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The dynamic of annual carbon allocation to wood in European forests is consistent with a combined source-sink limitation of growth: implications for modelling

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Received: 13 January 2015 – Accepted: 14 January 2015 – Published: 2 February 2015

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Published by Copernicus Publications on behalf of the European Geosciences Union.

Abstract

The extent to which forest growth is limited by carbon (C) supply (source control) or by cambial activity (sink control) will condition the response of trees to global changes. However, the physiological processes responsible for the limitation of forest growth are still under debate. The aim of this study is to evaluate the key drivers of the annual carbon allocation to wood along large soil and climate regional gradients in five tree species representative of the main European forest biomes (*Fagus sylvatica*, *Quercus petraea*, *Quercus ilex*, *Quercus robur* and *Picea abies*).

Combining field measurements and process-based simulations at 49 sites (931 site-years), we assessed the stand biomass growth dependences at both inter-site and inter-annual scales. Specifically, the relative influence of forest C balance (source control), direct environmental control (water and temperature controls of sink activity) and allocation adjustments related to age, past climate conditions, competition intensity and soil nutrient availability on growth were quantified.

The inter-site variability in stand C allocation to wood was predominantly driven by an age-related decline. The direct control of temperature or water stress on sink activity (i.e. independently from their effects on C supply) exerted a strong influence on the annual stand woody growth in all the species considered, including deciduous temperate species. The lagged effect of the past environment conditions was a significant driver of the annual C allocation to wood. Carbon supply appeared to strongly limit growth only in deciduous temperate species.

We provide an evaluation of the spatio-temporal dynamics of annual carbon allocation to wood in European forests. Our study supports the premise that European forest growth is under a complex control including both source and sink limitations. The relative influences of the different growth drivers strongly vary across years and spatial ecological gradients. We suggest a straightforward modelling framework to implement these combined forest growth limitations into terrestrial biosphere models.

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1 Introduction

Forests play a critical role in the global carbon (C) cycle. Inventory-based estimates show that forests have been a persistent carbon sink in recent decades, uptaking 60% of the cumulative world C fossil emissions between 1990 and 2007 (Pan et al., 2011). The fate of the entering C strongly relies on the C dynamics in trees, which determines its residence time in the forest ecosystem. Despite its importance for the future of the terrestrial C sink (Carvalhais et al., 2014; Friend et al., 2013), the C partitioning among tree organs and ecosystem respiration remains poorly understood (Brüggemann et al., 2011). In particular, considerable debates have arisen from the physiological mechanisms driving the increment of the forest woody biomass (Palacio et al., 2014; Wiley and Helliker, 2012). The fraction of the assimilated C stored in woody biomass can be inferred by combining biometric measurements to estimates of the C exchanges between the ecosystem and the atmosphere based on the Eddy-Covariance (EC) technique (Babst et al., 2014; Litton et al., 2007; Wolf et al., 2011). Global meta-analyses of such dataset (gathering data from different biomes and different species) revealed a strong correlation between gross primary production (GPP) and woody biomass increment (Litton et al., 2007; Zha et al., 2013). Accordingly, growth has for long been thought as C limited, through an hypothesized causal link between C supply and growth (source control, Sala et al., 2012). The environmental factors reported to affect growth (soil water content, temperature, nutrient, light and CO₂) were therefore supposed to operate through their effects on photosynthesis and respiration fluxes. This C-centric paradigm underlies most of the C allocation rules formalized in the terrestrial biosphere models (TBMs) currently used to evaluate the outcome of global changes on forests (Clark et al., 2011; Dufrêne et al., 2005; Krinner et al., 2005; Sitch et al., 2003).

The source control of tree growth has been questioned by several authors, arguing that cambial activity is more sensitive than C assimilation to a panel of environmental stresses (Fatichi et al., 2014), including water deficit (Muller et al., 2011; Tardieu

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et al., 2011) and low temperature (Körner, 2008). The onset of cambial activity is also known to be highly responsive to temperature (Lempereur et al., unpublished data; Rossi et al., 2011; Kudo et al., 2014), which in turn may partly determine annual cell production and forest growth (Lupi et al., 2010; Rossi et al., 2013).

5 Finally, the quality and quantity of available soil nutrients, particularly nitrogen, could affect growth independently of their impacts on C assimilation, due to the relatively constant stoichiometry of the tree biomass (Leuzinger and Hättenschwiler, 2013). These experimental evidences gave ways to an alternative understanding of tree C dynamic where growth is mostly limited by the direct effects of environmental factors (sink control). However, numerous key environmental factors (nutrient, temperature and water) affect both sink and source activities, and it is thus difficult to unscramble whether growth is more related to carbon supply or to the intrinsic sensitivity of cambium functioning to the environment (Fatichi et al., 2014). The extent to which forest growth is under a source- or a sink- control is of paramount importance to predict how trees will respond to global changes. Specifically, rising atmospheric CO₂ could possibly increase forest productivity, and hence the terrestrial C sink, only if growth is a source limited process. The implementation of the respective roles of source- and sink- controls on growth in TBMs is therefore a huge challenge for modellers as it will determine our ability to project the future of forest (Fatichi et al., 2014; Leuzinger et al., 2013).

10 The allocation of assimilated C within forest ecosystem is a complex integrative process that can be described on the basis of several non-exclusive principles (Franklin et al., 2012) among which are (i) allometric scaling, (ii) functional balance and (iii) evolution-based optimal responses. (i) Allometric scaling is based on the assumption that biophysical laws determine C partitioning within the different forest compartments. Current knowledge include vascular network optimality (Enquist, 2002) and functional homeostasis in water transport (Magnani et al., 2000) as main allocation constraints. (ii) Functional balance theory suggests a preferential allocation to the organ responsible for acquisition of the most limiting resource. In line with this principle a higher C

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allocation to fine root at the expense of woody growth has been reported on poor or dry soil (Chen et al., 2013; Keyes and Grier, 1981), along with a plausible higher allocation to root symbionts and exudates at the expense of biomass production (Vicca et al., 2012). (iii) Finally, optimal response postulates that allocation maximize a fitness proxy in a fixed environment. This hypothesis of fitness maximization is in line with the previously assumed dynamic reserve pool acting as temporary storage, possibly at the growth expense, to allow long-term survival of trees (Chapin et al., 1990; Sala et al., 2012). Indeed, time lags between C uptake and growth have been reported (Gough et al., 2009; Richardson et al., 2012). The optimal response theory also explains long-known life history traits such as the preferential allocation to reproduction in ageing plants that could lead to the observed age-related decline in woody biomass allocation (Genet et al., 2010; Thomas, 2011). Woody biomass increment therefore appears under the control of a panel of drivers which intensity effects are expected to strongly vary in space and time. As a consequence, local studies report contrasted agreements between C supply and woody growth (Gielen et al., 2013; Richardson et al., 2012), ranging from no significant relationships (Mund et al., 2010; Rocha et al., 2006) to tight links on seasonal (Babst et al., 2014; Granier et al., 2008; Zweifel et al., 2010) or annual (Ohtsuka et al., 2009; Peichl et al., 2010; Zweifel et al., 2010) time scales. Determining the key processes affecting woody growth at the different spatio-temporal scales is a necessary step to unify these apparently contradictory results in a common framework. Moreover, investigations should be conducted at the species level, as phylogeny may strongly constrain forest functioning (Carnicer et al., 2013; Drobyshev et al., 2013) and induce contrasted growth determinisms between taxa (Genet et al., 2010).

