Answers to the comments from Referee #1

We would like to thank you for the time you spent on our manuscript and for you constructive comments.

This manuscript discriminates between the drivers of woody growth at close to 1,000 site.years. Because some possible drivers – GPP, water stress, ... - are not directly measured in the experimental plots, a process-based model is used to estimate these drivers instead. Key conclusions are a hierarchy of all possible drivers according to their ability to explain either inter-annual woody growth variability or spatial woody growth variability. This hierarchy is – in my view – the main novelty brought by this manuscript, and a welcomed one. The method underlying this classification is partly questionable: the authors claim that the statistical models they use are robust to collinearity in explanatory variables but this claim is not sufficiently justified (see detailed comments). However, even if collinearity ends up being a problem, this would only add uncertainty to the results and would not greatly reduce the interest of the manuscript. As a result, and although some details could be improved, I think the manuscript is readable and worth being published.

We addressed your concern regarding collinearity implications in your dedicated specific comment.

In the following, we address each of your specific comments.

The claim that field measurements are combined with process-based simulations (e.g. p2214 l. 9, p2218 l3) disturbed me for a long time as I sought *to distinguish between what results came from the model structure and what really was observed on-site. Then I remembered that simulations are only used when measurements are not available, and that the dependent variable – woody growth – is measured (the confusion coming from the fact that the model also simulates woody growth). Unless I missed something, the study is mainly empirical, and only supplemented by process-based modelling to estimate some possible drivers of woody growth when more direct methods are not applicable. Therefore, although I do not dispute the "combination", I would recommend clarifying this by removing the term "combination" throughout the text, and highlighting that modelling is only here to estimate explanatory variables (or drivers) when these can't be measured.*

Our study is indeed mainly empirical. We only used process-based modelling to estimate potential drivers that could not be directly measured in the field, as stated in your comment. We clarified this point in the abstract and in the manuscript by removing the word "combination" in the description of our approach. Rather, we briefly explained why process-based modelling was used to complement field measurements (e.g., l26, l133, l420).

P2215 l4 This 60% figure does not directly come from Pan et al (2011). Their estimate of 2.6 PgC yr-1 divided by AR5's estimate of 8.3 PgC yr-1 for fossil fuel emissions would land around 30%. How do you get this 60%?

We evocated the gross carbon uptake by the established forests and tropical regrowth forests, which amount to 73 PgC over the period 1990 to 2007, "equivalent to 60% of cumulative fossil emissions in the period" (Pan et al., 2011). We acknowledge that this statement was confusing as 1) we did not explicitly mentioned in the manuscript that we addressed gross carbon uptake 2) Literature usually reports the figures that you mentioned i.e. the proportion of anthropogenic C emission captured in established forests. We therefore modified our sentence based on Pan et al.

(Table 3) as follows “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).” (l51-53)

P2215 l26 An overview of the mechanisms potentially underlying cambial activity other than C availability would be useful here (they are provided later in the discussion).

We added a short description of the cell processes into play. “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).” (l73-82)

P2219 l16-22 The key features (e.g. list of explanatory variables) of the empirical model and the allometric function should be provided in the manuscript itself (not in the SM).

We added a description of the empirical model, with a focus on its parametrization. “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).” (l173-185)

Because of the number of relations involved, it was difficult to provide all the species-specific allometric equations in the manuscript. Rather, we reported in the manuscript all the references that we used (l190-192). The allometric functions used in our work and their parametrizations are extensively described in appendix S3 and S4.

P2219 l22 What does “historical basal area” mean? Basal area measured before the measurement years? Since when?

The “historical stand basal area” is the past stand basal area, that we calculate using the past trajectory of the stand CBH distribution obtained thanks to the empirical model described above. We clarified this point in the manuscript (l186-188).

P2220 l6-12 Although SWC and SNA can unquestionably be put in the “plot fertility” category, putting LAI and LNC in the same category is debatable as these variables *depend among others on management and stand age as well as fertility.*

We acknowledge that the relation between LNC and plot fertility is debatable. We chose to include this variable because some studies report a significant link between LNC and soil type (see for example Le Maire et al, 2005, Tree Physiology 25, 859-872, Figure 4). However we did not found a significant link between C allocation to growth and any of the variable included in the “fertility” category, possibly because they are poor proxy of the actual plot fertility. LAI was not used to characterize plot fertility in the statistical analyses (l205-206).

P2222 l1-4 How are these water stress indices defined? As water stress ends up being high in the hierarchy of drivers of woody growth, it is important to explain it is characterized.

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}).

We added this description to the manuscript (l249-261).

P2222 l24-26 See general comment. The statistical models used are apparently: Pearson's correlations, multiple linear regression, and random forest. The robustness of the first two to collinearity in explanatory variables is not justified (and indeed, it would be difficult to justify it) and the justification provided for random forest (p 2224 l23-25) is that the collinearity problem is diminished by the random selection of variables participating in the classification. I'm clearly not an expert of this algorithm, but I fail to see how random selection reduces collinearity: if two variables (eg. GPP and water stress) are strongly correlated in the sample, selecting sometimes one and sometimes the other will not diminish the fact that they both tend to provide the same clusters and that therefore it's difficult to say whether it's GPP or water stress which explains why the clusters are "different". I acknowledge that I may be missing some background here, but so will many readers so your claim should either be better justified or dropped. If dropped, then the results should be discussed with the collinearity problem in mind.

We acknowledge that the presentation of the empirical models regarding their ability to deal with correlation among predictors was misleading. Pearson's correlation and multiple linear regressions are indeed not able to handle highly correlated variables. Consequently, we changed the manuscript and we highlighted that the correlations among the explanatory variables that were used in this study generally were lesser than 0.7, which has been reported as the level above which collinearity begins to severely affect model performance (Dormann et al., 2013). One exception was for the important correlation among components of the tree C balance (because NPP = GPP – Ra). As a consequence the tree C balance components were introduced one at a time in the models, as previously specified in section 2.4.2. The effectiveness of Random forest methods in identifying “true” predictors among a large number of correlated candidate predictors have been empirically (i.e. comparing RF to traditional models) highlighted in many studies in the last decade (e.g. Archer and Kimes, 2008; Cutler et al., 2007; Genuer et al., 2010). The reason often given is that the iterative sample of predictors allows for an independent evaluation of each variable importance. As a consequence, the ranking of variable importance obtain in RF appears to be a more robust procedure than traditional model selection in the face of collinearity, and RF “does not suffer some of the shortcomings of traditional variable selection methods, such as selecting only one or two variables among a group of equally good but highly correlated predictors” (Cutler et al., 2007). However to our knowledge, the theoretical causes of the effectiveness of RF, along with the limit of its application, remain debated (see Gregorutti et al., 2015 arXiv:1310-5726). These controversies are however beyond the scope of this paper and our field of science. We clarified the section 2.4.1. with regards to the ability of models to deal with collinearity and we added the mainlines of the above discussion (l280-295).

P2225 l10-15 How variable is Ra? If GPP and NPP are both correlated with AWBI and Ra is not, an obvious possibility is that Ra is broadly constant in CASTANEA. Can you rule this out?

The coefficient of variation of the simulated annual NPP, GPP and Ra is 10.8% ± 3, 7.4% ± 2, 6.8% ± 3, respectively (the values are mean CV ± standard deviation among sites). NPP, GPP and Ra appear to have comparable annual variability, which lead us to think that it is unlikely that the low Ra-AWBI correlation would be a consequence of the low variability of Ra. Previous studies report that GPP has a preponderant role in the annual variability of net ecosystem productivity of European forests (e.g. Delpierre et al., 2012), which could explain its strong link with annual growth. We reported the CV values in the manuscript (l361).

*P2226 "between" sites is more appropriate than "among" I think. There is a typo in line 5: "*did *not revealed".*

We rephrased this sentence (l375).

P2228 l5-10 One of your key explanations is species difference. Would species difference reconcile these cited works? More generally, how do your results help in solving the apparent paradox between these cited works?

