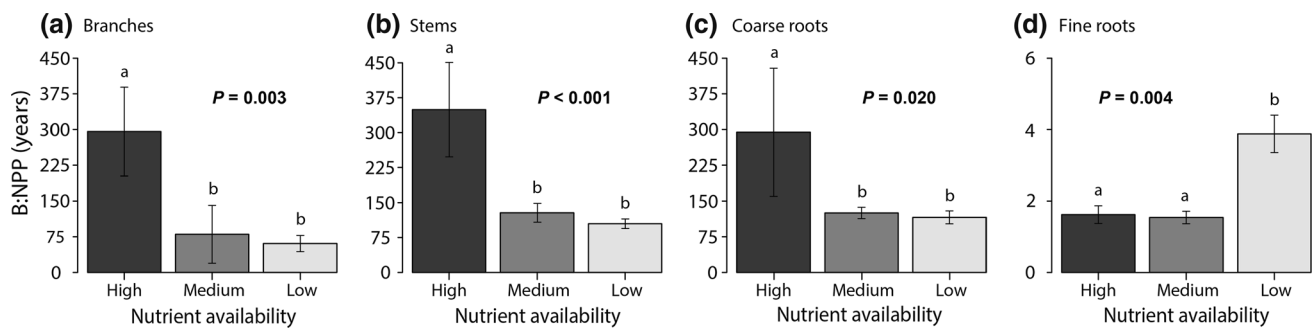
Fig. 3 B:NPPs of **a** branches, **b** stems, **c** coarse roots, and **d** fine roots for different levels of nutrient availability. The branch, stem, and coarse-root B:NPPs have been adjusted to the stationary state (200 years) using the equations in Fig. 1. Exact values can also be found in

Table S2. *Different letters* above the *bars* indicate significant differences using Tukey's HSD test for multiple comparisons at the 0.05 level
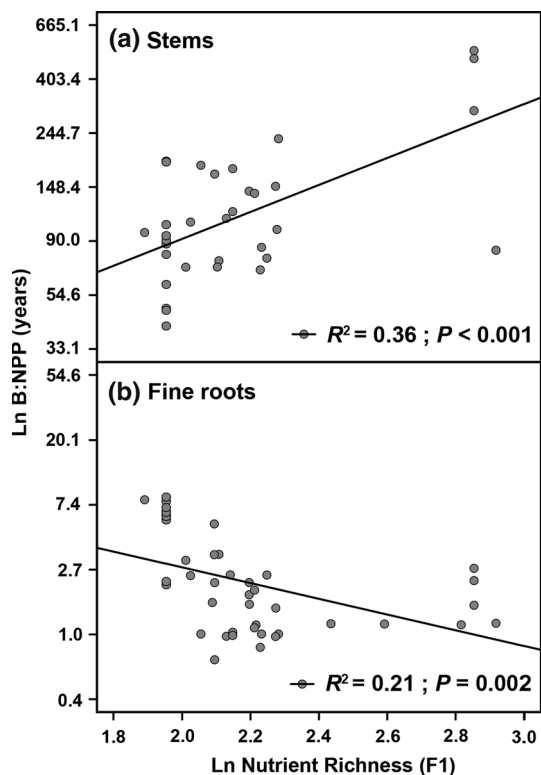

Fig. 4 Relationships of the B:NPPs of **a** stems and **b** fine roots with nutrient richness

possible combined effect that nutrient availability and management can have on biomass production (Campioli et al. 2015), B:NPP did not differ significantly between managed and unmanaged forests in any compartment.

Carbon stocks in the biomasses of branches and stems increased with nutrient availability (Table S2, Fig. 5; $P < 0.05$). Fine roots had the opposite trend, but the results were not statistically significant. Production (NPP) varied little (Table S2, Fig. 5) among nutrient classes. The differences in B:NPP with nutrient availability were thus due

to differences in stand biomass rather than to differences in NPP.