The gap between the lessons drawn from global studies regarding universal C allocation rules in forest and our understanding of the cell processes underpinning cambial activity appears to be the current main obstacle toward a better understanding of forest growth drivers. In this regard, species-specific studies evaluating the dynamic of C partitioning to annual woody growth along soil and climate regional gradients

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constitute a key missing link. Unfortunately, advances are so far precluded by the scarcity of datasets combining EC and growth measurement from the same sites (Luyssaert et al., 2007). Here, we released this constraint by combining stand and soil measurements from a permanent plot network and process-based simulations of forest annual and seasonal C balance (Fig. 1) over 49 forest sites. Simulations were performed using a process-based model (CASTANEA, Dufrêne et al., 2005) thoroughly validated against EC data over Europe (LeMaire et al., 2005; Davi et al., 2005; Delpierre et al., 2009, 2012) and applied here with site-specific parameterizations. Relating biometric measurements to different variables linked to C source and sink activity, we evaluated the key drivers of the annual C allocation to stand woody growth in five species representative of the main European forest biomes: *Fagus sylvatica*, *Quercus petraea* and *Quercus robur* for temperate deciduous broadleaf forests, *Picea abies*, found in high latitude and high altitude evergreen needleleaf forests and *Quercus ilex*, a Mediterranean evergreen broadleaf species. Specifically, the relative influence of forest annual and seasonal C balance (source control), direct environmental control (water and temperature controls of sink activity) and allocation adjustments related to age, past climate conditions, competition intensity and soil nutrient availability on tree growth were considered (Fig. 1). We aimed to (1) quantify the relative contributions of source- and sink- controls in the spatio-temporal dynamic of forest woody growth across a wide range of environmental contexts and (2) provide transferable information to help refining the representation of forest growth causalities in TBMs.

2 Materials and methods

We based our analyses on three complementary data sources: field measurements, climatic variables from atmospheric reanalysis (Vidal et al., 2010) and process-based simulated data. This hybrid approach allowed to extensively assessing and disentangling the effects of previously reported environmental and endogenous drivers of C allocation to woody growth (Fig. 1).

2.1 Study sites and field data

Our investigation gathered field measurements from 48 plots from the French permanent plot network for the monitoring of forest ecosystem (RENECOFOR, Ulrich, 1997) and from the heavily-instrumented Puéchabon site (Martin-StPaul et al., 2013).

5 Location and general climatic features are given in Fig. 2 and Table 1, a complete description of the sites is available in Sect. S1 in the Supplement.

2.1.1 Growth measurements and historical stand growth reconstruction

Growth measurements consisted of (i) dendrochronological sampling: 12 to 30 overstorey trees per plots were cored to the pith at breast height with an incremental borer (in 1994 in the RENECOFOR and in 2008 at the Puéchabon site, Lebourgeois, 10 1997; Ourcival, unpublished data). The tree circumferences at breast height (CBHs) and total heights were also measured. Average stand age was inferred from the tree ring series. (ii) Forest inventories: extensive CBH surveys were conducted on every plot on a 0.5 ha area (Cluzeau et al., 1998; Gaucherel, Guiot and Misson, 2008; Ourcival, 15 unpublished data).

Tree ring series were combined to the CBH surveys to reconstruct the historical CBHs of every tree on the plots (over 8 to 43 years, Sect. S1). The scaling from the sampled trees to the entire stand tree CBH distribution involved an empirical tree competition model calibrated annually (Guillemot et al., 2014, Sect. S2). The historical total woody stand biomass was then calculated using tree level allometric 20 functions (Sect. S3) and past annual woody biomass increments (AWBIs) were inferred (Sect. S4). Historical stand basal area was additionally considered as a proxy for within-stand competition intensity (SBA, Table 2, Kunstler et al., 2011), along with the number of stems (numstem, Table 2).

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2.1.2 Measurement of stand characteristics

Stand measurements included soil water holding capacity (SWC), leaf area index (LAI), leaf nitrogen content (LNC) and soil nutrient availability (SNA). SWC was estimated from soil depth and texture measured on two soil pits per plots (Brêthes and Ulrich, 1997). LAI was estimated from litter collection (Pasquet, 2002) and sunlit LNC was determined annually on 8 trees from 1993 to 1997 (Croisé et al., 1999). SNA was assessed through the carbon (C):nitrogen (N) soil biomass ratio, the absolute value of the soil cation-exchange capacity and its percent base saturation (Ponette, 1997). These soil indices were measured at 3 depths (0–10, 10–20, 20–40 cm) and used to ranked soil plots in three nutrient classes, from low to high nutrient availability (Supplement S5). SNA, SWC and LNC were used to characterize plot fertility in the statistical analyses (Table 2).

2.2 Climate data

Meteorological variables at the hourly temporal scale (8 km resolution) were obtained from the SAFRAN atmospheric reanalysis (Vidal et al., 2010): global radiation, rainfall, wind speed, air humidity and air temperature. Temperature, which was associated to the averaged altitudes of the SAFRAN cells, was corrected using plot-specific elevation measurements (considering a lapse rate of 0.6 K per 100 m, Supplement S1). These variables were used for the climate forcing of the CASTANEA model (Dufrêne et al., 2005, see next section). In addition, two annual temperature indices were derived as proxies for winter frost damage and low temperature stress during the growth period (frost and templim, respectively, Table 2).

2.3 Process-based simulated data

We used the CASTANEA model for simulating an ensemble of diagnostic variables linked to the C source and the sink activity of the forest stands. The eco-physiological

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process-based model CASTANEA aims at simulating carbon and water fluxes and stocks of an even-aged monospecific forest stand at the rotation time scale. The stand-atmosphere C fluxes simulated by the CASTANEA model on an hourly basis have been thoroughly validated against EC data over Europe (Davi et al., 2005; Delpierre et al., 2009, 2012; LeMaire et al., 2005). Importantly, the biophysical hypotheses formalized in the model are able to reproduce the complex mechanisms interplay leading to the inter-annual stand C balance variability (Delpierre et al., 2012), which has been recognized as a strong challenge for TBMs (Keenan et al., 2012). A complete description of CASTANEA is given in Dufrêne et al. (2005), with subsequent modifications from Davi et al. (2009) and Delpierre et al. (2012). For the purpose of the present study, CASTANEA was parameterized with site-specific SWC and LNC. Measured LAI and total woody biomass were used to initialize the model simulations. The model ability to reproduce the annual variability in LAI and the forest growth at regional scale has been recently validated (Guillemot et al., 2014). Standing woody biomass was nonetheless forced on each year to the observed values as the model was here used for diagnostic purposes.