Our study was based on 4 species with contrasted autecology, in order to be representative of the main European biomes. Consequently these species face different environmental conditions, described in Table 1 and in the Supplement. A limit of this approach is that it is not possible to evaluate whether the differences highlighted among species (especially the ranking in variable importance, Fig. 4) result from the environment of from species-specific (genetic) growth response. Common-garden experiment could be very relevant in this respect, but will require studying seedlings and not mature trees. More generally, the paradox that we report in C flux – growth agreements is not solved in this study: our aim was to highlight C allocation drivers across 49 sites, but the relative impacts of these drivers has not been evaluated at the site level. We only argue that in the modelling framework that we present in section 4.4., the simulated growth is subject to the combined controls of C supply and changes in C allocation due to endogenous adjustments and/or modulations of sink activity. 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 (l569-575). The processes reported in our work should now be implemented in an integrated allocation scheme as part of a process-based model. Using such a model at contrasted sites to quantify the relative importance of each process in the resulted simulated annual growth should allow bringing more light on this paradox, as already initiated by recent studies (http://www.biogeosciences-discuss.net/12/2745/2015/bgd-12-2745-2015.pdf and Schiestl-Aalto, Kulmala, Mäkinen, Nikinmaa, & Mäkelä, 2015, New Phytologist).

Table 4 Which data has been centered and scaled? Why?

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 (l311).

Answers to comments from Referee #2

We would like to sincerely thank you for the time you spent on our manuscript and for your insightful comments and suggestions.

Because you pointed some misspelling in your comments, the entire manuscript was edited for correct English language and style.

Very well written and presented study, though the interpretation of the results at times could be viewed as overreaching. The main issue is that the C source is modeled, and therefore the relationship (or lack thereof) between C source and biomass increment are highly dependent on the accuracy of the modeled C source. Unfortunately there is no data available to estimate the accuracy of the modeled C source at the studied sites (with the exception of Puechabon, though no validation is presented here). The authors claim that the model has been widely validated at European sites. Of course practically all models are, but the quality of their extrapolation to other sites remains subject to the idiosyncrasies of those sites.

The issue is that authors repeatedly highlight the lack of relationship between source dynamics and biomass increments as evidence for a sink limitation, but do not acknowledge that there could be errors in the modeled C source that are responsible for the lack of relationship. Indeed the modeled C source is regularly presented in a way that could lead the reader to believe the authors are presenting observed C source. The C source should be referred to as the modeled C source at all times, and the impact of the potential disjoint between modeled and actual C source should be discussed in an open and non-defensive way.

Regardless of the above, the findings and approach used in this study are a novel and valuable contribution to a growing area of interest. I have no doubt it will be of interest to the readers of Biogeosciences.

We acknowledge that process-based modelling is a source of uncertainty that was not properly discussed in the first version of our paper. As a consequence, we clarified throughout the text whether the considered explanatory variable was simulated or measured (e.g., l354, l360, l366, l392). We additionally discuss in section 4.4. the potential impact of model uncertainty on our results and the fact that the quality of our simulations remain subject to the idiosyncrasies of the sites used in this work. Among other considerations, we acknowledge that “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. […] 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).” (l583-594).

However, as stated in the paper, the uncertainty of the simulated C fluxes was considered in both spatial and temporal 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 (Appendix 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. Consequently, the results discussed in the paper proved to be significant even when considering the reported uncertainty of CASTANEA flux simulations (l321-326, l.349-350, l409).

In the following, we address each of your specific comments.

Detailed comments:

Page 2215

Line 4: 60% of the fossil fuel emissions. Please check this. The airborne fraction ranges between 30-40%, meaning oceans and terrestrial ecosystems together take up about 60%. Estimates suggest the ocean accounts for 30%, which would leave 30% for global ecosystems (which includes all ecosystem types, not just forests).

We evocated the gross carbon uptake by the established forests and tropical regrowth forests, which amount to 73 PgC over the period 1990 to 2007, "equivalent to 60% of cumulative fossil emissions in the period" (Pan et al., 2011). We acknowledge that this statement was confusing as 1) we did not explicitly mentioned in the manuscript that we addressed gross carbon uptake 2) Literature usually reports the figures that you mentioned i.e. the proportion of anthropogenic C emission captured in established forests. We therefore modified our sentence based on Pan et al. (Table 3) as follows "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)." (l51-53) We chose the term "established forests" rather than "global ecosystems" because it makes more sense in the context of our work, as Pan et al. reported that “within the limits of reported uncertainty, the entire terrestrial C sink is accounted for by C uptake of global established forests”.

Page 2216:

Line 7: Constant – constrained.

We followed your suggestion and corrected the manuscript (l84).

Line 7: This sentence structure is confusing. Perhaps rephrase as: “The above experimental evidence suggests that growth is mostly limited by the direct effects...”

We followed your suggestion and corrected the manuscript (l85-86).

Line 15: The statement that rising CO2 could increase the terrestrial sink only if growth is a source limited process is misleading. There are multiple pathways through which CO2 can increase the sink. For example, increased root exudates under elevated CO2, and increased allocation to roots in general, is now widely accepted. This is thought to alleviate nutrient limitation. Water use efficiency also increases under elevated CO2. This can alleviate water limitation, thus enhancing sink strength.

We acknowledge that our statement was naive and we accordingly corrected the sentence: ”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.” (l89-91)

Line 19: the future of forest? Perhaps be more specific.

We further explained our statement in a new sentence :” 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” (l93-95).

Page 2217

Line 13: the intensity effects of which

We corrected the manuscript and clarified this sentence. “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.” (l114-116).

Line 26: in forests

We followed your suggestion and corrected the manuscript (l127).

Page 2218

Line 5: I would suggest increasing the font on this schematic. It will be quite small in the final print version.

We increased the font of the schematic for a better readability.

Line 25: ‘allowed to extensively assessing’. Please revise for proper language use.

We corrected the sentence as follows: “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).” (l154-155).

Page 2220 Line 10: used to rank

We rephrased this sentence (l204).

Page 2221

Line 6-7: The level of CASTANEA agreement with observed interannual variability in the Delpierre et al., 2012 study is indeed impressive. Are we to believe, however, that the model does similarly well for site for which there is no calibration data such as the ones included in this study? It is quite likely that when it was first applied to the sites in the Delpierre et al. study it did not do well at all, until some site specific characteristics were accounted for by adjusting parameters. This is the weak point of this study – we have no way of knowing if the model does a good job of reproducing variability in NPP at the studied sites. If it does not do a good job, then it is no surprise that modeled C source diagnostic variables were not found to be related to actual carbon allocation.

We acknowledge that the use of process-based modelling is a source of uncertainty that was not properly discussed in the first version of our work and that remain unknown in the absence of EC measurements at our study sites. Dedicated discussion of this point can be found in our above general answer.

Line 23: 2 day resolution

We followed your suggestion and corrected the manuscript (l241).

Page 2222

Line 12: State which carbon fluxes.

The considered C fluxes are GPP, NPP and Ra. We clarified this point in the sentence (l270).

Line 15: The age related trend.

We rephrased this sentence (l274).

Line 22: I’m not sure collinearity is the right word here, as the relationships are not necessarily linear. Perhaps covariance?

We agree that covariance is better here, as a more general statement (l281). Thank you for this suggestion.

Line 23: could hamper

We followed your suggestion and corrected the manuscript (l282).

Page 2223

Line 5: gathered – grouped.

We followed your suggestion and corrected the manuscript (l296).

Page 2224

Line 14: important – large.

We followed your suggestion and corrected the manuscript (l333).

Page 2225

Line 7: The elementary components of the simulated seasonal forest C balance. It should be made clear in all instances when referred to Castanea output that this is indeed model output.

We clarified in all instances whether the considered variables is simulated or not (e.g., l354, l360, l366, l392).

You are not simulating C balance, as the forest C balance also includes heterotrophic respiration. Please revise throughout the manuscript.

We acknowledge that this statement was confusing because we only simulated tree-atmosphere C fluxes. We therefore changed all the occurrences of “forest C balance” referring to our study to “tree C balance” (e.g., l237, l281, l286, l534).