Leaf habit was responsible for the largest differences in foliage B:NPP (Table S2). Foliage B:NPP averaged approximately 1 year in deciduous forests and 4.3 ± 0.4 years in evergreen forests (Table S2). Branch B:NPP was longer in evergreen than deciduous forests (Table 2). Evergreen foliage B:NPPs were positively correlated with water deficit, and fine-root B:NPPs were higher in forests with low water stress (Table 2). The seasonality of precipitation, however, was the most (positively) correlated variable with fine-root B:NPP, explaining 58 % of its variance. High values of annual thermal amplitude were also correlated with high fine-root B:NPPs. Evergreen foliage and fine-root B:NPPs were marginally positively correlated with stand age (Fig. 2; Table 2).

Discussion

Our results identified large differences in B:NPPs among forest compartments but only small differences among tree species (Tables 1 and S2, Fig. 3). The slow-growing species in this study may thus have similar structural and functional properties, which allowed us to compare the role of exogenous controls of B:NPP spatial variability. The B:NPPs were mostly driven by climate in non-woody tissues but by age and nutrient availability in woody tissues.

The role of climate in non-woody compartments

Climate played a significant role in determining the B:NPPs of non-woody compartments such as foliage and fine roots but not of branches, stems, and coarse roots. The negative correlation between foliar B:NPPs and water deficit may indicate that forests under high water stress are unable to sustain as much leaf biomass as forests with good
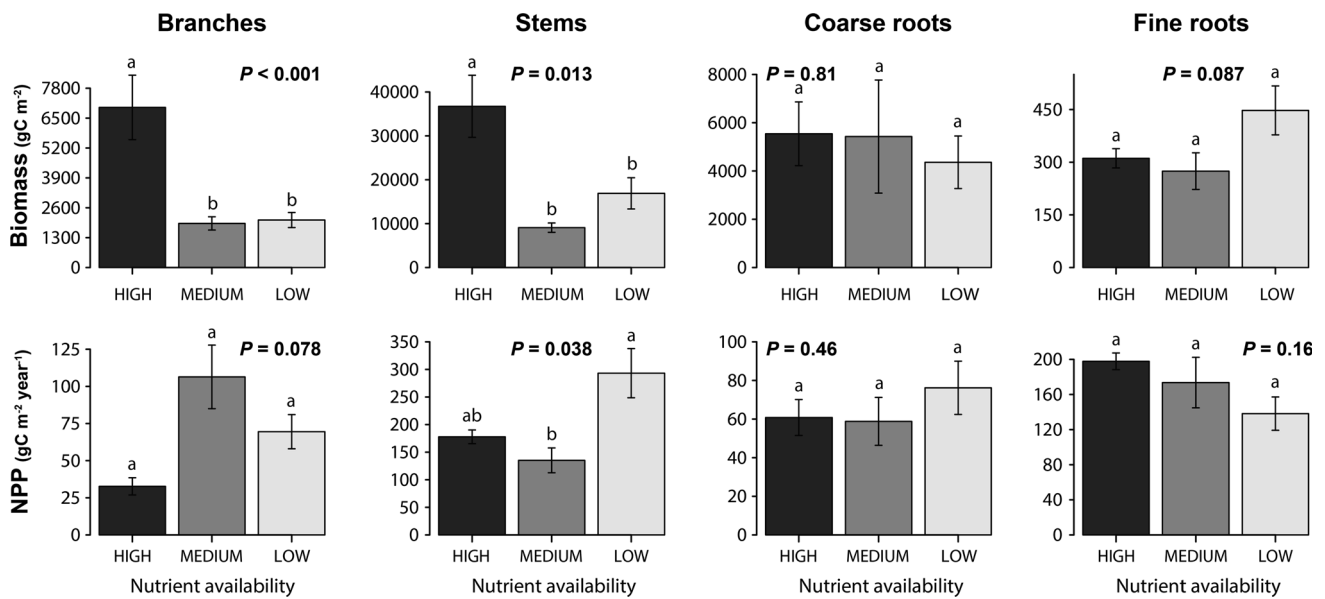
Fig. 5 Stand biomass and NPP of branches, stems, coarse roots, and fine roots for different levels of nutrient availability. The biomasses for branches, stems, and coarse roots have been adjusted to the stationary state (200 years) using an asymptotic exponential function (see"Materials and methods") 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

hydric conditions, as previous studies have reported (Fernández-Martínez et al. 2014b).

