The dynamic of the 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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Abstract

The extent to which wood growth is limited by carbon (C) supply (i.e., source control) or by cambial activity (i.e., sink control) will strongly determine the responses of trees to global changes. Nevertheless, the physiological processes that are responsible for limiting forest growth are still debated. The aim of this study was to evaluate the key determinants of the annual C allocation to wood along large soil and climate regional gradients for five tree species representative of the main European forest biomes (*Fagus sylvatica*, *Quercus petraea*, *Quercus ilex*, *Quercus robur* and *Picea abies*).

The drivers of stand biomass growth were assessed on both inter-site and inter-annual scales. Our dataset included field measurements performed at 49 sites (931 site-years) and it was complemented with process-based simulations when possible explanatory variables could not be directly measured. Specifically, the relative influences of tree 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 the stand C allocation to wood was predominantly driven by age-related decline. The direct effects of temperature and water stress on sink activity (i.e., effects independent from their effects on the C supply) exerted a strong influence on the annual stand wood growth in all of the species considered, including deciduous temperate species. The lagged effect of the past environmental conditions (e.g., the previous year's water stress and low C uptake) significantly affected the annual C allocation to wood. The C supply appeared to strongly limit growth only in temperate deciduous species.

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

1 Introduction

Forests play a critical role in the global carbon (C) cycle. Inventory-based estimates indicate that established forests have been a persistent carbon sink for decades, sequestering almost 30% of the world's total anthropogenic C emissions between 1990 and 2007 (Pan et al., 2011). The fate of the sequestered C is highly dependent on the C dynamic in trees, which determines the residence time of C in forest ecosystems. Despite its importance for the future terrestrial C sink (Carvalhais et al., 2014; Friend et al., 2013), the partitioning of C among tree organs and ecosystem respiration remains poorly understood (Brüggemann et al., 2011). In particular, there has been considerable amount of debate regarding the physiological mechanisms that drive the increment of the forest woody biomass (Palacio et al., 2014; Wiley and Helliker, 2012). The fraction of assimilated C stored in woody biomass can be inferred by combining biometric measurements with estimates of the C exchange between the ecosystem and atmosphere, based on the eddy-covariance (EC) technique (Babst et al., 2014; Litton et al., 2007; Wolf et al., 2011). Global meta-analyses (that included data from various biomes and species) have revealed a strong correlation between the observed gross primary production (GPP) and the woody biomass increment (Litton et al., 2007; Zha et al., 2013). Accordingly, growth has long been thought to be C limited, because of the hypothesized causal link between C supply and growth (i.e., source control, Sala *et al.* 2012). The environmental factors that have been reported to affect growth (soil water content, temperature, nutrient content, light and CO_2) 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) that are currently used to evaluate the effects of global changes on forests (Clark et al., 2011; Dufrêne et al., 2005; De Kauwe et al., 2014; Krinner et al., 2005; Sitch et al., 2003).

Source control of wood growth is a mechanism that has been questioned by several authors, who argue that cambial activity is more sensitive than C assimilation to several environmental stressors (Fatichi et al., 2014). In particular, the decrease in cell turgor that occurs because of water stress strongly affects cell division and expansion (Woodruff and Meinzer, 2011) before there is any strong reduction in the gas exchange (Muller et al., 2011; Tardieu et al., 2011). Similarly, cell division is affected by low temperatures before it is affected by photosynthesis (Körner, 2008). The onset of cambial activity is also known to be highly responsive to temperature (Delpierre et al., 2015; Kudo et al., 2014; Lempereur et al., 2015; Rossi et al., 2011) and, in turn, may partly determine annual cell production and wood growth (Lupi et al., 2010; Rossi et al., 2013). Finally, the quality and quantity of available soil nutrients, particularly nitrogen (N), could affect growth independently of their impacts on C assimilation, because of the relatively constrained stoichiometry of tree biomass (Leuzinger and Hättenschwiler, 2013). These studies suggest that growth is limited by the direct effects of environmental factors (i.e., sink control). However, numerous key environmental factors (e.g., nutrients, temperature and water) affect both sink and source activities, and it is thus difficult to determine whether wood growth is more related to C supply or to the intrinsic environmental sensitivity of cambium functioning (Fatichi et al., 2014). The extent to which wood growth is under source or sink control is of paramount importance for predicting how trees will respond to global changes and specifically how increasing atmospheric CO_2 will affect forest productivity and the future terrestrial C sink. The implementation of the respective roles of source and sink controls on growth in TBMs is therefore a substantial challenge for modellers, because it may determine our ability to project future forest C sink, diebacks and distributions (Cheaib et al., 2012; Fatichi et al., 2014; Leuzinger et al., 2013).

The allocation of assimilated C within forest ecosystems is a complex, integrative process that can be described by several non-exclusive principles (Franklin et al., 2012), including i) allometric scaling, ii) functional balance and iii) evolution-based optimal responses. i) The allometric scaling principle is based on the assumption that biophysical laws determine C partitioning among the different forest compartments. Important allocation constraints include vascular network optimality (Enquist, 2002) and functional homeostasis in water transport (Magnani et al., 2000). ii) The functional balance principle suggests that the organ responsible for acquiring the limiting resource is preferentially allocated C. Consistent with this principle, higher C allocation to fine roots at the expense of C allocation to wood growth has been reported for poor or dry soils (Chen et al., 2013; Keyes and Grier, 1981). In addition, a possibly greater allocation to root symbionts and exudates at the expense of biomass production has also been reported (Vicca et al., 2012). iii) Finally, the optimal response principle postulates that allocation maximizes fitness in a fixed environment. This hypothesis agrees with the idea that a dynamic reserve pool act as temporary storage, possibly at the expense of growth, to promote long-term tree survival (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., 2013). The optimal response principle is consistent with several well-known life history traits, such as preferential allocation to reproduction in ageing plants, which could lead to age-related declines in woody biomass allocation (Genet et al., 2010; Thomas, 2011). The woody biomass increment therefore appears to be under the control of multiple factors. The effects of these drivers are expected to strongly vary in space and time. Consequently, studies have reported conflicting relationships between the C supply and wood growth (Gielen et al., 2013; Richardson et al., 2013), ranging from no significant relationships (Mund et al., 2010; Rocha et al., 2006) to close relationships 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 that affect wood growth on different spatio-temporal scales is necessary to explain these apparently contradictory results using a common framework. Moreover, investigations should be conducted at the species level, because phylogeny may strongly constrain forest functioning (Carnicer et al., 2013; Drobyshev et al., 2013) and induce different growth determinants among taxa (Genet et al., 2010).

There is a gap between the knowledge obtained from global studies of universal C allocation rules in forests and our understanding of the cell processes that underlie cambial activity; currently, this gap appears to be the primary obstacle to a more complete understanding of wood growth drivers. In this regard, species-specific studies that evaluate the dynamic of C partitioning to annual wood growth along soil and climate gradients would be highly useful but are lacking. Unfortunately, there is a scarcity of datasets that combine EC and growth measurements at the same sites (Luyssaert et al., 2007). Here, we released this constraint by complementing stand and soil measurements at a permanent plot network of 49 forest sites with process-based simulations of annual and seasonal tree C balance (Fig. 1). Simulations were performed using a process-based model (CASTANEA, Dufrêne *et al.* 2005) that was thoroughly validated using EC data from throughout Europe (Davi et al., 2005; Delpierre et al., 2009, 2012) and was applied using site-specific parameters. By relating biometric measurements to variables that explain the C source and sink activity, we evaluated the key drivers of the annual C allocation to stand wood growth in five species that are representative of the main European forest biomes: *Fagus sylvatica*, *Quercus petraea* and *Quercus robur* for temperate deciduous broadleaf forests; *Picea abies*, for high-latitude and high-altitude evergreen needleleaf forests;

and *Quercus ilex*, an evergreen broadleaf species from Mediterranean forests. Specifically, the relative influence of annual and seasonal (from one month to the year) tree C balance (source control), direct environmental control (water and temperature effects on 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 to the spatio-temporal dynamic of forest wood growth across a wide range of environmental contexts and (2) provide information that can be used to refine 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 simulation data. This hybrid approach allowed us to assess and disentangle the effects of previously reported environmental and endogenous drivers of C allocation to wood growth (Fig. 1).

2.1 Study sites and field data

We gathered field measurements from 48 plots from the French Permanent Plot Network for the Monitoring of Forest Ecosystems (RENECOFOR, Ulrich, 1997) and the Puéchabon tower flux site (Martin-StPaul *et al.* 2013). The location and general climatic features of these plots are shown in Fig. 2 and Table 1. Complete site description is available in Supplement S1.