An ensemble of variables was simulated and aggregated on an annual basis (Table 2):

1. *The elementary components of the forest C balance*: gross primary productivity (GPP) and autotrophic respiration (R_a), along with the net balance (net primary productivity, $NPP = GPP - R_a$). For a given year y , we aggregated the hourly simulated C fluxes over different seasonal time periods including starts ranging from day 30 to 190, and ends ranging from day 190 to 350, with a 2 days resolution. Carbon fluxes were also summed (i) over the species-specific biomass growth periods reported in the literature (GPP_{gp} , $R_{a_{gp}}$ and NPP_{gp} , Supplement S10) and (ii) over the whole preceding year ($y - 1$) as a proxy of forest C status induced by past climate conditions (lagged effect, GPP_{y-1} , $R_{a_{y-1}}$ and NPP_{y-1}).

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2. *Bioclimatic water stress indices*: the intensity and the duration of the water stress over the growth period were evaluated ($WS_{int_{gp}}$ and $WS_{per_{gp}}$, respectively, Sect. S7). Water stress indices were also calculated over the whole preceding year ($y - 1$) (lagged effect of water stress, $WS_{int_{y-1}}$, $WS_{per_{y-1}}$).

3. *The onset of the biomass growth* ($camb_{onset}$). We used in this work a new growth onset module (Delpierre et al., unpublished results) based on a temperature sum trigger (Sect. S8).

2.4 Statistical analyses

2.4.1 General overview

The statistical analyses were conducted in three complementary steps in each studied species: (1) we calculated the correlation between annual woody biomass increments (AWBIs) and the C fluxes aggregated seasonally (from 1 month to the year) to evaluate the direct agreement between C supply and annual biomass growth changes. (2) AWBI dependences to C source and sink activity were evaluated at spatial (inter-site) scale in order to highlight the influence of site characteristics on biomass growth. Age-related trend in C allocation to woody biomass was also evaluated in this step. By using age differences among sites we covered a large chronosequence (including stands from approx. 30 to 150 years, Table S1 in the Supplement). (3) AWBI dependences were finally assessed at temporal scale to highlight the drivers responsible for the inter-annual growth biomass variability.

Because numerous key environmental factors affect both forest sink and source activities, there may be a strong collinearity between forest C balance and environmental stress proxies (Fatichi et al., 2014) that could hampered the inferential interpretation of classical statistical tests (Graham, 2003). The statistical models used in the study were consequently selected for their reliability in the presence of confounded variables (see below). Explanatory variables considered in spatial and

temporal analyses are presented in Table 2 and Fig. 1. Analyses were conducted with the R software (R Development Core Team, 2013, packages lme4, randomForest and MuMIn). Because *Quercus petraea* and *Quercus robur* are difficult to distinguish in the field and have a high hybridization rate (Abadie et al., 2012), these two species have been gathered in the analyses and referred to as temperate oaks in the following.

2.4.2 Correlations between growth and C fluxes

Pearson correlations between AWBIs and simulated C fluxes aggregated over seasonal time periods were assessed separately for each site. The highest median correlation values per species were retained and tested against zero using Wilcoxon signed rank tests. Critical correlations (threshold values for a significant difference with the retained maximum correlation) were determined in order to evaluate the sensitivity of correlation values to changes in the C flux aggregation periods.

2.4.3 Spatial biomass growth dependences

The spatial growth dependences were evaluated using a selection of multiple regressions based on the information-theoretic approach (Burnham and Anderson, 2002). AWBIs and the considered explanatory variables were averaged per plots. The variables entering the linear models were centered and scaled so that the values of the normalized coefficient estimates indicated the relative influence of predictors on AWBI. Elementary components of the forest C balance (NPP, GPP and Ra) were introduced one at a time in the models. For each species, multiple regressions containing all possible combinations of the explanatory variables were fitted. Models were compared using the second order Akaike criterion (AICc) and all models with an Akaike weight of at least 1 % of the best approximating (lower AICc) model were considered plausible (Burnham and Anderson, 2002). We retained finally the variables that appeared in at least 95 % of the selected models. Models fitted on *P. abies* data were restricted to a maximum of 3 explanatory variables due to the low amount of data ($n = 6$, Table 1).

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Q. ilex ($n = 1$) was not considered in spatial analyses. The uncertainty of the simulated C fluxes was considered in the analyses using a bootstrap procedure (Chernick, 2011): all linear models were fitted 1000 times, randomly sampling at each iteration the C fluxes values within the root mean square error of the CASTANEA simulations (Supplement S9) to obtain for each variable a parameter estimate distribution. We finally retained explanatory variables with parameter estimate distributions excluding zero value in a bilateral 5 % probability level.

2.4.4 Temporal biomass growth dependences

The temporal analysis was conducted on standardized AWBI series: a double-detrending process was applied for each series, based on an initial linear regression, followed by a fitting of a cubic smoothing spline with 50 % frequency response cut-off (Mérian et al., 2011). For analysing the temporal dependences of biomass growth we used a Random Forest (RF) learning method (Breiman, 2001), which was made possible by the important amount of data ($n = 931$ site-year). The RF learning method is a non-parametric method used to rank the contribution of different explanatory variables and evaluate their marginal effects on a variable of interest without assuming a priori dependence forms. The principle of RF is to combine 500 binary decision trees built using bootstrap samples from the initial dataset. Decisions aimed to reduce the heterogeneity of the explained variable in the resulting branches. For each of the 500 built trees the data not involved in the tree construction are used for validation. Tree predictions and errors are then averaged to provide final RF results. Consequently, RF does not overfit and does not need cross-validation (Cutler et al., 2007). A subset of explanatory variables is randomly chosen at each node, reducing the effect of collinear variables on the output. RF was used to select important variables related to growth temporal variability (Genuer et al., 2010). Variable selection relied on permutation importance: the increasing of the global mean square error when a given variable is randomized in the validation subsamples. The form of the dependences was discussed thanks to partial dependence plots (graphical depiction of the marginal effect of

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a given variable; Cutler et al., 2007). We used this information (variable selection and dependence forms) to test for the significance of the temporal AWBI dependences within the linear model. Uncertainties on the simulated C fluxes were considered in the linear models as for the spatial growth dependence analysis.

3 Results

3.1 Agreement between woody biomass growth and carbon fluxes

The elementary components of the seasonal forest C balance revealed contrasted agreement with the inter-annual variability in AWBI (Table 3). Seasonal gross primary productivity (GPP) and net primary productivity (NPP) were strongly linked to AWBIs with a comparable agreement between species. However, autotrophic respiration (R_a) revealed weak and often non-significant correlations with AWBIs across the 49 studied plots. The highest correlations were obtained for flux aggregation periods that (i) were generally consistent within a species for GPP and NPP but different for R_a (ii) strongly differed among species (Table 3). Notably, the GPP and NPP in temperate deciduous species were summed from the beginning of May to the beginning of August or September, in temperate oaks and *F. sylvatica*, respectively. The longest GPP and NPP aggregation periods were obtained in *P. abies* (from the beginning of February to mid-September) and the shortest were found in *Q. ilex* (from the beginning of July to mid-August). Minor (less than 20 days) changes in the flux aggregation period associated to the maximum flux-AWBI correlation usually affected marginally the correlation values (Sect. S6). As a consequence, aggregation periods differing less than 13 days (start or end) from the values reported in Table 3 were generally not significantly lower than the maximum values (see critical values in Sect. S6).