Page 2226 Line 7: “no retained models included...” Please state whether this is for all species or just the temperate oaks.

This statement is for all species. We clarified this point in the manuscript (l377).

Page 227

Fig 5: These partial dependencies are very interesting. It would help the reader if the footer contained information on how they were derived.

We added to the Figure caption a short technical description of partial plot in random forest : ” 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.”

Page 2227

Line 25: “Our results have far reaching....” This is unnecessary.

We removed this sentence (l423).

Page 2228

Line 23: fluxes – flux

We followed your suggestion and corrected the manuscript (l445).

Page 2232

Line 21: It is disingenuous to cite a paper over a decade old in support of the claim that current models do not simulate the IAV of growth well. There are multiple studies that show quite accurate simulation of tree ring IAV using GPP driven modeling (e.g., http://www.biogeosciences.net/11/6711/2014/bg-11-6711-2014.html).

We acknowledge that recent studies report very satisfactory simulations of annual growth based on C source modelling. We rather would like to emphasize that there is a risk of “getting the right answers for the wrong reason” (Fatichi *et al.* 2014) because of the high correlation usually found between GPP and cambial activity. Because the simulated fundamental processes are different, even if they obtain similar performances against observations, this could be of great importance for productivity projections under climate change. We therefore modified our sentence : ”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).” (l547-550).

Line 20-25. You need to add another explanation here – the possibility that modeled C source is not accurate enough. Even if your model is globally applicable with absolute confidence as it is presented here, it will still be unable to account for forest disturbances such as insect outbreaks, and various extreme events. This is a very important issue and must be discussed.

We added a further discussion of the possible implications of process-based modelling on our results, based on your suggestions. A dedicated discussion of this point can be found in our above general answer.

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

J. Guillemot[1], N. K. Martin-StPaul[1,2], E. Dufrêne[1], C. François[1], K. Soudani[1], J. M. Ourcival[3] and N. Delpierre[1]

[1]{Laboratoire Ecologie, Systématique et Evolution, Université Paris Sud, CNRS, AgroParisTech, UMR8079, F-91405 Orsay, France}

[2]{Ecologie des Forêts Méditerranéennes, INRA, UR629, F-84914 Avignon, France}

[3]{CEFE, CNRS, Université de Montpellier, Université Paul-Valéry Montpellier, EPHE, UMR5175, F-34293 Montpellier, France}

Correspondence to: J. Guillemot (joannes.guillemot@gmail.com)

~~**J. Guillemot[1,2,3], N. K. Martin-StPaul[1,2,3], E. Dufrêne[1,2,3], C. François[1,2,3], K. Soudani[1,2,3], J. M. Ourcival[4] and N. Delpierre[1,2,3]**~~

~~[1]{Université Paris Sud, Laboratoire Ecologie, Systématique, Evolution, UMR8079, F-91405 Orsay, France}~~

~~[2]{CNRS, Laboratoire Ecologie, Systématique, Evolution, UMR8079, F-91405 Orsay, France}~~

~~[3]{AgroParisTech, Laboratoire Ecologie, Systématique, Evolution, UMR8079, F-91405 Orsay, France}~~

~~[4]{CNRS, Centre d’Ecologie Fonctionnelle et Evolutive, UMR5175, F-34293 Montpellier, France}~~

~~Correspondence to: J. Guillemot (joannes.guillemot@gmail.com)~~

Abstract

The extent to which ~~forest~~ wood growth is limited by carbon (C) supply (i.e., source control) or by cambial activity (i.e., sink control) will strongly determine~~s~~ the responses of trees to global changes. ~~However~~Nevertheless, the physiological processes that are responsible for ~~the~~ limiting~~ation of~~ forest growth are still ~~under~~ debated. The aim of this study ~~is~~ was to evaluate the key ~~drivers~~ determinants of the annual ~~carbon~~ C allocation to wood along large soil and climate regional gradients ~~in~~ for 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.~~ 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 ~~forest~~ 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 ~~an~~ age-related decline. The direct ~~control~~ effects of temperature ~~or~~ and water stress on sink activity (i.e., effects independent~~independently~~ from their effects on the C supply) exerted a strong influence on the annual stand wood~~y~~ 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) ~~was a~~ significantly affected ~~driver of~~ the annual C allocation to wood. The C~~Carbon~~ supply appeared to strongly limit growth only in ~~deciduous~~ temperate deciduous species.

We provide an evaluation of the spatio-temporal dynamics of the annual ~~carbon~~ C allocation to wood in European forests. Our study supports the premise that European forest growth is ~~under~~ subject to~~a~~ complex control processes that include~~ing~~ both source and sink limitations. The relative influences of the ~~different~~ growth drivers strongly vary with time and across ~~years and~~ 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 ~~show~~ indicate that established forests have been a persistent carbon sink for~~in recent~~ decades, sequestering~~uptaking~~ almost 3~~6~~0% of the ~~cumulative~~ world's total anthropogenic C ~~fossil~~ emissions between 1990 and 2007 (Pan et al., 2011). The fate of the ~~entering~~ sequestered C ~~strongly relies~~is highly dependent on the C dynamic~~s~~ in trees, which determines ~~its~~ the residence time of C in ~~the~~ forest ecosystems. Despite its importance for the future ~~of the~~ terrestrial C sink (Carvalhais et al., 2014; Friend et al., 2013), the ~~C~~ 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~~s have arisen from~~ regarding the physiological mechanisms that drive~~ing~~ 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~~ with estimates of the C exchange~~s~~ between the ecosystem and ~~the~~ atmosphere, based on the ~~Eddy~~eddy-~~Covariance~~ covariance (EC) technique (Babst et al., 2014; Litton et al., 2007; Wolf et al., 2011). Global meta-analyses ~~of such dataset~~ (that~~gathering~~ included data from various~~different~~ biomes and ~~different~~ 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 ~~for~~ long been thought ~~as~~ to be C limited, because of the ~~through an~~ 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~~outcome~~ 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).

S~~The s~~ource control of ~~tree~~ wood growth is a mechanism that has been questioned by several authors, who argue~~ing~~ that cambial activity is more sensitive than C assimilation to ~~a panel of~~ several environmental stressors~~es~~ (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). ~~, including water deficit (Muller et al., 2011; Tardieu et al., 2011) and low temperature (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~~,~~ ~~which~~ in turn, may partly determine annual cell production and ~~forest~~ 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 ~~due to~~ the relatively ~~constant~~ constrained stoichiometry of ~~the~~ tree biomass (Leuzinger and Hättenschwiler, 2013). ~~These experimental evidences~~These studies ~~gave ways to an alternative understanding of tree C dynamic where~~suggest that growth is ~~mostly~~ 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 ~~unscramble~~ determine whether wood growth is more related to ~~carbon~~ C supply or to the intrinsic environmental sensitivity of cambium functioning ~~to the environment~~ (Fatichi et al., 2014). The extent to which ~~forest~~ wood growth is under ~~a~~ source~~-~~ or~~ a~~ ~~-~~sink~~-~~ control is of paramount importance ~~to~~ for predicting how trees will respond to global changes and ~~.~~s~~ S~~pecifically ~~, rising~~how increasing atmospheric CO_2 will affect~~could possibly increase~~ forest productivity~~, and hence the~~ and the future 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~~ substantial challenge for modellers, because~~as~~ it ~~will~~ may determine our ability to project ~~the~~ future ~~of~~ 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 ~~on the basis of~~by several non-exclusive principles (Franklin et al., 2012), ~~among which are~~including i) allometric scaling, ii) functional balance and iii) evolution-based optimal responses. i) ~~Allometric~~ The allometric scaling principle is based on the assumption that biophysical laws determine C partitioning among ~~within~~ the different forest compartments. ~~Current knowledge~~Important allocation constraints include ~~include~~ vascular network optimality (Enquist, 2002) and functional homeostasis in water transport (Magnani et al., 2000) ~~as main allocation constraints~~. ii) The f~~F~~unctional balance ~~theory~~ principle suggests ~~a preferential allocation to~~ that the organ responsible for acquiring ~~sition of~~ the ~~most~~ limiting resource is preferentially allocated C. ~~In line~~Consistent with this principle~~, a~~ higher C allocation to fine roots at the expense of C allocation to wood~~y~~ growth has been reported ~~on~~for poor or dry soils (Chen et al., 2013; Keyes and Grier, 1981).~~,~~ In addition,~~along with~~ a possibly~~lausible~~ ~~higher~~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 ~~a~~ fitness ~~proxy~~ in a fixed environment. This hypothesis ~~of fitness maximization is in line~~agrees with the ~~previously assumed~~idea that a dynamic reserve pool act~~ing~~ as temporary storage, possibly at the expense of growth ~~expense~~, to ~~allow~~ promote long-term tree 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., 2013). The optimal response ~~theory~~ principle is consistent with several~~also explains~~ well~~long~~-known life history traits, such as ~~the~~ preferential allocation to reproduction in ageing plants, ~~that~~ which could lead to ~~the observed~~ age-related declines in woody biomass allocation (Genet et al., 2010; Thomas, 2011). ~~Woody~~ The woody biomass increment therefore appears to be under the control of ~~a panel of drivers~~multiple factors. T~~-~~he ~~which intensity effects~~effects of these drivers ~~are~~ are expected to strongly vary in space and time. ~~As a consequence~~Consequently, ~~local~~ studies have reported ~~contrasted agreements~~conflicting relationships between the C supply and wood~~y~~ 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~~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 that affect~~ing~~ wood~~y~~ growth on~~at~~ ~~the~~ different spatio-temporal scales is ~~a~~ necessary ~~step~~ to explain ~~unify~~ these apparently contradictory results ~~in~~using a common framework. Moreover, investigations should be conducted at the species level, ~~as~~ because phylogeny may strongly constrain forest functioning (Carnicer et al., 2013; Drobyshev et al., 2013) and induce different ~~contrasted~~ growth ~~determinisms~~ determinants ~~between~~ among taxa (Genet et al., 2010).