2.1.1 Growth measurements and historical stand growth reconstruction

Growth measurements were obtained by two methods: *i)* Dendrochronological sampling, in which 12 to 30 overstory trees per plot were cored to the pith at breast height with an incremental borer. Cores were collected in 1994 at the RENECOFOR sites and in 2008 at the Puéchabon site (Lebourgeois 1997; J.M. Ourcival, *unpublished data*). Tree circumferences at breast height

(CBHs) and total heights were also measured. The average stand age was inferred from the tree ring series. *ii)* Forest inventories, in which extensive CBH surveys were conducted in a 0.5 ha area of every plot (Cluzeau *et al.* 1998; Gaucherel, Guiot & Misson 2008; J.M. Ourcival, unpublished data).

Tree ring series were combined with the CBH surveys to reconstruct the historical CBHs of every tree on the plots (over 8 to 43 years, Supplement S1). The entire stand tree CBH distribution was reconstructed from the CBHs of the sampled trees using an empirical tree competition model (Deleuze et al., 2004). This model stipulates that only trees with a CBH above a given threshold (σ, the minimum circumference needed to gain direct access to sunlight), have a significant growth. Overstory trees then have an annual basal area growth rate that is proportional to their size, according to a slope coefficient, γ. Following the work of Guillemot *et al.* (2014), the model was calibrated annually, beginning at year (n) of the core sampling and used iteratively to reconstruct the past stand CBH growth. The σ parameter was first defined using an empirical relationship with the maximum CBH of the stand tree distribution from year (n). The γ parameter was then adjusted using the tree rings measured on the sampled trees in year (n-1). The parameterized model was finally used to predict the basal area increments of all the trees in the distribution, and consequently the tree CBH distribution in the year (n-1). A detailed description of the iterative process can be found in Supplement S2 and in Guillemot *et al.* (2014).

The inferred past trajectory of the stand CBH distribution was used to calculate the historical number of stems (*numstem*, Table 2) and stand basal area, which we considered to be a proxy for within-stand competition intensity (*SBA*, Table 2, Kunstler *et al.* 2011). The historical total woody stand biomass was also calculated (Supplement S3) using species-specific tree level allometric functions (Bontemps et al., 2009, 2012; Dhôte and Hercé, 1994; Seynave et al., 2005; Vallet et al., 2006) and wood density models (Bouriaud et al., 2004; Wilhelmsson et al., 2002; Zhang et al., 1993). For *Q. ilex*, we used the appropriate function from Rambal et al. (2004) to calculate the stand woody biomass from CBHs. Past annual woody biomass increments (AWBIs) were then inferred (Supplement S4).

2.1.2 Measurements of stand characteristics

The stand measurements included the soil water holding capacity (SWHC), leaf area index (LAI), leaf N content (LNC) and soil nutrient availability (SNA). The SWHC was estimated via the soil depth and texture measured at two soil pits per plot (Brêthes and Ulrich, 1997). The LAI was estimated from litter collection (Pasquet, 2002), and the sunlit LNC was determined annually for 8 trees between 1993 and 1997 (Croisé et al., 1999).

SNA was assessed as the soil's C:N biomass ratio, the absolute value of the cation-exchange capacity and the per cent base saturation (Ponette, 1997). These soil indices were measured at 3 depths (0 to 10, 10 to 20, 20 to 40 cm) and were used to categorize the soil plots into three nutrient classes, from low to high nutrient availability (Supplement S5). The SNA, SWHC and LNC were used to characterize plot fertility in the statistical analyses (Table 2).

2.2 Climate data

The following meteorological variables at the hourly temporal scale (with 8km spatial 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 related to the average altitudes of the SAFRAN cells, was corrected using plot-specific elevation measurements (assuming a lapse rate of 0.6 °K per 100 m, Supplement S1). These variables were used for climate forcing in the CASTANEA model (Dufrêne *et al.* 2005, see the following section). In addition, two annual temperature indices were used as proxies of winter frost damage and low temperature stress during the growing period (*frost* and $templim_{gp}$, respectively, Table 2).

2.3 Process-based simulation data

We used the CASTANEA model to simulate an ensemble of diagnostic variables that are related to the C source and sink activity of forest stands. The eco-physiological process-based CASTANEA model aims to simulate C and water fluxes and stocks of a monospecific, sameaged forest stand on a rotation time scale. The hourly stand-atmosphere C fluxes predicted by the CASTANEA model have been thoroughly validated using EC data from throughout Europe (Davi et al., 2005; Delpierre et al., 2009, 2012). Importantly, the biophysical hypotheses that were formalized in this model are able to reproduce the interplay of the complex mechanisms that lead to inter-annual variability in the stand C balance (Delpierre et al., 2012); modelling this interplay has been recognized as a substantial challenge for TBMs (Keenan et al., 2012). A complete description of CASTANEA is provided in Dufrêne *et al.* (2005), and subsequent modifications are described in Davi *et al.* (2009) and Delpierre *et al.* (2012). For the purpose of the present study, CASTANEA was parameterized with site-specific SWHC and LNC values. The measured LAI and total woody biomass were used to initialize the model simulations. The model's ability to reproduce the annual variability in LAI and the forest growth has been recently validated (Guillemot et al., 2014). Nevertheless, the annual standing woody biomass was forced to conform to the observed values, because the model was used for diagnostic purposes in this study.

Several groups of variables were simulated and aggregated on an annual basis (Table 2):

1. *The elementary components of the tree C balance*. These components included the GPP, autotrophic respiration (Ra), and net balance (i.e., net primary productivity, NPP = GPP – Ra). For a given year y, we aggregated the hourly simulated C fluxes over different seasonal time periods, with starting days that ranged from 30 to 190 and ending days that ranged from 190 to 350, at a 2-day resolution. The C fluxes were also summed i) for the species-specific biomass growth periods reported in the literature (GPP_{gp}, Ra_{gp} and NPP_{gp}, Supplement S6) and ii) for the entire preceding year (y-1) as a proxy of the forest C status induced by past climate conditions (lagged effect, GPP_{y-1}, Ra_{y-1} and NPP_{y-1}).

2. *Bioclimatic water stress indices*. These indices included the intensity and duration of water stress (WS_int_{gp} and WS_per_{gp}, respectively, Supplement S7) during species-specific growing periods that have been reported in the literature (Supplement S6). The CASTANEA model simulated the daily soil water balance, based on a bucket soil sub-model with 2 layers (a top soil layer and a total soil layer that includes the top soil layer,

Dufrêne et al., (2005)). WS_int_{gp} was then used to quantify the intensity of water stress by summing the *reduc* index on a daily basis (Granier et al., 1999).

$$reduc_t = \max\left(0, \min\left(1, \frac{SWC_t - SWC_{wilt}}{0.4 \times \left(SWC_{fc} - SWC_{wilt}\right)}\right)\right)$$

where SWC_t is the soil water content on day t (mm), SWC_{wilt} is the soil water content at the wilting point (mm) and SWC_{fc} is the soil water content at field capacity (mm). WS_per_{gp} is the number of days of the current growth period during which the soil water content was less than 60% of the soil water holding capacity (Table 2, modified from Mund et al., (2010)). Water stress indices were also calculated for the entire preceding year (lagged effect of water stress, WS_int_{y-1} and WS_per_{y-1}).

3. *The onset of the biomass growth* (*camb_onset*). We used a new growth-onset module (David, (2011)*; N. Delpierre* and *N. K. Martin-StPaul, unpublished results*) based on a temperature sum trigger (Supplement S8).

2.4 Statistical analyses

2.4.1 General overview

Statistical analyses were conducted in three complementary steps for each studied species. (1) We calculated the correlation of the AWBIs and the C fluxes (GPP, NPP and Ra) aggregated seasonally (from 1 month to one year) to evaluate the relationship between the C supply and annual biomass growth changes. (2) The dependences of the AWBIs on the C source and the sink activity were evaluated on an inter-site spatial scale to determine the influence of the site characteristics on biomass growth. The relationship between the age and C allocation to woody biomass was also evaluated in this step. By using the age differences among sites, our chronosequence included a large range of ages (including stands that ranged in age from approximately 30 to 150 years-old, Table S1). (3) Finally, the drivers of AWBI were assessed temporally to determine the factors that were responsible for variability in the inter-annual biomass growth.

Because many environmental factors affect both forest sink and source activities, there may be strong covariance among the tree C balance and proxies of environmental stress (Fatichi et al., 2014) that could hamper the inferential power of classical statistical tests (Graham, 2003). However, the explanatory variables used in this study generally had correlation coefficients of less than 0.7, the level above which collinearity begins to severely affect model performance (Dormann et al., 2013). One exception was the correlation of components of the tree C balance (because NPP = GPP – Ra). Consequently, the tree C balance components were introduced one at a time into the models. In addition, temporal growth dependencies were evaluated using the random forest (RF) learning method (Breiman, 2001). A number of studies have empirically demonstrated the effectiveness of RF at identifying the "true" predictors among a large number of correlated candidate predictors (e.g., Archer and Kimes, 2008; Cutler et al., 2007; Genuer et al., 2010). The explanatory variables considered in our spatial and temporal analyses are presented in Table 2 and Fig. 1. Analyses were conducted with the R software (R Development Core Team 2013), using the packages lme4 (Bates et al., 2007), randomForest (Liaw and Wiener, 2002) and MuMIn (Barton and Barton, 2014). 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 were grouped in the analyses and are hereafter collectively referred to as "temperate oaks".