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3.2 Spatial dynamics of carbon allocation to woody biomass growth

The among-sites biomass growth variability was well explained by the selected multiple regression models ($R^2 \geq 0.6$), highlighting contrasted growth dependences among species (Table 4). Carbon supply (GPP_{gp} , Table 2) was positively related to biomass growth in *F. sylvatica* and *P. abies*, whereas temperate oaks did not revealed a significant link between average AWBI and photosynthesis among sites (Fig. 3a). Notably no retained models included NPP_{gp} or Ra_{gp} . Stand age appeared as an important growth biomass driver in temperate oaks and *F. sylvatica*. Accordingly, stand age explained a substantial part of the AWBI to C supply ratio in all species, although the relationship was not significant in *P. abies* (Fig. 3b). The fraction of C sequestered in woody biomass decreased with stand age (Table 4, Fig. 3b) and was halved in temperate oaks and *F. sylvatica* for stands from 50 to 150 years (from 0.3 to 0.13 and from 0.25 to 0.1, respectively). Additionally, we reported a significant and positive effect of stand basal area on both AWBI (Table 4) and AWBI to GPP_{gp} ratio (data not shown) in temperate oaks.

3.3 Temporal dynamics of carbon allocation to woody biomass growth

The ranking of the biomass growth drivers using the RF-based variable importance highlighted strongly contrasted temporal AWBI dependences among species (Fig. 4). The growth of temperate deciduous species appeared to be under a more complex environmental control than *P. abies* and *Q. ilex*, with several variables explaining a substantial part of the AWBI annual variability (Fig. 4a and b). C supply (GPP_{gp}) was strongly related to AWBI in temperate oaks and *F. sylvatica*, and to a lesser extent, in *P. abies* (Fig. 4a–c), with positive marginal effects (Fig. 5a, e and h). Water stress duration over the study period ($WS_{per_{gp}}$) was the predominant driver of the AWBI variability in *Q. ilex*, and was also strongly related to the growth of temperate deciduous species. Low temperature over the growing period (templim) was the most important dependence in *P. abies* and also explained a part of AWBI variability in temperate oaks.

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Water and temperature stress indices had negative and quasi-linear marginal effects on AWBI (Fig. 5). Finally, environmental lagged effects contributed substantially to explain AWBI variability in all species: water stress intensity of the previous year ($WS_{int_{y-1}}$) was reported to affect growth in *F. sylvatica* and *Q. ilex* whereas C supply of the previous year (GPP_{y-1}) affected temperate oaks and *P. abies* stands. Lagged effects generally revealed threshold marginal dependences, with a significant negative effect on AWBI only for high water stress or low C supply (Fig. 5). The effect of the retained variables (Fig. 4) was evaluated in multiple regressions using dummy variables to test for the significance of slope changes when threshold appears on partial plots (Fig. 5). Models explained approx. 20 % of the AWBI variability of temperate oaks and *P. abies*, and approx. 40 % in *F. sylvatica* and *Q. ilex* (Table 5). All the explanatory variables had significant effects, but *templim* was not retained in temperate oaks after the bootstrap procedure accounting for the uncertainty of C flux simulations. We reported significant slope changes in the effect of GPP_{y-1} in temperate oaks and in the effect of GPP_{gp} in *P. abies* (Table 5). The models including NPP_{gp} and NPP_{y-1} revealed the same AWBI dependences that the models described above with a reduced explanatory power, whereas models including Ra_{gp} and Ra_{y-1} were not significant (data not shown).

4 Discussion

This study quantified the C annually allocated to woody biomass increment in five species representative of the main European forest biomes. Combining field measurements, climatic database and process-based simulations, our approach released the constraint imposed by EC data scarcity to characterize the annual partitioning of C to wood at 49 sites (931 site-years). We were thus able to highlight the species-specific drivers of the spatio-temporal dynamic of C allocation to woody growth along large ecological gradients. Our results have far reaching implications for the representation of biomass growth causalities in TBMs.

4.1 On correlating forest carbon balance to woody biomass growth

Relating EC-based estimation of forest C balance and biometric measurements of woody biomass growth has been the concern of an increasing number of local studies. The results are expected to enhance our understanding of the ecosystem C dynamics but provide conflicting conclusions so far. The reported correlation between woody biomass growth and forest C gain indeed ranges from non-significant correlations (Mund et al., 2010; Richardson et al., 2012; Rocha et al., 2006) to tight links (Babst et al., 2014; Ohtsuka et al., 2009; Peichl et al., 2010; Zweifel et al., 2010). Accordingly, the agreements between AWBI and C fluxes reported in this study strongly varied among sites in each studied species (Table 3). Annual woody biomass increment was nonetheless consistently related to GPP_{gp} and NPP_{gp} , and only marginally to Ra_{gp} in a majority of sites (Table 3). Babst et al. (2013) reported a similar dependence of biomass growth to the C fluxes at 5 sites spanning a wide latitude range across Europe. The authors attributed this result to a common sensitivity of C assimilation and biomass growth to the water balance. Our results also support the view that biomass growth and forest C balance components are under the control of distinct but partially correlated processes (Beer et al., 2007; Fatichi et al., 2014) that may or may not induce consistent annual changes, depending on the environmental conditions faced by trees. Maximum correlation values were observed in *F. sylvatica* and temperate oaks for flux aggregation periods that were consistent with the previously reported phenology of woody biomass increment (Table 3, Michelot et al., 2012, Sect. S10). Granier et al. (2008) and Babst et al. (2013) accordingly reported high agreements between AWBI and forest C fluxes summed until the time of growth cessation (August/September). Fluxes aggregation periods were however strongly incoherent with the timing of woody growth in *Q. ilex* and *P. abies* (M. Lempereur et al., unpublished data; Cuny et al., 2012) which indicates that the inter-annual variation in AWBI is not solely, and in some cases (here in *Q. ilex* and *P. abies*) not primarily, depending on the C fuelled from photosynthesis. Specifically, the agreement between growth and a short period of C flux aggregation

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occurring in early summer that we reported in *Q. ilex* is in line with the major effect of growth cessation on the annual biomass increment that have been attributed to a drought-induced limitation of cambial activity at the Puéchabon site (Lempereur et al., unpublished data). The processes underlying the long flux aggregation period related to the annual biomass increment in *P. abies* possibly involves the effect of late winter temperature on cambium phenology (Rossi et al., 2011). Overall our results suggest that using growth-flux correlation coefficients when investigating the source-limitation of growth or the seasonality of C allocation to woody tissue can lead to misleading conclusions.