There is a gap between the knowledge obtained from~~lessons drawn from~~ global studies of~~regarding~~ universal C allocation rules in forests and our understanding of the cell processes ~~underpinning~~ that underlie cambial activity; currently, this gap appears to be the ~~current main~~primary obstacle ~~toward a better~~to a more complete understanding of ~~forest~~ wood growth drivers. In this regard, species-specific studies that evaluate~~ing~~ the dynamic of C partitioning to annual wood~~y~~ growth along soil and climate ~~regional~~ gradients ~~constitute a key missing link~~would be highly useful but are lacking. Unfortunately, ~~advances are so far precluded by the~~there is a scarcity of datasets that combine~~ing~~ EC and growth measurements ~~from~~at the same sites (Luyssaert et al., 2007). Here, we released this constraint by ~~combining~~ complementing stand and soil measurements at ~~from~~ a permanent plot network of 49 forest sites ~~and~~ with process-based simulations of ~~forest~~ annual and seasonal tree C balance (Fig. 1)~~ over 49 forest sites~~. Simulations were performed using a process-based model (CASTANEA, Dufrêne *et al.* 2005) that was thoroughly validated using~~against~~ EC data from throughout ~~over~~ Europe ~~((Dufrêne et al., 2005)~~(Davi et al., 2005; Delpierre et al., 2009, 2012) and was applied ~~here with~~ using site-specific ~~parameterizations~~parameters. By r~~R~~elating biometric measurements to ~~different~~ variables ~~linked to~~that explain the C source and sink activity, we evaluated the key drivers of the annual C allocation to stand wood~~y~~ 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*, ~~found in~~for high~~-~~-latitude and high-~~-~~altitude evergreen needleleaf forests; and *Quercus ilex*, an ~~Mediterranean~~ evergreen broadleaf species from Mediterranean forests. Specifically, the relative influence of ~~forest~~ annual and seasonal (from one month to the year) tree C balance (source control), direct environmental control (water and temperature ~~controls~~ effects on~~f~~ 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~~-~~

Code de champ modifié

controls ~~in ~~to the spatio-temporal dynamic of forest wood~~y~~ growth across a wide range of environmental contexts and (2) provide ~~transferable ~~information ~~to help~~that can be used to ~~refin~~refine~~ing~~ 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 ~~simulation data. This hybrid approach allowed ~~to ~~us to ~~extensively ~~assess~~ing~~ and ~~disentangling ~~disentangle the effects of previously reported environmental and endogenous drivers of C allocation to wood~~y~~ growth (Fig. 1).

2.1 Study sites and field data

~~Our investigation~~We gathered field measurements from 48 plots from the French P~~p~~ermanent P~~p~~lot N~~n~~etwork for the M~~m~~onitoring of F~~f~~orest E~~e~~cosystems (RENECOFOR, Ulrich, 1997) and ~~from ~~the ~~heavily instrumented ~~Puéchabon tower flux site (Martin-StPaul *et al.* 2013). The l~~L~~ocation and general climatic features of these plots are shown~~given~~ in Fig. 2 and Table 1. ~~, a~~ ~~c~~Complete site description ~~of the sites ~~is available in ~~Appendix~~Supplement -S1.

2.1.1 Growth measurements and historical stand growth reconstruction

Growth measurements ~~consisted of~~were obtained by two methods: *i)* D~~d~~endrochronological sampling, in which~~:~~ 12 to 30 overstorey trees per plot~~s~~ were cored to the pith at breast height with an incremental borer. Cores were collected ~~(~~in 1994 ~~in ~~at the RENECOFOR sites and in 2008 at the Puéchabon site~~,~~ (Lebourgeois 1997; J.M. Ourcival, *unpublished data*). T~~he t~~ree circumferences at breast height (CBHs) and total heights were also measured. The ~~A~~average stand age was inferred from the tree ring series. *ii)* Forest inventories, in which~~:~~ extensive CBH surveys were conducted~~ on every plot on~~ 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 ~~to~~ with the CBH surveys to reconstruct the historical CBHs of every tree on the plots (over 8 to 43 years, ~~Appendix~~Supplement -S1). The entire stand tree CBH distribution was reconstructed from the~~The scaling from the sampled trees to the entire stand tree~~ CBHs of the sampled trees using~~ distribution involved~~ 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). ~~calibrated annually (Guillemot *et al.* 2014, Appendix S2).~~ The historical total woody stand biomass was ~~then~~ 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) ~~(Appendix S3)~~ 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. P~~p~~ast annual woody biomass increments (AWBIs) were then inferred (~~Appendix~~Supplement -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).~~

Mis en forme : Retrait : Première ligne : 0 cm

Mis en forme : Police :(Par défaut) Times New Roman, 12 pt

Mis en forme : Police :(Par défaut) Times New Roman, 12 pt

Mis en forme : Police :(Par défaut) Times New Roman, 12 pt

Mis en forme : Police :(Par défaut) Times New Roman, 12 pt

Mis en forme : Police :(Par défaut) Times New Roman, 12 pt

Mis en forme : Police :(Par défaut) Times New Roman, 12 pt

Mis en forme : Police :(Par défaut) Times New Roman, 12 pt

Mis en forme : Police :(Par défaut) Times New Roman, 12 pt

Mis en forme : Police :(Par défaut) Times New Roman, 12 pt

Mis en forme : Police :Italique

Mis en forme : Retrait : Première ligne : 0 cm

2.1.2 Measurements of stand characteristics

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

SNA was assessed as ~~through~~ the soil's C:N~~carbon (C):nitrogen (N) soil~~ biomass ratio, the absolute value of the ~~soil~~ cation-exchange capacity and the ~~its~~ 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~~ranked~~ soil plots into three nutrient classes, from low to high nutrient availability (~~Appendix~~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 ~~M~~meteorological variables at the hourly temporal scale (with 8~~–~~km 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 ~~associated~~ related to the average~~d~~ altitudes of the SAFRAN cells, was corrected using plot-specific elevation measurements (~~considering~~ assuming a lapse rate of 0.6 °K per 100 m, ~~Appendix~~Supplement ~~–~~S1). These variables were used for ~~the~~ climate forcing ~~of~~ in the CASTANEA model (Dufrêne *et al.* 2005, see the following~~next~~ section). In addition, two annual temperature indices were ~~derived~~ used as proxies of~~for~~ winter frost damage and low temperature stress during the growing~~th~~ period (*frost* and *templim*$_{gp}$, respectively, Table 2).