Fine-root B:NPPs were strongly correlated with intra-annual climatic variability (thermal amplitude and especially the seasonality of precipitation). This relationship supports previous findings, suggesting that the B:NPPs of fine roots decrease with climatic seasonality (Gill and Jackson 2000). Climatic seasonality may lead to periods of extreme weather (e.g., drought or cold) during the year that may kill fine roots, thus decreasing their lifespan. This negative effect of seasonality may also indicate that warmer forests (with less seasonality) need a higher fine-root NPP to sustain the same pools of fine-root biomass (Gill and Jackson 2000) due to the higher metabolic rates.

In contrast to foliage and fine roots, the B:NPPs of woody tissues were not correlated with climate, perhaps because woody tissues are organs that accumulate much biomass in a very recalcitrant form and are therefore relatively insensitive to meteorological conditions. Also, the turnover of woody tissues is primarily associated with tree mortality and is therefore less sensitive to normal meteorological conditions (without considering events of extreme weather causing disturbances such as windthrows, storms, or heat waves causing mass mortality).

The role of nutrient availability in woody and non-woody compartments

The positive effect of nutrient availability on woody B:NPPs was driven by the larger carbon pools in nutrient-rich than in nutrient-poor forests, not by an increase in biomass production (NPP), which remained fairly constant among the classes of nutrient availability (Table S2). Because nutrient-rich forests presented larger carbon pools, we can thus infer that either necromass production is higher in nutrient-poor forests or that nutrient-rich forests allocate more photosynthates into woody compartments than nutrient-poor forests (Vicca et al. 2012). Woody compartments have longer B:NPPs than non-woody organs (Tables 1, S2; Fig. 3), so our findings also suggest that nutrient-rich forests are more likely to act as carbon sinks than nutrient-poor forests (Fernández-Martínez et al. 2014a). Nutrient-rich forests thus accumulate more biomass, and the carbon is more likely to reside longer in the living biomass because of higher allocation in forest compartments with high B:NPP.

In contrast to woody compartments, fine-root B:NPPs are shorter in nutrient-rich forests, supporting previous research suggesting that nutrient-poor forests increase the lifespan of fine roots to increase nutrient-use efficiencies and thus to avoid nutrient losses (Reich et al. 1992; Aerts 1995; Ryser 1996). Foliar B:NPPs were not significantly correlated with nutrient richness, which may be linked to the hypothesised higher resorptive capacity of leaves than of fine roots (Freschet et al. 2010).

Methodological considerations

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

from our estimates of B:NPP suggests that our results should be interpreted with caution. Turnover times in leaves and fine roots could theoretically be calculated as the pool-to-flux ratio, because biomass in these compartments reaches a steady state at relatively young ages (Ryan et al. 1997; Chen et al. 2007). This methodology (simple B:NPP calculation) to evaluate turnover times, however, may certainly underestimate the real average time that an amount of carbon will reside in compartments where biomass increases with time (i.e., branches, stems, and coarse roots), leading to a strong association between turnover time and age (Fig. 1). Biomass in woody compartments, however, tends to a steady state with age (Houghton 2009; Fernández-Martínez et al. 2014b), so the pool-to-flux ratio might provide reliable estimates in old-growth forests that have already reached a stationary state when the inputs equal the outputs (NPP – necromass production = 0). The alternative to studying only old-growth forests is to adjust the pool-to-flux ratio to a theoretical stationary state of the stands following an asymptotic function describing the increase in pool-to-flux ratio with age, which is the methodology we have chosen. By adjusting B:NPPs to the stationary state, we can provide surrogates of turnover times that should be useful to forest managers and the modelling community.

Conclusions

We detected large differences in B:NPPs among forest compartments but only small differences among tree species (Tables 1, S2; Fig. 3). Once the effect of stand age was removed for compartments without stationary behaviour (Fig. 1), nutrient availability (Fig. 4) and climate (mostly water deficit and seasonality) were identified as playing crucial roles in determining the B:NPPs of woody and non-woody tissues, respectively (Table 2).

Compliance with ethical standards

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