4.2 The between-site variability in carbon allocation to woody biomass growth is related to ontogeny and competition intensity

We highlighted an age-related decline of C partitioning to woody biomass at spatial scale in all three species (Fig. 3b). This result had previously been reported in *F. sylvatica* stands using measurements of the main C compartments along a chronosequence (Genet et al., 2010). Different non-exclusive processes can explain this age-related trend. The increase of tree height is associated with an increase in xylem hydraulic resistance that may lead to a decline in the turgor of living cells with potential negative consequence on cambial activity (Woodruff et al., 2004). This constraint may result in a height-related sink-limitation of growth (Woodruff and Meinzer, 2011) in line with our report. Concurrently, life-history traits such as a predominant effort toward reproduction in aged stands could also be involved, although the interactions between growth and reproduction mechanisms are still under debate (Hoch et al., 2013; Thomas, 2011) and remain to be properly represented in TBMs. Only the GPP component of the forest C balance was retained in the final models (Table 4), indicating that the increase of maintenance respiration with standing biomass was probably not involved in the age-related decline in biomass growth (Drake et al., 2011; Tang et al., 2014). While the hydraulic constraint on C assimilation associated with tree height has been thought as an important driver (Ryan et al., 2006;

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Tang et al., 2014), recent local studies have evidenced that changes in demography and stand structure rather than decrease in tree functioning may primarily explain the age-related decline observed in stand woody growth (Binkley et al., 2002; Xu et al., 2012). Our result suggests that changes in C allocation should also be considered, as no mortality occurred in the studied plots over the measurement period (data not shown). We additionally evidenced a significantly higher C partitioning to woody biomass in temperate oak stands with high competition intensity (i.e. high stand basal area, Table 3). Reports regarding the effect of competition on C allocation dynamic are so far conflicting (Litton et al., 2007) showing no large and consistent effect. Besides, no significant effect of soil nutrient availability was evidenced along the studied ecological gradient whereas a recent meta-analysis reported that this factor affects positively C partitioning to forest biomass at global scale (Vicca et al., 2012). The RENECOFOR network only includes relatively fertile sites (Supplement S5) which could explain this result but remains putative at this stage. More studies are thus required to further specify the contribution of the different drivers to the variation in the C partitioning to woody biomass along local to global environmental gradients.

4.3 The inter-annual variability in woody biomass growth is consistent with combined source-sink limitations

Water or temperature stresses exerted a significant direct control on the inter-annual variation of woody biomass growth (i.e. independently from their effects on C assimilation) in every species and biomes (Table 5 and Figs. 4 and 5). Cambial growth has been reported to be inhibited at lower water stress level than photosynthesis (Muller et al., 2011; Tardieu et al., 2011). Indeed, the drought-induced decrease in cell turgor strongly affects the cell divisions (Woodruff and Meinzer, 2011) and cell wall expansion (Cosgrove, 2005; Lockhart, 1965) before gas exchange modulation comes into play. Similarly, there is evidence that cell growth processes, such as cell division, are affected earlier by low temperature than photosynthesis (Körner, 2008). While these evidences documented the plausible mechanisms of the sink control of

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biomass growth at the cell scale, there is still considerable debate as to whether sink or source actually limit growth of the world's forests (Palacio et al., 2014; Wiley and Helliker, 2012). The typically observed large C reserve pools (Hoch et al., 2003; Würth et al., 2005) have been interpreted as a consequence of overabundant C supply and thus as an evidence of a sink control of tree growth (Körner, 2003). However, recent works suggest that a source limitation of growth may be compatible with large C reserve pools if part of this mobile C is sequestered rather than stored (Millard and Grelet, 2010) or if C storage is an active tree response to environmental stress (Dietze et al., 2014; Wiley and Helliker, 2012). Using an alternative methodology (i.e. not based on C storage measurement) our results suggest that sink limitation has a significant effect on the annual woody biomass growth in five species representative of contrasted European biomes, including deciduous temperate forests. As sink limitation implies periods with significant C supply but no growth, this result also corroborates recent empirical studies reporting a significant role of growth duration in the annual variability of tree radial increment (Lempereur et al., unpublished data; Cuny et al., 2012; Brzostek et al., 2014). We additionally reported that past environment constraints significantly affected the C partitioning to woody growth in every species and biomes (Table 5 and Figs. 4 and 5). The lagged effect of previous year low C supply (GPP_{y-1}) possibly indicates a preferential C allocation to storage at the expense of growth in trees facing C reserve pool depletion (Bansal and Germino, 2008; Wiley et al., 2013). Richardson et al. (2012) accordingly reported a strong agreement between AWBI and EC-based estimation of the previous year carbon supply in a mature maple stand. The important detrimental effect of low previous year C supply on the temperate oak woody growth (Fig. 4) may be related to its growth phenology as this species relied on C reserve to achieve a large part of the annual biomass growth before leaf expansion in spring (Barbaroux et al., 2003). The lagged effect of high water stress intensity in *F. sylvatica* and *Q. ilex* (Fig. 4) may be linked to the past drought-induced mortalities of buds or fine roots (Leuschner et al., 2001; López et al., 2003). Indeed, pre-built buds are thought to strongly regulate the cambial activity of the next year (Palacio et al., 2012; Zweifel

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et al., 2006) and a recent meta-analysis highlighted preferential allocation to fine roots at the expense of woody growth in stands facing constraining environment (Chen et al., 2013). Finally, our results suggest that C supply (GPP_{gp}) is an important driver of the annual biomass woody growth in temperate deciduous forest (Daudet et al., 2005).

GPP was the component of the forest C balance most closely related to the annual variability of growth, which is in line with its preponderant role in the annual variability of net ecosystem productivity of European forests (Delpierre et al., 2012). Overall, our findings support the premise that forest woody biomass growth is under a complex control including both source and sink limitations, following the principle of Liebig's law: while numerous processes potentially influence woody growth, the stand growth at a given site and a given time is limited only by the most constraining factor. The C (source) limitation of growth can thus only occur when other factors are non-limiting (Fatichi et al., 2014), which is expected to be rare in strongly constrained environment such as Mediterranean or mountainous areas (Fig. 4).