2.3 Process-based ~~simulated~~ simulation data

We used the CASTANEA model ~~for~~ to simulate~~ing~~ an ensemble of diagnostic variables that are related~~linked~~ to the C source and~~ the~~ sink activity of ~~the~~ forest stands. The eco-physiological process-based CASTANEA model ~~CASTANEA~~ aims ~~at~~ to simulate~~ing~~ ~~carbon~~ C and water fluxes and stocks of a~~n even-aged~~ monospecific, same-aged forest stand on ~~at the~~a rotation time scale. The hourly stand-atmosphere C fluxes ~~simulated~~ predicted by the CASTANEA model ~~on an hourly basis~~ have been thoroughly validated using~~against~~ EC data from throughout~~over~~ Europe (Davi et al., 2005; Delpierre et al., 2009, 2012). Importantly, the biophysical hypotheses that were formalized in this~~e~~ model are able to reproduce the interplay of the complex mechanisms ~~interplay leading~~that lead to~~ the~~ inter-annual variability in the stand C balance ~~variability~~ (Delpierre et al., 2012); modelling this interplay~~, which~~ has been recognized as a ~~s~~substantial~~trong~~ challenge for TBMs (Keenan et al., 2012). A complete description of CASTANEA is ~~given~~ provided in Dufrêne *et al.* (2005), ~~with~~ and subsequent modifications ~~from~~ 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. ~~Measured~~ 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 ~~at regional scale~~ has been recently validated (Guillemot et al., 2014). Nevertheless, the annual s~~S~~tanding woody biomass was ~~nonetheless~~ forced ~~on each year~~to conform to the observed values, because~~as~~ the model was ~~here~~ used for diagnostic purposes in this study.

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

1. *The elementary components of the ~~forest~~ tree C balance*. These components included the ~~:~~ ~~gross primary productivity (G~~GPP~~), and~~ autotrophic respiration (Ra), ~~along with~~and ~~the~~ 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. ~~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~~The C fluxes were also

summed i) ~~over ~~for the species-specific biomass growth periods reported in the literature (GPP_{gp}, Ra_{gp} and NPP_{gp}, ~~Appendix~~Supplement ~~ S10~~S6) and ii) for~~over~~ the ~~whole ~~entire preceding year (y-1) as a proxy of ~~f~~the forest C status induced by past climate conditions (lagged effect, GPP_{y-1}, Ra_{y-1} and NPP_{y-1}).

~~1.~~

2. *Bioclimatic water stress indices*. These indices included~~:~~ the intensity and ~~the ~~duration of ~~the ~~water stress (WS_int_{gp} and WS_per_{gp}, respectively, Supplement S7) ~~over the~~during species-specific growing~~th~~ periods that have been reported in the literature (Supplement S6).~~were evaluated (WS_int_{gp} and WS_per_{gp}, respectively, Appendix S7).~~ 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 ~~over ~~for the ~~whole~~ entire preceding year ~~(y-1)~~ (lagged effect of water stress, WS_int_{y-1} and~~,~~ WS_per_{y-1}).

~~2.~~

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

Mis en forme : Retrait : Gauche : 1.27 cm, Sans numérotation ni puces

Mis en forme : Numéros + Niveau : 1 + Style de numérotation : 1, 2, 3, … + Commencer à : 1 + Alignement : Gauche + Alignement : 0.63 cm + Retrait : 1.27 cm

Mis en forme : Police :Non Italique

Mis en forme : Police :Non Italique

Mis en forme : Police :Non Italique

Mis en forme : Police :Non Italique

Mis en forme : Police :Non Italique

Mis en forme : Police :Non Italique

Mis en forme : Police :Non Italique

Mis en forme : Police :Italique

Code de champ modifié

Mis en forme : Retrait : Gauche : 1.27 cm, Sans numérotation ni puces

Mis en forme : Indice

Mis en forme : Indice

Mis en forme : Indice

Mis en forme : Police :Non Italique, Non Exposant/ Indice

Mis en forme : Police :Non Italique, Non Exposant/ Indice

Mis en forme : Police :Non Italique, Non Exposant/ Indice

Mis en forme : Police :Non Italique, Non Exposant/ Indice

Mis en forme : Police :Non Italique, Non Exposant/ Indice

2.4 Statistical analyses

2.4.1 General overview

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

~~drivers responsible for the inter-annual growth biomass variability.~~

Because ~~numerous key~~many environmental factors affect both forest sink and source activities, there may be ~~a~~ strong ~~collinearity~~ covariance ~~between~~ among the ~~forest~~ tree C balance and proxies of environmental stress ~~proxies~~ (Fatichi et al., 2014) that could hamper~~ed~~ the inferential ~~interpretation~~ 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 statistical models used in the study were consequently selected for their reliability in the presence of confounded~~

Mis en forme : Espacement automatique entre les caractères asiatiques et latins, Espacement automatique entre les caractères asiatiques et les chiffres

~~variables (see below). E~~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 ~~have been~~were ~~gathered ~~grouped in the analyses and are hereafter collectively referred to as "temperate oaks"~~ in the following~~.

2.4.2 Correlations between growth and C fluxes

Pearson correlations between the AWBIs and simulated C fluxes ~~aggregated ~~in ~~over ~~different seasonal time periods were ~~assessed ~~calculated separately for each site. The highest median correlation value for each~~s~~ ~~per ~~species was~~ere~~ 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 ~~in order ~~to evaluate the sensitivity of the correlation values to changes in the C flux ~~aggregation ~~aggregation periods.

2.4.3 ~~Spatial ~~Drivers of spatial variations in biomass growth~~ dependences~~

The drivers of spatial variations in biomass growth ~~dependences ~~were evaluated using ~~a selection of ~~multiple regression models using an~~s based on the~~ information-theoretic approach (Burnham and Anderson, 2002). The AWBIs and the considered explanatory variables were averaged ~~per~~ for each plot~~s~~. The variables ~~entering ~~introduced into the linear models were centered and scaled such~~o~~ that the~~ values of the~~ir normalized coefficient estimates indicated the relative influence of the predictors on the AWBI. The e~~E~~lementary components of ~~the forest ~~tree C balance (NPP, GPP and Ra) were introduced one at a time into the models. For each species, multiple regression models~~s~~ that contain~~ing ~~ed all possible combinations of the explanatory variables were fitted. The m~~M~~odels were compared using the second-~~-~~order Akaike information criterion (AIC~~c~~), and all models with an Akaike weight of at least 1% of the best approximating (lowest~~r~~ AIC~~c~~) model were considered to be plausible (Burnham and Anderson, 2002). Ultimately, ~~We ~~we retained

~~finally~~ the variables that appeared in at least 95% of the selected models. Models fitted ~~on~~ using *P. abies* data were restricted to a maximum of 3 explanatory variables because of~~due to~~ the ~~low amount of data~~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 ~~considered~~ assessed in the analyses using a bootstrap procedure (Chernick, 2011): all linear models were fitted 1000 times, and~~randomly sampling~~ at each iteration, the C flux~~es~~ values were randomly sampled within the root mean square error of the CASTANEA simulations (~~Appendix~~Supplement –S9) to obtain ~~for each variable~~ a parameter estimate distribution for each variable. We finally retained the explanatory variables with parameter estimate distributions that excluded~~ing~~ the zero value at~~in~~ a ~~bilateral~~ two-tailed~~5%~~ probability level of 5%.