2.4.2 Correlations between growth and C fluxes

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

2.4.3 Drivers of spatial variations in biomass growth

The drivers of spatial variations in biomass growth were evaluated using multiple regression models using an information-theoretic approach (Burnham and Anderson, 2002). The AWBIs and the considered explanatory variables were averaged for each plot. The variables introduced into the linear models were centred and scaled such that their normalized coefficient estimates indicated the relative influence of the predictors on the AWBI. The elementary components of tree C balance (NPP, GPP and Ra) were introduced one at a time into the models. For each species, multiple regression models that contained all possible combinations of the explanatory variables were fitted. The models were compared using the second-order Akaike information criterion (AIC), and all models with an Akaike weight of at least 1% of the best approximating (lowest AIC) model were considered to be plausible (Burnham and Anderson, 2002). Ultimately, we retained the variables that appeared in at least 95% of the selected models. Models fitted using *P. abies* data were restricted to a maximum of 3 explanatory variables because of the small sample size (n=6, Table 1). *Q. ilex* (n=1) was not considered in the spatial analyses. The uncertainty of the simulated C fluxes was assessed in the analyses using a bootstrap procedure (Chernick, 2011): all linear models were fitted 1000 times, and at each iteration, the C flux values were randomly sampled within the root mean square error of the CASTANEA simulations (Supplement S9) to obtain a parameter estimate distribution for each variable. We finally retained the explanatory variables with parameter estimate distributions that excluded the zero value at a two-tailed probability level of 5%.

2.4.4 Drivers of temporal variations in biomass growth

A temporal analysis was conducted on the standardized AWBI series: a double-detrending process was applied to each series based on an initial linear regression model, followed by fitting a cubic smoothing spline with a 50% frequency response cut-off (Mérian et al., 2011). For analysing the temporal variations in biomass growth we used an RF learning method (Breiman, 2001), which was possible because of the large sample size (n = 931 site-years). The RF learning method is a non-parametric method that is used to rank the contribution of different explanatory variables and evaluate their marginal effects on a variable of interest without assuming an *a priori* dependence. The RF method combined 500 binary decision trees that were built using bootstrap samples from the initial dataset. The decisions trees aimed to reduce the heterogeneity of the explained variable in the resulting branches. For each of the 500 trees, the data that were not involved in the tree construction were used for validation. The tree predictions and errors were then averaged to provide the final RF results. The RF method does not overfit or require cross-validation (Cutler et al., 2007). A subset of explanatory variables was randomly chosen at each node, thus reducing the effect of collinear variables on the output. The RF method was used to select variables that explained the temporal variability in biomass growth (Genuer et al., 2010). Variable selection relied on permutation importance, i.e., the existence of an increase in the global mean square error when a given variable was randomized in the validation subsamples. The forms of the dependences were illustrated by partial dependence plots (graphical depiction of the marginal effect of 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. The uncertainty in the simulated C fluxes was considered in the linear models, following the procedure described in the spatial analysis section.

3 Results

3.1 Relationship between woody biomass growth and C fluxes

The elementary components of the simulated seasonal tree C balance differed in terms of their relationships with the inter-annual variability of the AWBI (Table 3). The simulated seasonal GPP and NPP were linked to AWBIs with a comparable agreement between species. However, the simulated Ra had weak and often non-significant relationships with the AWBIs across the 49 studied plots. The strongest correlations were obtained for flux aggregation periods that i) were generally consistent within a species for GPP and NPP but different for Ra and ii) strongly differed among species (Table 3). The coefficients of variation of the simulated annual NPP, GPP and Ra across the 49 studied sites were 10.8% ± 3, 7.4% ± 2, and 6.8% ± 3, respectively. GPP and NPP were summed from the beginning of May to the beginning of August and September, in temperate oaks and *F. sylvatica*, respectively. The longest GPP and NPP aggregation periods were obtained for *P. abies* (from the beginning of February to mid-September), and the shortest period were found for *Q. ilex* (from the beginning of July to mid-August). Minor (less than 20 days) changes in the flux aggregation period associated with the maximum simulated flux-AWBI correlation usually marginally affected the correlation values (Supplement S10). Consequently, aggregation periods that were less than 13 days different (either in terms of their starting or ending dates) from the values reported in Table 3 were generally not significantly lower than the maximum values (see the critical values presented in Supplement S10).

3.2 Spatial dynamic of C allocation to woody biomass growth

The inter-site variability in biomass growth was well explained by the selected multiple regression models ($R^2 \geq 0.6$). We highlighted that species varied in terms of their inter-site dependences (Table 4). The simulated C supply during the growth period (GPP_{gp}, Table 2) was positively correlated with biomass growth in *F. sylvatica* and *P. abies*, whereas there was no significant relationship between the average AWBI and photosynthesis among sites for temperate oaks (Fig. 3A). Notably, the final models did not include NPP_{gp} or Ra_{gp} for any species. The stand age was an important driver of biomass growth in temperate oaks and *F. sylvatica*. The stand age explained a substantial portion of the AWBI:C supply ratio in all species, although the relationship was not significant for *P. abies* (Fig. 3B). The fraction of C sequestered in woody biomass decreased with stand age (Table 4, Fig. 3B) and was reduced by half in temperate oaks and *F. sylvatica* stands that were between 50 and 150 years of age (from 0.3 to 0.13 and from 0.25 to 0.1, respectively). Additionally, we identified a significant and positive effect of stand basal area on both AWBI (Table 4) and the AWBI:GPP_{gp} ratio (*data not shown*) in temperate oaks.

3.3 Temporal dynamic of carbon allocation to woody biomass growth

The ranking of the drivers of biomass growth obtained using the RF algorithm indicated that the temporal AWBI dependences varied among species (Fig. 4). The growth of temperate deciduous species was under a more complex environmental control than the growth of *P. abies* and *Q. ilex*, with several variables explaining a substantial portion of the annual variability in AWBI (Fig. 4A, B). Simulated C supply (GPP_{gp}) was strongly related to the AWBI of temperate oaks and *F. sylvatica* and, to a lesser extent, *P. abies* (Fig. 4A, B, C), with positive marginal effects (Fig. 5 a, e, h). The duration of water stress during the growth period (WS_per_{gp}) was the predominant driver of the AWBI variability of *Q. ilex*, and was also strongly related to growth in temperate deciduous species. Low temperatures during the growth period ($templim_{gp}$) most substantially affected *P. abies* and also explained a portion of the variability in AWBI of temperate oaks. The simulated water and temperature stress indices had negative and quasi-linear marginal effects on the AWBI (Fig 5). Finally, environmental lagged effects contributed substantially to the AWBI variability in all species: the water stress intensity of the previous year (WS_int_{y-1}) affected the growth of *F. sylvatica* and *Q. ilex*, whereas the simulated C supply of the previous year (GPP_{y-1}) affected temperate oaks and *P. abies*. Lagged effects generally revealed threshold in marginal dependences, with a significant negative effect on AWBI only under high water stress or low C supply (Fig. 5). The effects of the retained variables (Fig. 4) were evaluated via multiple regression models that used dummy variables to test for the significance of slope changes when thresholds appeared on partial plots (Fig. 5). The models explained approximately 20% of the variability in the AWBI for temperate oaks and *P. abies*, and approximately 40% of the variability for *F. sylvatica* and *Q. ilex* (Table 5). All of the explanatory variables had significant effects, but *templim* was not retained in the models for temperate oaks after the bootstrap procedure that accounted for the uncertainty of the C flux simulations. We observed significant changes in the slopes of the effect of GPP_{y-1} on temperate oaks and the effect of GPP_{gp} on *P. abies* (Table 5). The models with NPP_{gp} and NPP_{y-1} variables revealed the same AWBI dependences as the models described above, but with reduced explanatory power. The models with Ra_{gp} and Ra_{y-1} variables were not significant (*data not shown*).

4 Discussion

This study quantified the C that is allocated annually to the woody biomass increment for five species that are representative of the main European forest biomes. By complementing field measurements from a permanent plot network with process-based modelling, our approach circumvented the limitation of EC data scarcity and characterized the annual partitioning of C into woody biomass at 49 sites (931 site-years). We were thus able to identify the species-specific drivers of the spatiotemporal dynamics of the allocation of C to wood growth along ecological gradients.