4.4 Toward an integrated modelling framework

Most of the models currently used to project the outcome of global changes on forest represent woody growth as a fraction coefficient of the total C uptake (source control of growth, De Kauwe et al., 2014). This carbon-centric perspective overlooks the possibility of a sink control of growth, contradicting evidences found in this and earlier local studies (reviewed by Fatichi et al., 2014) and possibly explaining the low ability of TBMs to simulate the inter-annual variability of woody growth (Le Roux et al., 2001). On the basis of our analysis of the spatio-temporal dynamics of C allocation to woody growth at regional scale, we here suggest a straightforward way toward a combined source-sink-driven forest growth modelling framework (Fig. 6). In this view, a potential site-specific allocation coefficient is first defined to represent the effect of soil fertility on C allocation to wood (Vicca et al., 2012). In a second step, this coefficient is adjusted to the physiological state of the stand using the dependence of C allocation to ontogeny, competition intensity and lagged environmental stresses. The age-related

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decline in forest growth has been highlighted as an important modelling goal (Magnani et al., 2000; Zaehle et al., 2006) but has so far been implemented through a negative effect of the increasing stand respiration on the forest C balance, contradicting current knowledge (Ryan et al., 2006). The resulting annual allocation coefficient is finally modulated by the direct water and temperature constraints on growth. Leuzinger et al. (2013) accordingly improved the LPJ terrestrial biosphere model predictions at the cold tree-line using a representation of the direct temperature limitation of growth. Our approach can be seen as an intermediate step toward a more mechanistic representation of C allocation to woody biomass (Hölttä et al., 2010). It further synthesizes our current knowledge of forest growth dependences and has the potential to unify in the same modelling framework seemingly contradictory observations. The simulated growth is indeed under the combined controls of C supply and changes in C allocation due to endogenous adjustments and/or modulations of the sink activity (Fig. 6). These controls result from distinct processes, independently represented in the modelling framework. The relative influence of the different processes, i.e. the simulated growth causalities, are thus likely to vary both spatially and temporally depending on the environmental conditions faced by trees, possibly shedding light on the contrasted results reported by correlative studies. While comparable to previous reports (Lebourgeois et al., 2005; Mérian et al., 2011), the proportion of the annual growth variability explained by our approach remained moderate (Table 5). Plausible explanations include: (i) unreported management interventions that could have skewed the historical stand growth reconstruction (ii) potentially important growth drivers not considered here, such as changes in C partitioning due to mast seeding (Mund et al., 2010), genetic differentiation (Vitasse et al., 2014) or allometry-mediated tree acclimation to drought (Martin-StPaul et al., 2013). Nonetheless, our results suggest that implementing the presented C allocation dependences in TBMs will allow refining the projections of the outcome of global changes on forest growth, with implications on the predicted evolution of the forest C sink, forest dieback and tree species distributions (Cheaib et al., 2012).

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The Supplement related to this article is available online at
doi:10.5194/bgd-12-2213-2015-supplement.

Acknowledgements. We wish to thank the Office National des Forêts and the RENECOFOR network team, particularly Manuel Nicolas and Marc Lanier, for providing us with the database. The SAFRAN database was provided by Météo-France as part of the HYMEX project. J. Guillemot receives a PhD grant from the French Ministère de l'Enseignement Supérieur et de la Recherche and the University of Paris-Sud. A post-doctoral research grant to N. K. Martin-StPaul was provided by the Humboldt project within the GIS climat. As part as the ICP forests network data (icp-forests.net), the material used in this article is available, free of charge, upon request. Please contact M. Nicolas (manuel.nicolas@onf.fr, +00331 60 74 92 28, Office National des Forêts, Fontainebleau, 77300, France).

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Table 1. Climatic features of the studied sites. ETP is annual Penman–Monteith potential evapotranspiration, Precip. is annual precipitation, Temp. is annual temperature. Values are site averages \pm SD among sites.

| Species | Number of plots | Number of site-years | Elevation (m) | ETP (mm) | Precip. (mm) | Temp. ($^{\circ}$ C) | Source |
|----------------------------|-----------------|----------------------|----------------|----------------|----------------|-----------------------|----------------|
| <i>F. sylvatica</i> | 16 | 313 | 565 \pm 326 | 1010 \pm 121 | 1001 \pm 133 | 10.1 \pm 0.98 | RENECOFOR |
| <i>Q. petraea/Q. robur</i> | 26 | 484 | 193 \pm 76 | 999 \pm 71 | 821 \pm 96 | 10.7 \pm 0.63 | RENECOFOR |
| <i>P. abies</i> | 6 | 101 | 1056 \pm 313 | 933 \pm 44 | 1559 \pm 340 | 7.1 \pm 1.4 | RENECOFOR |
| <i>Q. ilex</i> | 1 | 43 | 270 | 1417 | 907 | 13.4 | Puéchabon site |

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Table 2. Description of the explanatory variables considered in the analyses. The type category indicates the source of the data: measurement (M), SAFRAN climate database (C) or CASTANEA simulations (S). Scale categories indicate the variables considered in spatial (S) and/or temporal (T) analyses.

| IDs | Description | Unit | Type | Scale |
|-----------------------------------|--|-------------------------|------|-------|
| age | Stand age | years | M | S |
| AWBI | Annual woody biomass increment | gCm^{-2} | M | ST |
| SBA | Stand basal area | m^2 | M | S |
| camb_onset | Onset of the cambial activity | day of the year | S | T |
| GPP _{gp} | Gross primary production of the current (y) growth period | gCm^{-2} | S | ST |
| GPP _{$y-1$} | Gross primary production of the previous ($y-1$) year | gCm^{-2} | S | T |
| frost | Sum of the average daily temperatures below -2°C during the last winter (year $y-1$ and y) | $^\circ\text{C}$ | C | ST |
| LNC | Leaf nitrogen content | gNgDM^{-1} | M | S |
| NPP _{gp} | Net primary production of the current (y) growth period | gCm^{-2} | S | ST |
| NPP _{$y-1$} | Net primary production of the previous ($y-1$) year | gCm^{-2} | S | T |
| numstem | Stem density | number ha^{-1} | M | S |
| SNA | Class of soil nutrient availability (1: low, 2: medium, 3: high) | unitless | M | S |
| SWC | Soil water holding capacity | mm | M | S |
| templim | Number of days of the current (y) growth period with an average temperature below 6°C | number of days | C | ST |
| Ra _{gp} | Autotrophic respiration of the current (y) growth period | gCm^{-2} | S | ST |
| Ra _{$y-1$} | Autotrophic respiration of the previous ($y-1$) year | gCm^{-2} | S | T |
| WS _{pergp} | Number of days of the current (y) growth period with a soil water content below 60% of the soil water holding capacity | number of days | S | ST |
| WS _{per$y-1$} | Number of days of the previous ($y-1$) year with a soil water content below 60% of the soil water holding capacity | number of days | S | T |
| WS _{intgp} | Water stress intensity index over the current (y) growth period | unitless | S | ST |
| WS _{int$y-1$} | Water stress intensity index of the previous ($y-1$) year | unitless | S | T |

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Table 5. Temporal dependences of the annual woody growth: multiple regression estimates. Data have been centered and scaled. GPP_{gp} is the gross primary production of the growth period, $WS_{per_{gp}}$ is a water stress index of the growth period, $WS_{int_{y-1}}$ is a water stress index of the previous year, $templim$ is a low temperature index of the growth period (Table 2). $D1$ and $D2$ are dummy variables ($D1 = 0$ if $GPP_{gp} < 1400 \text{ gCm}^{-2}$, $D1 = 1$ otherwise; $D2 = 0$ if $GPP_{y-1} < 1550 \text{ gCm}^{-2}$, $D2 = 1$ otherwise) see Fig. 5. ρ is the parameter of the first-order autoregressive process used to model the temporal autocorrelation of within-stand errors. Values: estimates [F values]. Estimate values differing from 0 are indicated (* $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$). Estimate with a Δ index indicates variable not retained in the bootstrap procedure (see main text).