2.4.4 Drivers of t~~T~~emporal variations in biomass growth ~~dependences~~

~~The~~ A temporal analysis was conducted on the standardized AWBI series: a double-detrending process was applied ~~for~~ to each series~~,~~ based on an initial linear regression model, followed by ~~a~~ fitting ~~of~~ a cubic smoothing spline with a 50% frequency response cut-off (Mérian et al., 2011). For analysing the temporal ~~dependences~~ variations in~~of~~ biomass growth we used an ~~Random Forest (~~ RF~~)~~ learning method (Breiman, 2001), which was ~~made~~ possible because of~~y~~ the ~~important~~ large ~~amount of data~~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 ~~forms~~. The ~~principle of~~ RF method ~~is to~~ combined 500 binary decision trees that were built using bootstrap samples from the initial dataset. ~~Decisions~~ The decisions trees aimed to reduce the heterogeneity of the explained variable in the resulting branches. For each of the 500 ~~built~~ trees, the data that were not involved in the tree construction were~~are~~ used for validation. The tree predictions and errors ~~are~~ were then averaged to provide the final RF results. ~~Consequently,~~The RF method does not overfit ~~and does not need~~or require cross-validation (Cutler et al., 2007). A subset of explanatory variables ~~is~~ was randomly chosen at each node, thus reducing the effect of collinear variables on the output. The RF method was used to select ~~important~~ variables that explained ~~related to~~ the ~~growth~~ temporal variability in biomass growth (Genuer et al., 2010). Variable selection relied on permutation importance, i.e.,~~:~~ the existence of an increase~~ing~~ in~~of~~ the global mean square error when a given variable was~~is~~ randomized in the validation subsamples. The forms of the dependences ~~was~~ were illustrated by ~~discussed thanks to~~ 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 u~~U~~ncertainty~~ies~~ ~~on~~ in the simulated C fluxes ~~were~~ was considered in the linear model~~ss~~, following the procedure described in~~as for~~ the spatial ~~growth dependence~~ analysis section.

3 Results

~~3.1 Agreement~~ Relationship between woody biomass growth and ~~carbon~~ C fluxes

3.1

The elementary components of the simulated seasonal ~~forest~~ tree C balance differed in terms of their relationships~~revealed contrasted agreement~~ with the inter-annual variability ~~in~~ of the AWBI (Table 3). The simulated s~~S~~easonal ~~gross primary productivity (~~GPP~~)~~ and ~~net primary productivity (~~NPP~~)~~ were ~~strongly~~ linked to AWBIs with a comparable agreement between species. However, the simulated ~~autotrophic respiration (~~Ra~~)~~ ~~revealed~~ had weak and often non-significant ~~correlations~~ relationships with the AWBIs across the 49 studied plots. The ~~highest~~ 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. ~~Notably, the~~ GPP and NPP ~~in temperate deciduous species~~ were summed from the beginning of May to the beginning of August ~~or~~ and September, in temperate oaks and *F. sylvatica*, respectively. The longest GPP and NPP aggregation periods were obtained ~~in~~ for *P. abies* (from the beginning of February to mid-September), and the shortest period were found ~~in~~ for *Q. ilex* (from the beginning of July to mid-August). Minor (less than 20 days) changes in the flux aggregation period associated ~~to~~ with the maximum simulated flux-AWBI correlation usually marginally affected ~~marginally~~ the

Mis en forme : Anglais

Mis en forme : Titre 2

correlation values (~~Appendix~~Supplement ~~S6~~S10). ~~As a consequence~~Consequently, aggregation periods ~~differing~~ that were less than 13 days different (~~start or end~~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 ~~Appendix~~Supplement ~~S6~~S10).

3.2 Spatial dynamic~~s~~ of ~~carbon~~ C allocation to woody biomass growth

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

Code de champ modifié

3.3 Temporal dynamic~~s~~ of carbon allocation to woody biomass growth

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

Mis en forme : Police :Italique

4 Discussion

This study quantified the C that is ~~annually~~ allocated annually to the woody biomass increment ~~in~~ for five species that are representative of the main European forest biomes. ~~Combining~~ By complementing field measurements from a permanent plot network with ~~, climatic database and~~ process-based modelling~~simulations~~, our approach ~~released~~ circumvented the ~~constraint~~ limitation ~~imposed by~~of EC data scarcity ~~to~~ and characterized the annual partitioning of C into woody biomass at 49 sites (931 site-years). We were thus able to ~~highlight~~ identify the species-specific drivers of the spatio~~-~~temporal dynamics of the ~~C~~ allocation of C to wood~~y~~ growth along ~~large~~ ecological gradients. ~~Our results have far reaching implications for the representation of biomass growth causalities in TBMs.~~

4.1 ~~On correlating~~The correlation between the ~~forest~~ tree C~~carbon~~ balance ~~to~~ and woody biomass growth

Relating EC-based ~~estimation~~ estimates of forest C balance and biometric measurements of woody biomass growth has been the ~~concern~~ focus of an increasing number of ~~local~~ studies. These studies ~~results are expected to~~ can enhance our understanding of ~~the~~ ecosystem C dynamics but have so far provided conflicting conclusions ~~so far~~. Indeed, t~~T~~he ~~reported~~ correlation between woody biomass growth and forest C gain ~~indeed ranges~~has been reported as both ~~from~~ non-significant ~~correlations~~ (Mund et al., 2010; Richardson et al., 2013; Rocha et al., 2006) ~~to~~ and highly significant ~~tight links~~ (Babst et al., 2014; Ohtsuka et al., 2009; Peichl et al., 2010; Zweifel et al., 2010). Accordingly, the ~~agreements~~ relationships between AWBI and C fluxes reported in this study strongly varied among sites ~~in~~ for each of the species studied ~~species~~ (Table 3). Nevertheless, the a~~A~~nnual woody biomass increment was ~~nonetheless~~ consistently related to GPP_{gp} and NPP_{gp}, and only marginally to Ra_{gp} ~~in~~ for the~~a~~ majority of sites (Table 3). ~~(~~Babst et al.~~,~~ (2014) ~~Babst *et al.* (2013)~~ reported a similar dependence of biomass growth ~~to~~ on~~the~~ C fluxes at 5 sites that spanned~~ing~~ a wide range of latitude ~~range across~~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 ~~forest~~ tree C balance ~~components~~ are under the control of distinct but partially correlated processes (Beer et al., 2007;

Code de champ modifié

Fatichi et al., 2014); these processes ~~that~~ may or may not induce consistent annual changes, depending on the environmental conditions faced by trees. For *F. sylvatica* and temperate oaks, ~~M~~maximum correlation values ~~were observed in *F. sylvatica* and temperate oaks for~~corresponded to flux aggregation periods that were consistent with the previously reported phenology of the woody biomass increment (Table 3, Michelot *et al.* 2012, ~~Appendix~~Supplement ~~-~~S10). ~~(~~Babst et al.~~,~~ (2014) and~~;~~ Granier et al.~~,~~ (2008) ~~accordingly~~ similarly reported ~~high agreements~~close relationships between the AWBI and forest C fluxes that were summed until ~~the time of~~cessation of growth ~~cessation~~ (August/September). The ~~F~~flux~~es~~ aggregation periods were, however, ~~strongly incoherent with~~not related to the timing of wood~~y~~ growth in *Q. ilex* ~~and~~ or *P. abies* (Cuny et al., 2012; Lempereur et al., 2015), which indicates that ~~the~~ inter-annual variation in the AWBI is not always solely (or even primarily, e.g.,~~, and in some cases (here in~~ *Q. ilex* and *P. abies*) ~~not primarily,~~ dependent~~ing~~ on the C ~~fuelled~~ derived from photosynthesis. Specifically, the agreement between the observed annual growth and a short period of C flux aggregation ~~occurring~~ in early summer that ~~we~~ was reported ~~in~~ for *Q. ilex* ~~is in line with~~corresponds to the ~~major~~ effect of growth cessation on the annual biomass increment, which ~~that~~ has~~ve~~ been attributed to a drought-induced limitation of cambial activity at the Puéchabon site ~~(~~(Lempereur et al., 2015)~~M. Lempereur, N. K. Martin-StPaul, J.M. Ourcival et al., unpublished data)~~. The processes that underlie~~ying~~ the relationship of the long flux aggregation period ~~related to~~and the annual biomass increment ~~in~~ of *P. abies* ~~possibly~~ may ~~involves~~ 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 ~~the~~ source ~~-~~limitation of growth or the seasonality of C allocation to woody ~~tissue~~ biomass can lead to misleading conclusions.