4.1 The correlation between the tree C balance and woody biomass growth

Relating EC-based estimates of forest C balance and biometric measurements of woody biomass growth has been the focus of an increasing number of studies. These studies can enhance our understanding of ecosystem C dynamics but have so far provided conflicting conclusions. Indeed, the correlation between woody biomass growth and forest C gain has been reported as both non-significant (Mund et al., 2010; Richardson et al., 2013; Rocha et al., 2006) and highly significant (Babst et al., 2014; Ohtsuka et al., 2009; Peichl et al., 2010; Zweifel et al., 2010). Accordingly, the relationships between AWBI and C fluxes reported in this study strongly varied among sites for each of the species studied (Table 3). Nevertheless, the annual woody biomass increment was consistently related to GPP_{gp} and NPP_{gp}, and only marginally to Ra_{gp} for the majority of sites (Table 3). Babst et al. (2014) reported a similar dependence of biomass growth on C fluxes at 5 sites that spanned a wide range of latitude in 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 tree C balance are under the control of distinct but partially correlated processes (Beer et al., 2007; Fatichi et al., 2014); these processes may or may not induce consistent annual changes, depending on the environmental conditions faced by trees. For *F. sylvatica* and temperate oaks, maximum correlation values corresponded to flux aggregation periods that were consistent with the previously reported phenology of the woody biomass increment (Table 3, Michelot *et al.* 2012, Supplement S10). Babst et al. (2014) and Granier et al. (2008) similarly reported close relationships between the AWBI and forest C fluxes that were summed until cessation of growth (August/September). The flux aggregation periods were, however, not related to the timing of wood growth in *Q. ilex* or *P. abies* (Cuny et al., 2012; Lempereur et al., 2015), which indicates that inter-annual variation in the AWBI is not always solely (or even primarily, e.g., *Q. ilex* and *P. abies*) dependent on the C derived from photosynthesis. Specifically, the agreement between the observed annual growth and a short period of C flux aggregation in early summer that was reported for *Q. ilex* corresponds to the effect of growth cessation on the annual biomass increment, which has been attributed to a drought-induced limitation of cambial activity at the Puéchabon site (Lempereur et al., 2015). The processes that underlie the relationship of the long flux aggregation period and the annual biomass increment of *P. abies* may include 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 either source limitation of growth or the seasonality of C allocation to woody biomass can lead to misleading conclusions.

4.2 Between-site variability in the C allocation to woody biomass growth is related to ontogeny and competition intensity

We highlighted an age-related decline in the C partitioning to woody biomass in all three species (Fig. 3B). This result had previously been observed in *F. sylvatica* stands using measurements of the main C compartments along a chronosequence (Genet et al., 2010). Several non-exclusive processes can explain this age-related trend. Increases in tree height are associated with increases in the hydraulic resistance of xylem, which may lead to declines in the turgor of living cells and result in potentially negative consequences on cambial activity (Woodruff et al., 2004). This constraint may result in a height-related sink-limitation of growth (Woodruff and Meinzer, 2011), which is consistent with our results. Additionally, life-history traits, such as a greater emphasis on reproduction in older stands, could also be involved. However, the interactions of growth and reproductive mechanisms are still under debate (Hoch et al., 2013; Thomas, 2011) and have yet to be properly represented in TBMs. Only the GPP component of the simulated tree C balance was retained in the final models (Table 4), thereby indicating that an increase in maintenance respiration with greater stand biomass most likely did not contribute to the age-related decline in biomass growth (Drake et al., 2011; Tang et al., 2014). Although height-related hydraulic constraints on C assimilation have been suggested to be an important driver (Ryan et al., 2006; Tang et al., 2014), recent studies have suggested that changes in demography and stand structure may primarily explain the age-related decline observed in stand wood growth (Binkley et al., 2002; Xu et al., 2012). Our results suggest that changes in the C allocation should also be considered, because no mortality occurred in our plots during the measurement period (*data not shown*). We additionally identified a significantly higher C partitioning to woody biomass in temperate oak stands with greater competition intensity (i.e., high stand basal area, Table 3). To date, reports regarding the effect of competition on C allocation dynamics are conflicting (Litton et al., 2007) and suggest no significant or consistent effect. Moreover, we found no significant effect of soil nutrient availability on the C allocation dynamics along the studied ecological gradient whereas a recent meta-analysis reported that this factor positively affects C partitioning to forest biomass on the global scale (Vicca et al., 2012). The RENECOFOR network only includes relatively fertile sites (Supplement S5), which could putatively explain the apparent tension between our results and the conclusions of the meta-analysis. Therefore, more studies are required to elucidate the contributions of the various drivers to the variation in C partitioning to woody biomass on scales that range from local to global.

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

Water and temperature stress exerted significant direct control on the inter-annual variation of woody biomass growth (i.e., independently from their effects on C assimilation) for every species and biome (Table 5 and Fig. 4 and 5). Cambial growth has been reported to be inhibited at lower water stress levels than photosynthesis (Muller et al., 2011; Tardieu et al., 2011). Indeed, drought-induced decrease in cell turgor strongly affects 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 more sensitive than photosynthesis to low temperatures (Körner, 2008). Although these findings documented the plausible mechanisms of sink control of biomass growth at the cellular scale, there is still considerable debate regarding whether the sink or the C source actually limit the 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 an overabundant C supply and thus evidence of sink control of tree growth (Körner, 2003). However, recent works have suggested 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. a methodology that is not based on C storage measurement) our results suggest that sink limitation has a significant effect on the annual woody biomass growth of five species that are representative of different European biomes, including deciduous temperate forests. Because sink limitation implies that there are periods with significant C supply but no growth, our results also corroborate recent empirical studies that reported a significant role of growth duration in the annual variability of tree radial increment (Brzostek et al., 2014; Cuny et al., 2012; Lempereur et al., 2015). Additionally, we observed that past environmental constraints significantly affected C partitioning to wood growth for each species and biome (Table 5 and Fig. 4 and 5). The lagged effect of the previous year's low C supply (GPP_{y-1}) possibly indicates a preferential C allocation to storage at the expense of growth in trees that face C reserve pool depletion (Bansal and Germino, 2008; Wiley et al., 2013). In support of this finding, Richardson *et al.* (2012) reported a strong relationship between the AWBI and the EC-based estimate of the previous year's C supply in a mature maple stand. The detrimental effect of a previous year's low C supply on temperate oak wood growth (Fig. 4) may be related to growth phenology, because this species relies on C reserves to achieve a large part of its annual biomass growth prior to leaf expansion in the spring (Barbaroux et al., 2003). The lagged effect of high water stress intensity on *F. sylvatica* and *Q. ilex* (Fig. 4) may be linked to previous 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 following year's cambial activity (Delpierre et al., 2015; Palacio et al., 2012; Zweifel et al., 2006) and a recent meta-analysis concluded that C is preferentially allocated to fine roots at the expense of wood growth in stands that face constraining environments (Chen et al., 2013). Finally, our results suggest that C supply (GPP_{gp}) is an important driver of the annual woody biomass growth in temperate deciduous forests (Daudet et al., 2005). GPP was the component of the simulated tree C balance that was most closely related to the annual variability in growth; this result indicates GPP's important role in explaining the annual variability in the net ecosystem productivity of European forests (Delpierre et al., 2012). Overall, our findings support the premise that forest woody biomass growth is subject to complex control processes that include both source and sink limitations, following Liebig's law: although numerous processes potentially influence wood growth, stand growth at a given site and a given year is predominantly limited by the most constraining factor. C (source) limitation of growth can thus only occur when other factors are non-limiting (Fatichi et al., 2014), a situation that 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 models that are currently used to project the outcome of global changes on forests represent wood growth as a fraction of the total C uptake (i.e., source control of growth, De Kauwe *et al.* 2014). This C-centric perspective overlooks the possibility of sink control of growth and thus ignores results such as those presented in this study and those of earlier local studies (reviewed by Fatichi *et al.* 2014). Consequently, this perspective possibly hampers the ability of TBMs to project future forest productivity (Fatichi *et al.* 2014). On the basis of our analysis of the spatiotemporal dynamics of C allocation to wood growth on a regional scale, we suggest a straightforward, combined source- and sink-driven forest growth modelling framework (Fig. 6). In this framework, a potential site-specific allocation coefficient is first defined to represent the effect of soil fertility on the C allocation to wood (Vicca et al., 2012). In a second step, this coefficient is adjusted to the physiological state of the stand by accounting for the dependences of the C allocation on ontogeny, competition intensity and lagged environmental stressors. Lagged environmental stressors are represented by a negative effect on the previous year's water stress index and low C uptake on the allocation coefficient. Inclusion of the age-related decline in forest growth has been highlighted as an important modelling goal (Magnani et al., 2000; Zaehle et al., 2006). However, this effect has thus far been incorporated in models by including a negative effect of the increasing stand respiration on the tree C balance, which contradicts current knowledge (Ryan et al., 2006). The resulting annual allocation coefficient is finally modulated by the direct water and temperature constraints on growth. In a similar fashion, Leuzinger *et al.* (2013) improved the Lund-Potsdam-Jena (LPJ) terrestrial biosphere model predictions for the cold tree-line by accounting for 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; Schiestl-Aalto et al., 2015). It synthesizes the current knowledge regarding forest growth dependences and has the potential to unify seemingly contradictory observations within a single modelling framework. The simulated growth is indeed subject to the combined controls of C supply and changes in C allocation due to endogenous adjustments and/or modulations of sink activity (Fig. 6). These controls result from distinct processes, which are independently represented in the modelling framework. The relative influences of the various processes, i.e., the simulated growth causalities, are thus likely to vary both spatially and temporally, depending on the environmental conditions faced by trees. Our approach has therefore the potential to shed light on the contrasted results reported by correlative studies. Although the value is comparable to those of previous studies (Lebourgeois et al., 2005; Mérian et al., 2011), the proportion of the annual growth variability that was explained by our approach was moderate (Table 5). Plausible explanations of this result include: i) unreported management interventions that may have skewed the historical stand growth reconstruction and ii) potentially important growth drivers that were not considered here, such as changes in C partitioning due to mast seeding (Mund et al., 2010), genetic differentiation among tree populations (Vitasse et al., 2014) or allometry-mediated tree acclimation to drought (Martin-StPaul et al., 2013). A third factor that hampered the ability of our empirical models to explain the annual growth variability is the potential disagreement between the CASTANEA outputs that were used as explanatory variables and the corresponding actual drivers. Although we argued that i) the CASTANEA model has been thoroughly validated at many EC sites from throughout Europe and ii) the presented growth dependences demonstrated their robustness against the reported uncertainties of the CASTANEA simulations, the quality of the simulations was limited by the idiosyncrasies of the sites we examined in this study. In particular, a number of past disturbances such as insect outbreaks, windthrow or unreported commercial thinning could have temporarily induced large discrepancies between the actual and simulated C fluxes (Grote et al., 2011; Hicke et al., 2012). The error that is attributable to model performance unfortunately remains unknown because of the absence of EC measurements at our study sites (except for the Puéchabon site, see Delpierre et al., 2012). Despite this additional uncertainty, the combined use of field measurements and process-based modelling allowed us to present the first species-specific evaluation of annual C allocation to growth along regional environmental gradients. Our results suggest that implementing the presented C allocation dependences in TBMs will refine the projections of the outcome of global changes on forest growth, and have implications for the predicted evolution of forest C sink, forest diebacks and tree species distributions (Cheaib et al., 2012).