| Estimates | Species | | | |
|----------------------|--|-----------------------------------|---------------------------------|----------------------------------|
| | <i>Q. petraea</i> / <i>Q. robur</i> | <i>F. sylvatica</i> | <i>P. abies</i> | <i>Q. ilex</i> |
| GPP_{gp} | 3.26×10^{-1} *** [96.7] | 4.87×10^{-1} *** [133.7] | 2.4×10^{-1} * [3.5] | |
| $WS_{per_{gp}}$ | -1.09×10^{-1} ** [5.9] | -2.04×10^{-1} *** [13.5] | | -5.8×10^{-1} *** [25.2] |
| $WS_{int_{y-1}}$ | | -2.37×10^{-1} *** [21.1] | | -2.2×10^{-1} * [6.3] |
| GPP_{y-1} | 3.82×10^{-1} * [3.3] | | -4×10^{-1} ** [3.2] | |
| $templim$ | -9.60×10^{-2} ** Δ [6.4] | | -1.26 *** [3.5] | |
| $D1$ | | | -2.4×10^{-1} *** [0.4] | |
| $D2$ | -3.9×10^{-1} ** [0.8] | | | |
| $D1 \cdot GPP_{gp}$ | | | 1.33 ** [8.2] | |
| $D2 \cdot GPP_{y-1}$ | -4×10^{-1} ** [6.4] | | | |
| ρ | 0.61 | 0.68 | 0.52 | 0.44 |
| P | $< 10^{-4}$ | $< 10^{-4}$ | 7.7×10^{-3} | $< 10^{-4}$ |
| adj. R^2 | 0.21 | 0.42 | 0.20 | 0.43 |

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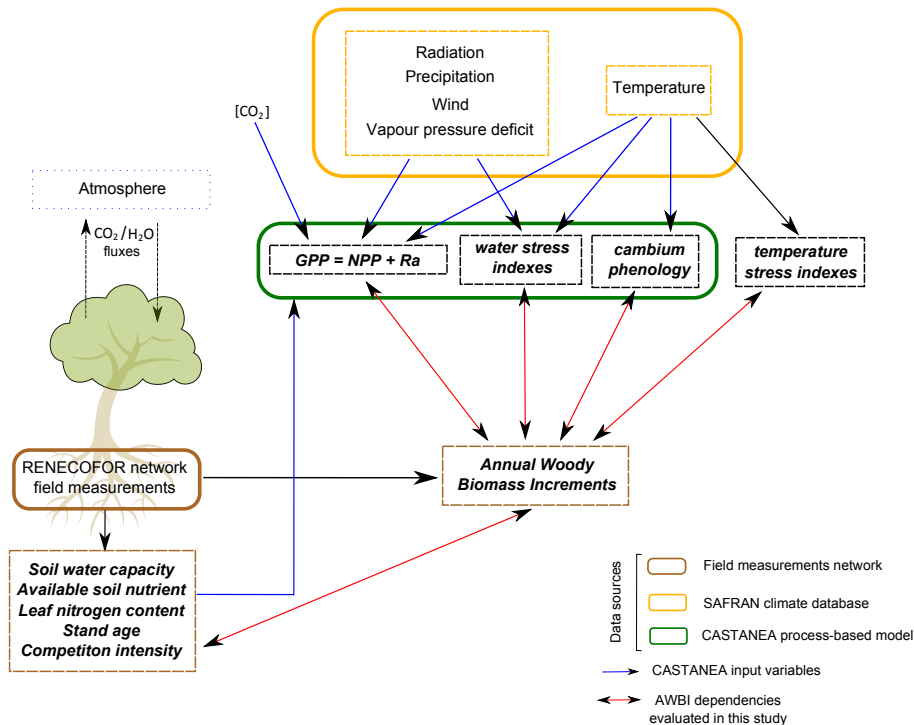


Figure 1. The conceptual framework and the three sources of data (field measurements, climate reanalysis, process-based simulations) used for the analyses.

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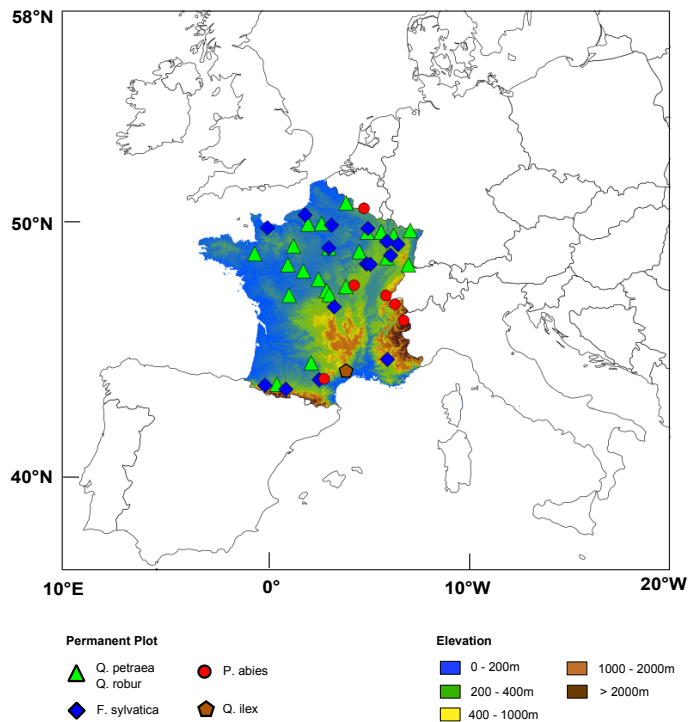


Figure 2. Location of the studied sites.

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J. Guillemot et al.

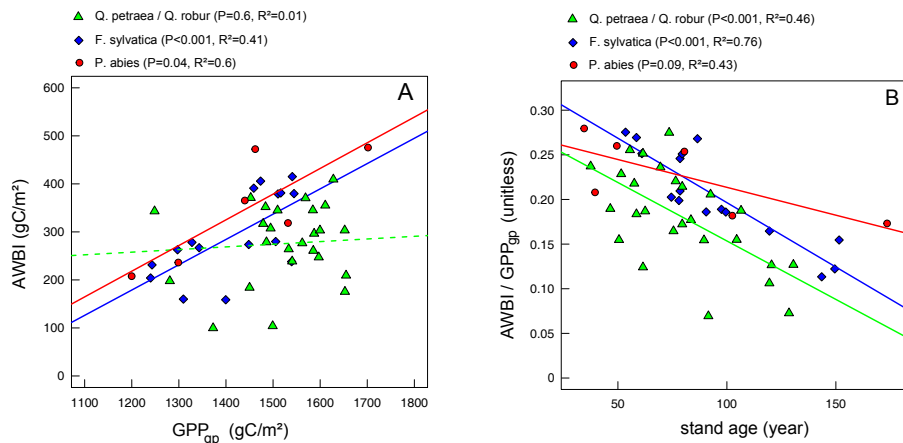


Figure 3. Spatial dependences of the annual woody growth. **(a)** Relationship between the annual woody biomass increment (AWBI) and the gross primary productivity of the growth period (GPP_{gp}) averaged over sites. **(b)** Age-related decline of the carbon partitioning to AWBI (AWBI/GPP_{gp}).