4.2 B~~The b~~etween-site variability in the ~~carbon~~ C allocation to woody biomass growth is related to ontogeny and competition intensity

We highlighted an age-related decline ~~of~~ in the C partitioning to woody biomass ~~at spatial scale~~ in all three species (Fig. 3B). This result had previously been ~~reported~~ observed in *F. sylvatica* stands using measurements of the main C compartments along a chronosequence (Genet et al., 2010). ~~Different~~ Several non-exclusive processes can explain this age-related trend. ~~The~~ I~~i~~ncreases ~~of~~ in tree height ~~is~~ are associated with ~~an~~ increases in the hydraulic resistance of xylem, which ~~hydraulic resistance that~~ may lead to ~~a~~ declines in the turgor of living cells ~~with~~ 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 ~~in line with~~ our ~~report~~results. ~~Concurrently~~Additionally, life-history traits, such as a ~~predominant~~ greater emphasis on~~effort toward~~ reproduction in ~~aged~~ older stands, could also be involved.~~,~~ ~~although~~ However, the interactions ~~between~~ of growth and reproductive~~on~~ mechanisms are still under debate (Hoch et al., 2013; Thomas, 2011) and ~~remain~~ have yet to be properly represented in TBMs. Only the GPP component of the simulated ~~forest~~ tree C balance was retained in the final models (Table 4), thereby indicating that ~~the~~ an increase ~~of~~ in maintenance respiration with greater stand~~ing~~ biomass ~~was probably~~most likely did not ~~involved~~ contribute to~~in~~ the age-related decline in biomass growth (Drake et al., 2011; Tang et al., 2014). ~~While the~~Although height-related hydraulic constraints on C assimilation ~~associated with tree height~~ have~~s~~ been ~~thought~~ suggested ~~as~~ to be an important driver (Ryan et al., 2006; Tang et al., 2014), recent ~~local~~ studies have ~~evidenced~~ suggested that changes in demography and stand structure ~~rather than decrease in tree functioning~~ may primarily explain the age-related decline observed in stand wood~~y~~ growth (Binkley et al., 2002; Xu et al., 2012). Our results suggest~~s~~ that changes in the C allocation should also be considered, ~~as~~ because no mortality occurred in ~~the~~ our~~studied~~ plots ~~over~~ during the measurement period (*data not shown*). We additionally ~~evidenced~~ identified a significantly higher C partitioning to woody biomass in temperate oak stands with ~~high~~ greater competition intensity (i.e., high stand basal area, Table 3). To date, r~~R~~eports regarding the effect of competition on C allocation dynamics are ~~so far~~ conflicting (Litton et al., 2007) ~~showing no large and consistent effect~~and suggest no significant or consistent effect. ~~Besides~~Moreover, we found no significant effect of soil nutrient availability on the C allocation dynamics~~was evidenced~~ along the studied ecological gradient whereas a recent meta-analysis reported that this factor ~~affects~~ positively affects C partitioning to forest biomass ~~at~~ on the global scale (Vicca et al., 2012). The RENECOFOR network only includes relatively fertile sites (~~Appendix~~Supplement –S5), which could putatively explain ~~this~~ the apparent tension between our results~~ but remains putative at this stage~~ and the conclusions of the meta-analysis. Therefore, m~~M~~ore studies are ~~thus~~ required to ~~further specify~~elucidate the contributions of the ~~different~~ various drivers to the variation in ~~the~~ C partitioning to woody biomass ~~along local to global environmental gradients.~~on scales that range from local to global.

4.3 I~~The i~~nter-annual variability in woody biomass growth is consistent with combined source-sink limitations

Water ~~or~~ and temperature stress~~es~~ exerted ~~a~~ significant direct control on the inter-annual variation of woody biomass growth (i.e., independently from their effects on C assimilation) ~~in~~ for every species and biome~~s~~ (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, ~~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~~more sensitive than photosynthesis to low temperatures (Körner, 2008). ~~While~~ Although these ~~evidences~~ findings documented the plausible mechanisms of ~~the~~ sink control of biomass growth at the cellular scale, there is still considerable debate ~~as to~~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 ~~as an~~ evidence of ~~a~~ 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 ~~in~~ of five species that are representative of ~~contrasted~~ different European biomes, ~~including~~ including deciduous temperate forests. ~~As~~ Because sink limitation implies that there are periods with significant C supply but no growth, ~~this~~ our results also corroborate~~s~~ recent empirical studies ~~reporting~~ 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). A~~We a~~dditionally, we ~~reported~~ observed that past environmental constraints significantly affected ~~the~~ C partitioning to wood~~y~~ growth ~~in every~~for each species and biome~~s~~ (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 ~~facing~~ that face C reserve pool depletion (Bansal and Germino, 2008; Wiley et al., 2013). In support of this finding, Richardson *et al.* (2012) ~~accordingly~~ reported a strong ~~agreement~~ relationship between the AWBI and the EC-based ~~estimation~~ estimate of the previous year's ~~carbon~~ C supply in a mature maple stand. The ~~important~~ detrimental effect of ~~low~~ a previous year's low C supply on ~~the~~ temperate oak wood~~y~~ growth (Fig. 4) may be related to ~~its~~ growth phenology, because~~as~~ this species relie~~d~~s on C reserves to achieve a large part of ~~the~~ its annual biomass growth ~~before~~ prior to leaf expansion in the spring (Barbaroux et al., 2003). The lagged effect of high water stress intensity ~~in~~ on *F. sylvatica* and *Q. ilex* (Fig. 4) may be linked to ~~the past~~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 ~~of the next year~~ (Delpierre et al., 2015; Palacio et al., 2012; Zweifel et al., 2006) and a recent meta-analysis ~~highlighted~~ concluded that C is preferentially allocated~~ion~~ to fine roots at the expense of wood~~y~~ growth in stands ~~facing~~ 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 ~~woody~~ growth in temperate deciduous forests (Daudet et al., 2005). GPP was the component of the simulated ~~forest~~ tree C balance that was most closely related to the annual variability ~~of~~ in growth;~~,~~ this result indicates GPP's important role in explaining the annual variability in~~which is in line with its preponderant role in the annual variability of~~ the net ecosystem productivity of European forests~~-~~ (Delpierre et al., 2012). Overall, our findings support the premise that forest woody biomass growth is ~~under a~~subject to complex control processes that include~~ing~~ both source and sink limitations, following ~~the principle of~~ Liebig's law: ~~while~~ although numerous processes potentially influence wood~~y~~ growth, ~~the~~ stand growth at a given site and a given ~~time~~ year is predominantly 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~~ 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 ~~of the~~ models that are currently used to project the outcome of global changes on forests represent wood~~y~~ growth as a fraction ~~coefficient~~ of the total C uptake (i.e., source control of growth, De Kauwe *et al.* 2014). This ~~carbon~~C-centric perspective overlooks the possibility of ~~a~~ sink control of growth~~, contradicting~~ and thus ignores results such as those presented in this study and those of earlier local studies ~~evidences found in this and earlier local studies~~ (reviewed by Fatichi *et al.* 2014). Consequently, this perspective possibly hampers the ability of TBMs to project future forest productivity~~and possibly~~ (Fatichi *et al.* 2014). ~~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 wood~~y~~ growth ~~at~~ on a regional scale, we ~~here~~ suggest a straightforward~~, way toward a~~ combined source- and ~~-~~sink-driven forest growth modelling framework (Fig. 6). In this ~~view~~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 ~~using~~ by accounting for the dependences of the C allocation ~~to~~ on ontogeny, competition intensity and lagged environmental ~~stresses~~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 t~~T~~he age-related decline in forest growth has been highlighted as an important modelling goal (Magnani et al., 2000; Zaehle et al., 2006). ~~but~~ However, this effect has thus far ~~has so far~~ been incorporated in models by including~~implemented through~~ a negative effect of the increasing stand respiration on the ~~forest~~ tree C balance, which contradicts~~ing~~ 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) ~~accordingly~~ improved the ~~LPJ~~ Lund-Potsdam-Jena (LPJ) terrestrial biosphere model predictions ~~at~~ for the cold tree-line ~~using~~ by accounting~~a~~ for ~~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; Schiestl-Aalto et al., 2015). It ~~further~~ synthesizes ~~our~~ the current knowledge ~~of~~ regarding forest growth dependences and has the potential to unify ~~in the same modelling framework~~ seemingly contradictory observations within a single modelling framework. The simulated growth is indeed ~~under~~ subject to 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, which are independently represented in the modelling framework. The relative influences of the ~~different~~ 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 ~~, possibly~~ shed~~ding~~ light on the contrasted results reported by correlative studies. ~~While~~ Although the value is comparable to those of previous ~~reports~~ studies (Lebourgeois et al., 2005; Mérian et al., 2011), the proportion of the annual growth variability that was explained by our approach ~~remained~~ was moderate (Table 5). Plausible explanations of this result include: i) unreported management interventions that ~~could~~ 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. O~~Nonetheless, o~~ur results suggest that implementing the presented C allocation dependences in TBMs will ~~allow~~ refine~~ing~~ the projections of the outcome of global changes on forest growth, ~~with~~ and have implications ~~on~~ for the predicted evolution of ~~the~~ forest C sink, forest diebacks and tree species distributions (Cheaib et al., 2012).