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Table 1. Climate of the study sites. ETP: annual Penman - Monteith potential evapotranspiration; Precip.: annual precipitation; Temp.: annual temperature. Values are site averages ± standard deviation among sites.

Species	number of plots	number of site-years	elevation (m)	ETP (mm)	Precip. (mm)	Temp. (°C)	Source
F. sylvatica	16	313	565 ± 326	1010 ± 121	1001 ± 133	10.1 ± 0.98	RENECOFOR
Q. petraea / Q. robur	26	484	193 ± 76	999 ± 71	821 ± 96	10.7 ± 0.63	RENECOFOR
P. abies	6	101	1056 ± 313	933 ± 44	1559 ± 340	7.1 ± 1.4	RENECOFOR
Q. ilex	1	43	270	1417	907	13.4	Puéchabon site

Table 2. Description of explanatory variables. The "Type" category indicates the source of the data: field measurement (M), SAFRAN climate database (C) or CASTANEA simulation (S). The "Scale" categories indicate whether the variable was considered in the spatial (S) and temporal (T) analyses.

IDs	Description	Unit	Type	Scale
age	Stand age	years	M	S
AWBI	Annual woody biomass increment	$gC.m^{-2}$	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	$gC.m^{-2}$	S	ST
GPP_{y-1}	Gross primary production of the previous (y-1) year	$gC.m^{-2}$	S	T
frost	Sum of the average daily temperatures below -2°C during the last winter (year y-1 and y)	°C	C	ST
LNC	Leaf nitrogen content	$gN.gDM^{-1}$	M	S
NPP_{gp}	Net primary production of the current (y) growth period	$gC.m^{-2}$	S	ST
NPP_{y-1}	Net primary production of the previous (y-1) year	$gC.m^{-2}$	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
SWHC	Soil water holding capacity	mm	M	S
$templim_{gp}$	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	$gC.m^{-2}$	S	ST
Ra_{y-1}	Autotrophic respiration of the previous (y-1) year	$gC.m^{-2}$	S	T
WS_per_{gp}	Number of days of the current (y) growth period with 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 soil water content below 60% of the soil water holding capacity	number of days	S	T
WS_int_{gp}	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

Table 3. Relationships of annual wood growth and the components of the seasonal forest carbon balance: NPP, GPP and Ra. The *start* and *end* terms (day of the year) indicate the carbon flux period that yielded the maximum value for the median of the growth-flux correlations among sites. The r term is the maximum obtained for the median of the site-specific Pearson correlation coefficients; values that are significantly different from 0 are indicated (* indicates P < 0.05 and ** indicates P < 0.001). The *σ* term is the standard deviation of the Pearson correlation values among sites.

Species	**GPP**				**Ra**				**NPP**			
	start	*end*	*r*	*σ*	*start*	*end*	*r*	*σ*	*start*	*end*	*r*	*σ*
F. sylvatica	124	258	0.62^{**}	0.18	96	200	-0.29^{*}	0.33	126	262	0.58^{**}	0.24
Q. petraea / Q. robur	136	214	0.59^{**}	0.25	98	192	0.31*	0.24	130	214	0.50^{**}	0.28
P. abies	32	262	0.52^{**}	0.38	78	348	0.11	0.52	32	200	0.49^{**}	0.29
Q. ilex	186	226	0.60		36	256	-0.26		186	226	0.58	

Table 4. Spatial dependences of annual wood growth: multiple regression estimates. The data have been centred and scaled. GPP_{gp} is the GPP of the growth period, age is the average age of the stand, and SBA is the stand basal area (Table 2). Values: estimates [F values]. All estimated values differed significantly from 0 ($P < 0.001$). All variables were retained in the bootstrap procedure (see main text).

Species	**Estimates**				
	GPP_{gp}	*age*	*SBA*	**P**	**adj. R^2**
Q. petraea / Q. robur		-8.88×10^{-1} [39.5]	4.27×10^{-1} [19.5]	***$<10^{-4}$***	**0.69**
F. sylvatica	5.07×10^{-1} [59.4]	-6.96×10^{-1} [61.6]		***$<10^{-4}$***	**0.88**
P. abies	8.25×10^{-1} [8.6]			***0.04***	**0.60**

Table 5. Temporal dependences of annual wood growth: multiple regression estimates. The data have been centred and scaled. GPP_{gp} is the GPP of the growth period, WS_per_{gp} is the water stress index of the growth period, WS_int_{y-1} is the water stress index of the previous year, and $templim_{gp}$ is the low temperature index of the growth period (see Table 2). D1 and D2 are dummy variables (D1 = 0 if $GPP_{gp} < 1400$ gC m^{-2}; otherwise, D1 = 1. D2 = 0 if $GPP_{y-1} < 1550$ gC m^{-2}; otherwise, D2 = 1; see Fig. 5). The ρ term is the parameter of the first-order autoregressive process that was used to model the temporal autocorrelation of the within-stand errors. Values: estimates [F values]. Estimated values that are significantly different from 0 are indicated (* indicates $P < 0.05$, ** indicates $P < 0.01$, and *** indicates $P < 0.001$). A Δ index indicates that the variable was not retained in the bootstrap procedure (see main text).

Estimates	**Species**			
	Q. petraea / Q. robur	*F. sylvatica*	*P. abies*	*Q. ilex*
GPP_{gp}	$3.26\times10^{-1\,***}$	$4.87\times10^{-1\,***}$	$2.4\times10^{-1\,*}$ [3.5]	
WS_per_{gp}	$-1.09\times10^{-1\,**}$	$-2.04\times10^{-1\,***}$		$-5.8\times10^{-1\,***}$
WS_int_{y-1}		$-2.37\times10^{-1\,***}$		$-2.2\times10^{-1\,*}$ [6.3]
GPP_{y-1}	$3.82\times10^{-1\,*}$ [3.3]		$-4\times10^{-1\,**}$ [3.2]	
$templim_{gp}$	$-9.60\times10^{-2\,**\Delta}$		-1.26^{***} [3.5]	
D1			$-2.4\times10^{-1\,***}$	
D2	$-3.9\times10^{-1\,**}$ [0.8]			
$D1 * GPP_{gp}$			1.33^{**} [8.2]	
$D2 * GPP_{y-1}$	$-4\times10^{-1\,**}$ [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**

Figure captions

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

Figure 2. **Locations of the study sites**.