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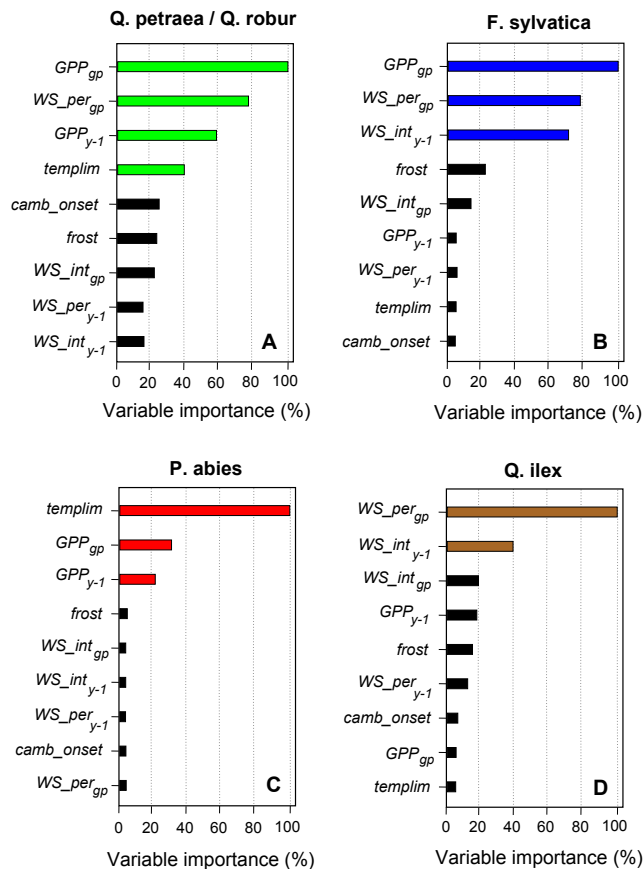


Figure 4. Temporal dependences of the annual woody growth: importance of explanatory variables from random forest classification. Importance is expressed as % of the importance of the explanatory variable ranked first. Variable IDs are given in Table 2. Colored variables were retained in the following analyses.

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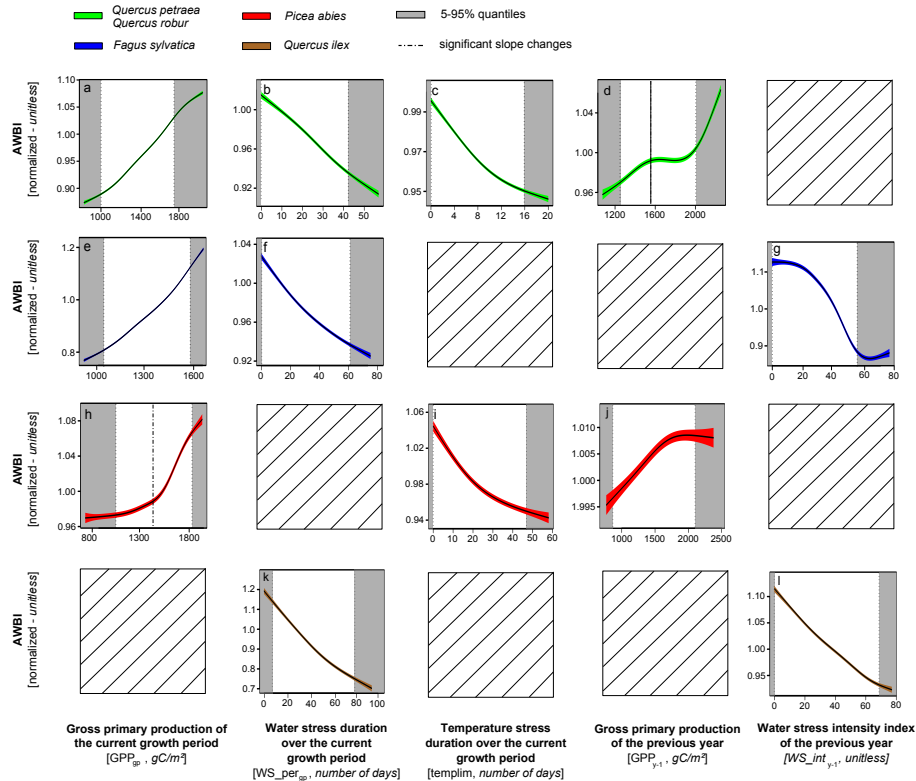


Figure 5. Temporal dependences of the annual woody growth: partial dependence describing the marginal effect of each explanatory variable on annual woody growth. Lines are smoothing splines with 50 % frequency response cut-off. Colored areas are 95 % confidence intervals. The part of the dependences corresponding to the 5 and 95 % data quantiles (grey areas) were not considered in the discussion.

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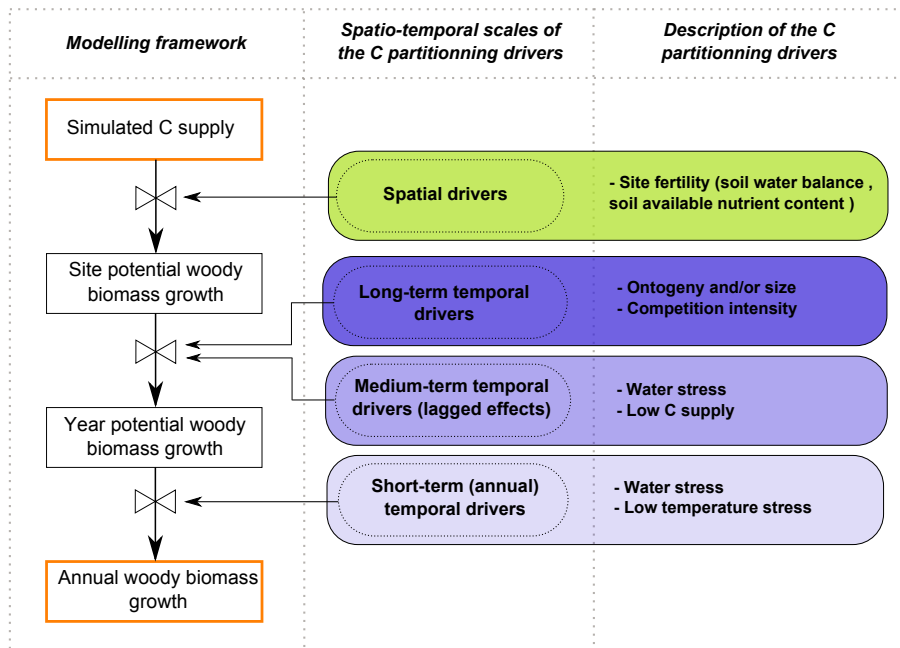


Figure 6. Modelling framework for a combined source-sink-driven representation of the carbon allocation to woody growth.

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