Figure 3. **Spatial dependences of annual wood growth.** A: Relationship of the AWBI and the GPP of the growth period (GPP_{gp}) averaged over sites. B: Age-related decline of the C partitioning to AWBI (AWBI / GPP_{gp}).

Figure 4. **Temporal dependences of annual wood growth: the roles of explanatory variables from RF classification**. Variable importance is expressed as the percentage of the importance of the top-ranked explanatory variable. The variable identifiers (IDs) are listed in Table 2. The coloured variables were retained in subsequent analyses.

Figure 5. **Temporal dependences of annual wood growth: marginal effects of each explanatory variable on the annual wood growth**. The lines represent smoothing splines with 50% frequency response cut-offs. The coloured areas indicate the 95% confidence intervals. The 5% and 95% data quantiles (grey areas) were not considered in the discussion. The marginal effect of a given variable X was obtained by fixing the value of X and averaging the RF predictions over all the combinations of observed values for the other predictors in the dataset (Cutler et al., 2007). The marginal predictions were collected over the entire range of X in the training data using a regular grid.

Figure 6. **Modelling framework for a combined source- and sink-driven representation of C allocation to wood growth**.

Figure 1.

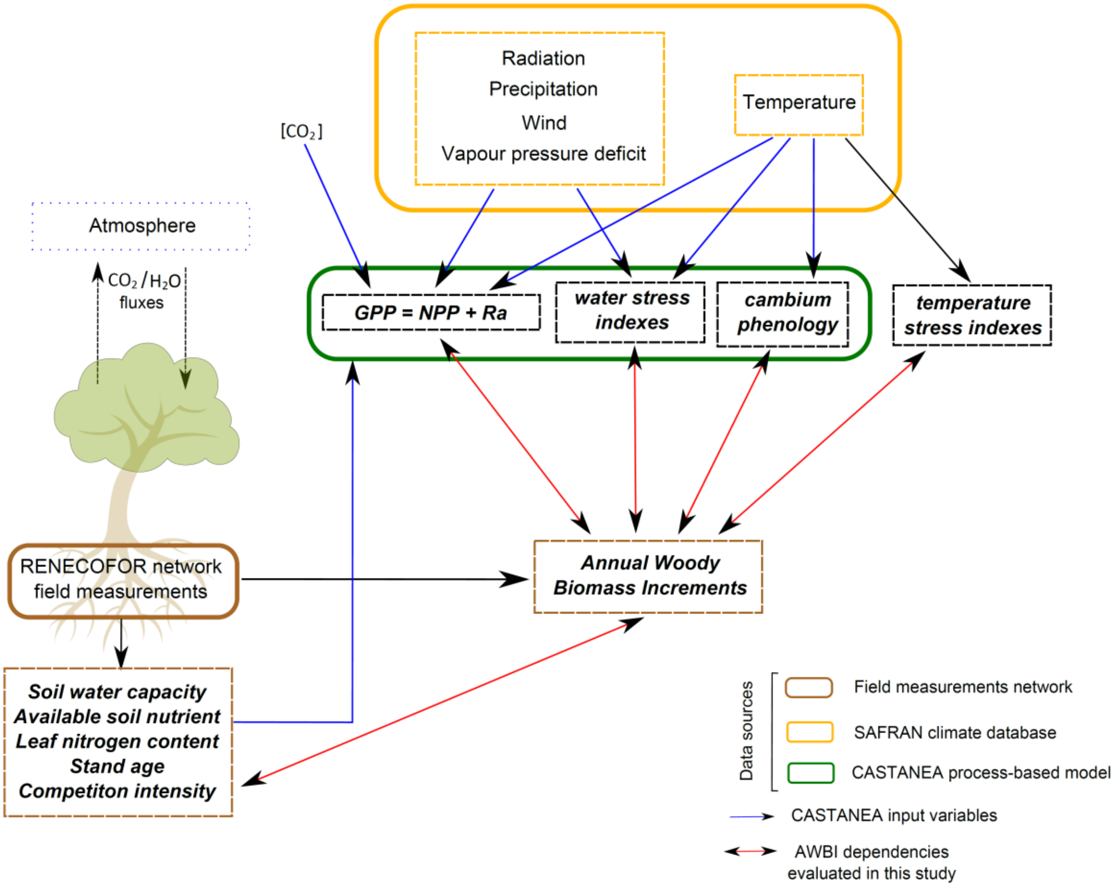

Radiation
Precipitation
Wind
Vapour pressure deficit
Temperature
[CO$_2$]
Atmosphere
CO$_2$ / H$_2$O fluxes
GPP = NPP + Ra
water stress indexes
cambium phenology
temperature stress indexes
RENECOFOR network field measurements
Annual Woody Biomass Increments
Soil water capacity
Available soil nutrient
Leaf nitrogen content
Stand age
Competiton intensity
Data sources
Field measurements network
SAFRAN climate database
CASTANEA process-based model
CASTANEA input variables
AWBI dependencies evaluated in this study

Figure 2.

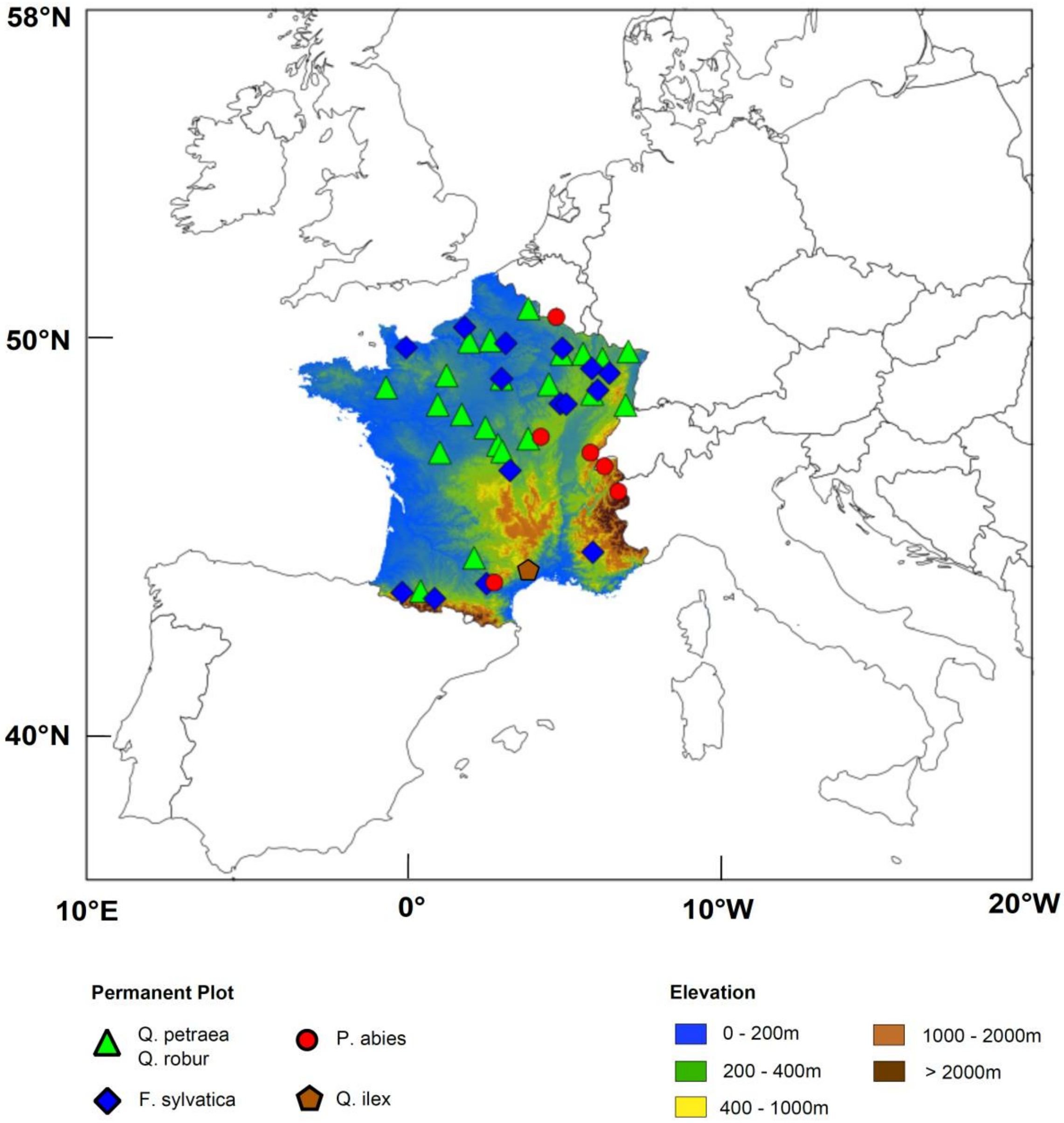

58°N
50°N
40°N
10°E
0°
10°W
20°W
Permanent Plot
Q. petraea
Q. robur
P. abies
F. sylvatica
Q. ilex
Elevation
0 - 200m
200 - 400m
400 - 1000m
1000 - 2000m
> 2000m

Figure 3.

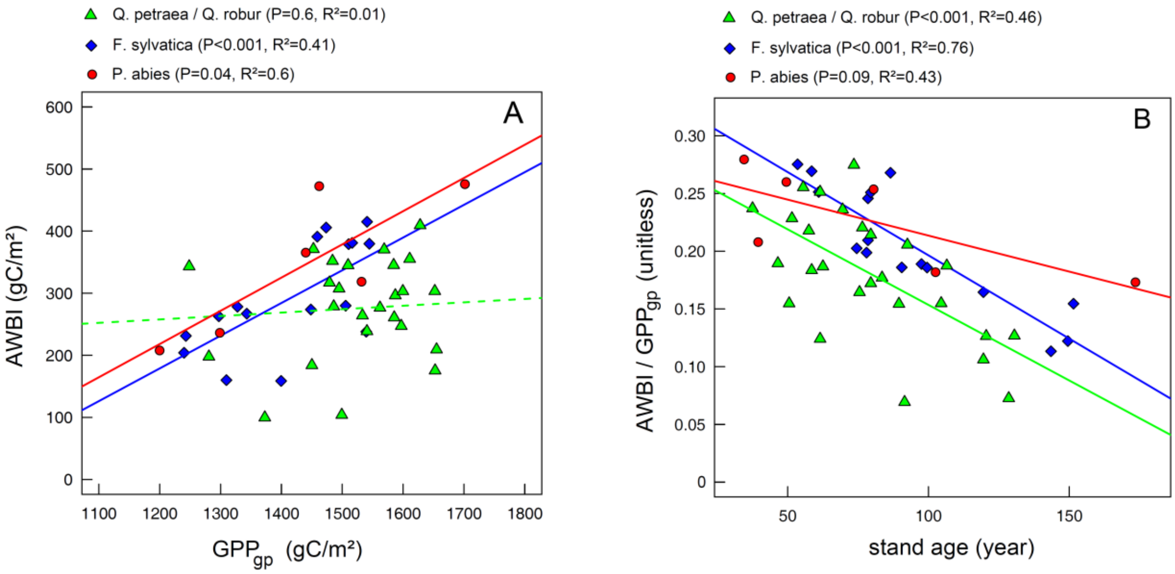

Q. petraea / Q. robur (P=0.6, R²=0.01)
F. sylvatica (P<0.001, R²=0.41)
P. abies (P=0.04, R²=0.6)
A
AWBI (gC/m²)
0
100
200
300
400
500
600
1100
1200
1300
1400
1500
1600
1700
1800
GPPgp (gC/m²)
Q. petraea / Q. robur (P<0.001, R²=0.46)
F. sylvatica (P<0.001, R²=0.76)
P. abies (P=0.09, R²=0.43)
B
AWBI / GPPgp (unitless)
0
0.05
0.10
0.15
0.20
0.25
0.30
50
100
150
stand age (year)

Figure 4.

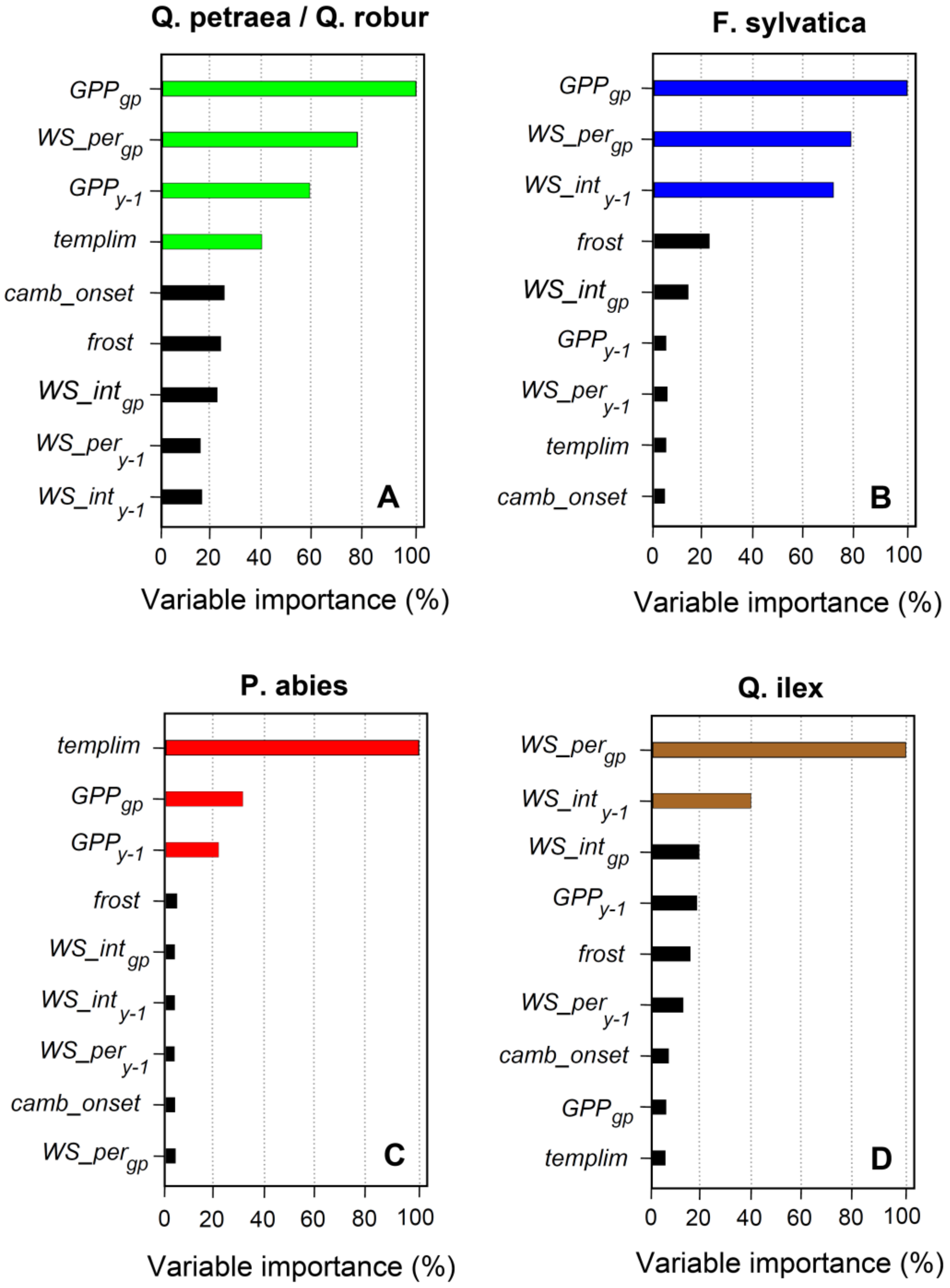
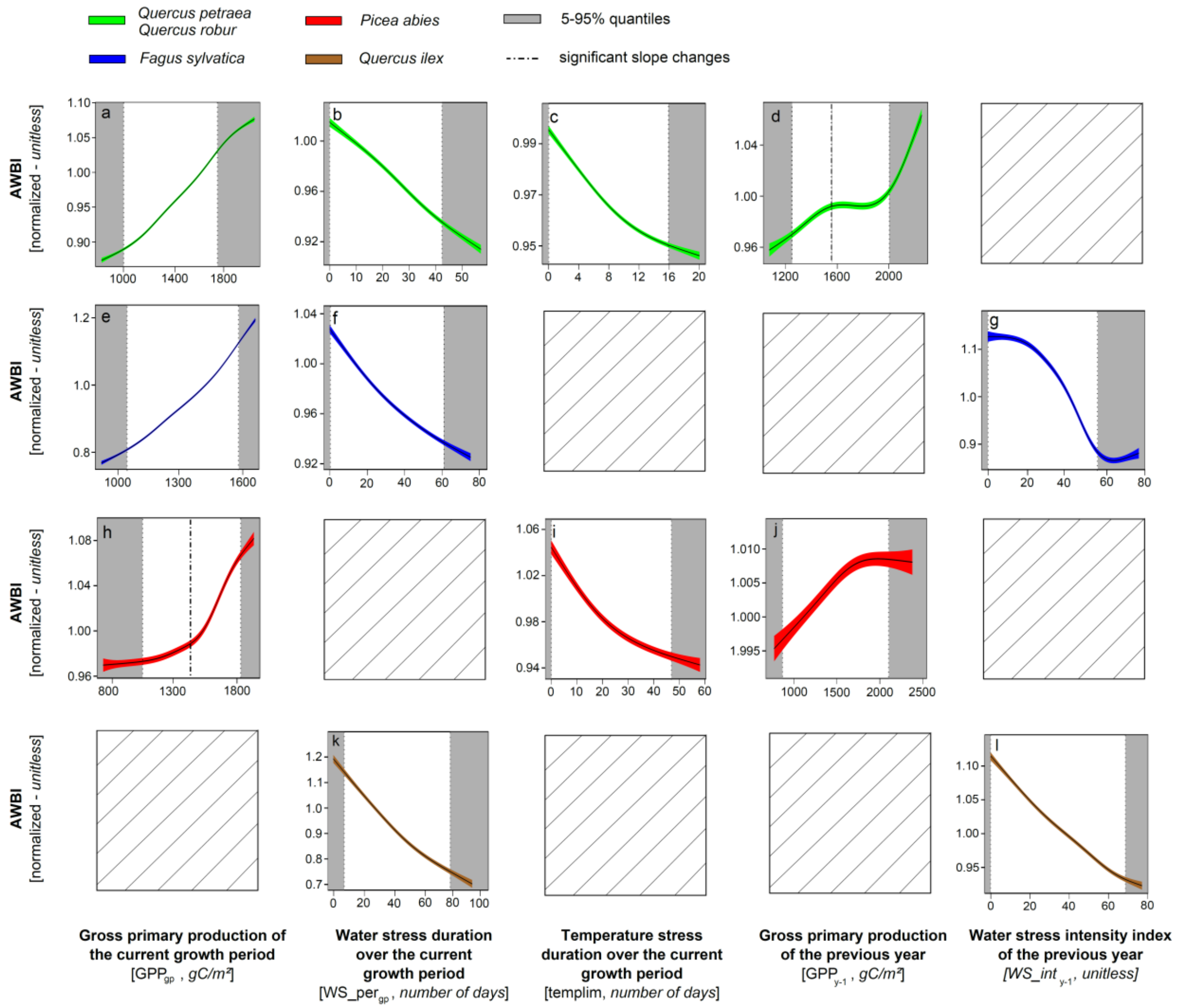
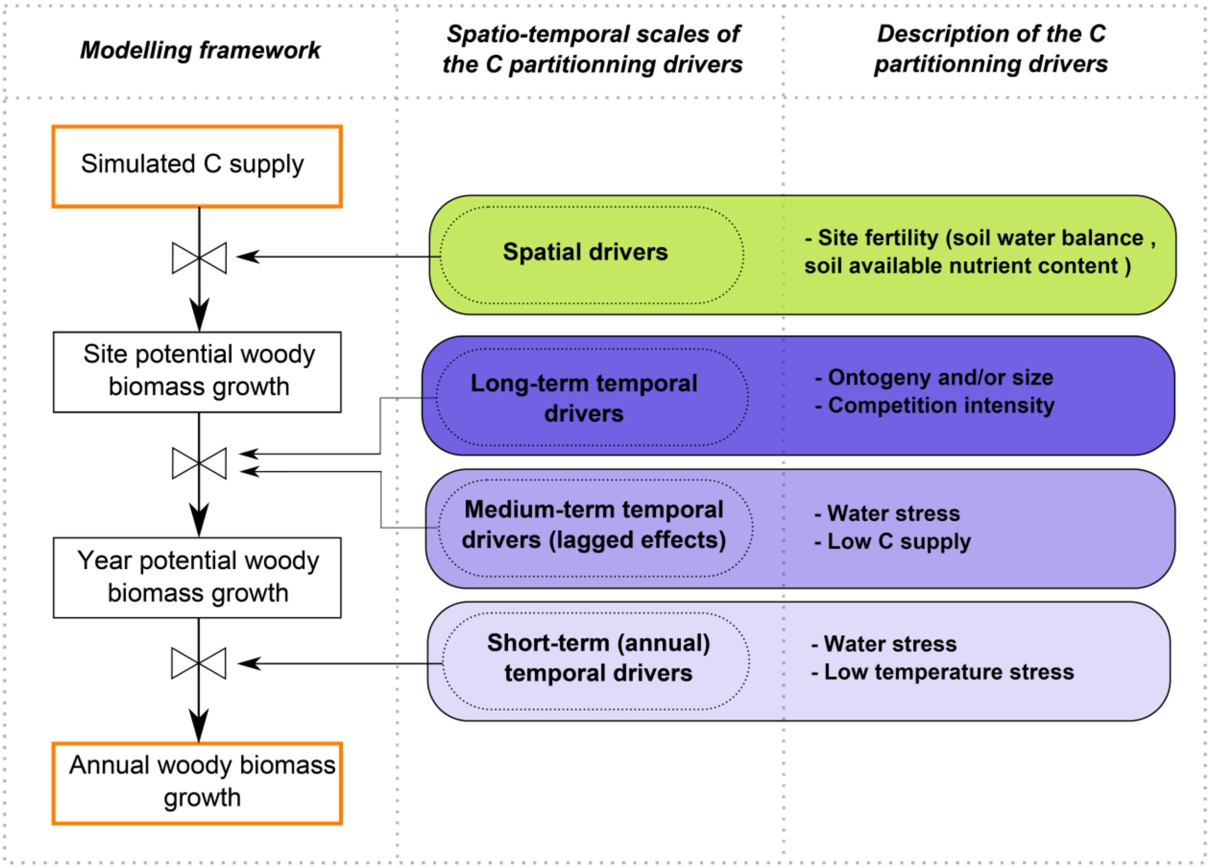

Q. petraea / Q. robur
GPP_{gp}
WS_per_{gp}
GPP_{y-1}
templim
camb_onset
frost
WS_int_{gp}
WS_per_{y-1}
WS_int_{y-1}
A
0
20
40
60
80
100
Variable importance (%)
F. sylvatica
GPP_{gp}
WS_per_{gp}
WS_int_{y-1}
frost
WS_int_{gp}
GPP_{y-1}
WS_per_{y-1}
templim
camb_onset
B
0
20
40
60
80
100
Variable importance (%)
P. abies
templim
GPP_{gp}
GPP_{y-1}
frost
WS_int_{gp}
WS_int_{y-1}
WS_per_{y-1}
camb_onset
WS_per_{gp}
C
0
20
40
60
80
100
Variable importance (%)
Q. ilex
WS_per_{gp}
WS_int_{y-1}
WS_int_{gp}
GPP_{y-1}
frost
WS_per_{y-1}
camb_onset
GPP_{gp}
templim
D
0
20
40
60
80
100
Variable importance (%)

Figure 5.



Quercus petraea
Quercus robur
Fagus sylvatica
Picea abies
Quercus ilex
5-95% quantiles
significant slope changes
AWBI
[normalized - unitless]
a
1.10
1.05
1.00
0.95
0.90
1000
1400
1800
b
1.00
0.96
0.92
0 10 20 30 40 50
c
0.99
0.97
0.95
0 4 8 12 16 20
d
1.04
1.00
0.96
1200 1600 2000
e
1.2
1.0
0.8
1000 1300 1600
f
1.04
1.00
0.96
0.92
0 20 40 60 80
g
1.1
1.0
0.9
0 20 40 60 80
h
1.08
1.04
1.00
0.96
800 1300 1800
i
1.06
1.02
0.98
0.94
0 10 20 30 40 50 60
j
1.010
1.005
1.000
1.995
1000 1500 2000 2500
k
1.2
1.1
1.0
0.9
0.8
0.7
0 20 40 60 80 100
l
1.10
1.05
1.00
0.95
0 20 40 60 80
Gross primary production of the current growth period
[GPP_gp , gC/m²]
Water stress duration over the current growth period
[WS_per_gp , number of days]
Temperature stress duration over the current growth period
[templim, number of days]
Gross primary production of the previous year
[GPP_y-1 , gC/m²]
Water stress intensity index of the previous year
[WS_int y-1, unitless]

Figure 6.


Modelling framework
Spatio-temporal scales of the C partitionning drivers
Description of the C partitionning drivers
Simulated C supply
Spatial drivers
- Site fertility (soil water balance , soil available nutrient content)
Site potential woody biomass growth
Long-term temporal drivers
- Ontogeny and/or size
- Competition intensity
Medium-term temporal drivers (lagged effects)
- Water stress
- Low C supply
Year potential woody biomass growth
Short-term (annual) temporal drivers
- Water stress
- Low temperature stress
Annual woody biomass growth