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 RENECOFOR database. The SAFRAN database was provided by Météo-France as part of the HYMEX project. J.G. ~~receives~~ received 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.M.-S. was provided by the Humbolt project within the GIS ~~climat~~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 (~~.~~ p~~P~~lease contact M. Nicolas, ~~(~~manuel.nicolas@onf.fr, +00331 60 74 92 28, Office National des Forêts, Fontainebleau, F-77300, France).

References

Abadie, P., Roussel, G., Dencausse, B., Bonnet, C., Bertocchi, E., Louvet, J., Kremer, A. and Garnier-Géré, P.: Strength, diversity and plasticity of postmating reproductive barriers between two hybridizing oak species (Quercus robur L. and Quercus petraea (Matt) Liebl.), J. Evol. Biol., 25(1), 157–173, 2012.

Archer, K. J. and Kimes, R. V: Empirical characterization of random forest variable importance measures, Comput. Stat. Data Anal., 52(4), 2249–2260, 2008.

Babst, F., Bouriaud, O., Papale, D., Gielen, B., Janssens, I. A., Nikinmaa, E., Ibrom, A., Wu, J., Bernhofer, C., Köstner, B., Grünwald, T., Seufert, G., Ciais, P. and Frank, D.: Above-ground woody carbon sequestration measured from tree rings is coherent with net ecosystem productivity at five eddy-covariance sites, New Phytol., 201(4), 1289–1303, doi:10.1111/nph.12589, 2014.

Bansal, S. and Germino, M. J.: Carbon balance of conifer seedlings at timberline: relative changes in uptake, storage, and utilization., Oecologia, 158(2), 217–27, doi:10.1007/s00442-008-1145-4, 2008.

Barbaroux, C., Breda, N. and Dufrene, E.: Distribution of above-ground and below-ground carbohydrate reserves in adult trees of two contrasting broad-leaved species (Quercus petraea and Fagus sylvatica), New Phytol., 157(3), 605–615 [online] Available from: http://doi.wiley.com/10.1046/j.1469-8137.2003.00681.x, 2003.

Barton, K. and Barton, M. K.: Package “MuMIn,” Version, 1, 18, 2014.

Bates, D., Sarkar, D., Bates, M. D. and Matrix, L.: The lme4 package, R Packag. version, 2(1), 2007.

Beer, C., Reichstein, M., Ciais, P., Farquhar, G. D. and Papale, D.: Mean annual GPP of Europe derived from its water balance, Geophys. Res. Lett., 34(5), 2007.

Binkley, D., Stape, J. L., Ryan, M. G., Barnard, H. R. and Fownes, J.: Age-related Decline in Forest Ecosystem Growth: An Individual-Tree, Stand-Structure Hypothesis, Ecosystems, 5(1), 58–67, doi:10.1007/s10021-001-0055-7, 2002.

Bontemps, J.-D., Hervé, J.-C. and Dhôte, J.-F.: Long-term changes in forest productivity: a consistent assessment in even-aged stands, For. Sci., 55(6), 549–564, 2009.

Bontemps, J.-D., Herve, J.-C., Duplat, P. and Dhôte, J.-F.: Shifts in the height-related competitiveness of tree species following recent climate warming and implications for tree community composition: the case of common beech and sessile oak as predominant broadleaved species in Europe, Oikos, 121(8), 1287–1299, doi:10.1111/j.1600-0706.2011.20080.x, 2012.

Bouriaud, O., Bréda, N., Le Moguédec, G. and Nepveu, G.: Modelling variability of wood density in beech as affected by ring age, radial growth and climate, Trees - Struct. Funct., 18(3), 264–276, doi:10.1007/s00468-003-0303-x, 2004.

Breiman, L.: Random forests, Mach. Learn., 45(1), 5–32, 2001.

Brêthes, A. and Ulrich, E.: RENECOFOR - Caractéristiques pédologiques des 102 peuplements du réseau., Off. Natl. des forêts, Département des Rech. Tech., 1997.

Brüggemann, N., Gessler, a., Kayler, Z., Keel, S. G., Badeck, F., Barthel, M., Boeckx, P., Buchmann, N., Brugnoli, E., Esperschütz, J., Gavrichkova, O., Ghashghaie, J., Gomez-Casanovas, N., Keitel, C., Knohl, a., Kuptz, D., Palacio, S., Salmon, Y., Uchida, Y. and Bahn, M.: Carbon allocation and carbon isotope fluxes in the plant-soil-atmosphere continuum: a review, Biogeosciences, 8(11), 3457–3489, doi:10.5194/bg-8-3457-2011, 2011.

Brzostek, E. R., Dragoni, D., Schmid, H. P., Rahman, a F., Sims, D., Wayson, C. a, Johnson, D. J. and Phillips, R. P.: Chronic water stress reduces tree growth and the carbon sink of deciduous hardwood forests., Glob. Chang. Biol., doi: 10.1111/gcb.12528, doi:10.1111/gcb.12528, 2014.

Burnham, K. P. and Anderson, D. R.: Model selection and multi-model inference: a practical information-theoretic approach, Springer., 2002.

Carnicer, J., Barbeta, A., Sperlich, D., Coll, M. and Peñuelas, J.: Contrasting trait syndromes in angiosperms and conifers are associated with different responses of tree growth to temperature on a large scale., Front. Plant Sci., 4(October), 409, doi:10.3389/fpls.2013.00409, 2013.

Carvalhais, N., Forkel, M., Khomik, M., Bellarby, J., Jung, M., Migliavacca, M., Mu, M., Saatchi, S., Santoro, M. and Thurner, M.: Global covariation of carbon turnover times with climate in terrestrial ecosystems, Nature, 2014.

Chapin, F. S., Schulze, E.-D. and Mooney, H. A.: The ecology and economics of storage in plants, Annu. Rev. Ecol. Syst., 21, 423–447, 1990.

Cheaib, A., Badeau, V., Boe, J., Chuine, I., Delire, C., Dufrêne, E., François, C., Gritti, E. S., Legay, M., Pagé, C., Thuiller, W., Viovy, N. and Leadley, P.: Climate change impacts on tree ranges: model intercomparison facilitates understanding and quantification of uncertainty., Ecol. Lett., 15(6), 533–44, doi:10.1111/j.1461-0248.2012.01764.x, 2012.

Chen, G., Yang, Y. and Robinson, D.: Allocation of gross primary production in forest ecosystems: allometric constraints and environmental responses, New Phytol., 200(4), 1176–1186, 2013.

Chernick, M. R.: Bootstrap methods: A guide for practitioners and researchers, Wiley., 2011.

Clark, D. B., Mercado, L. M., Sitch, S., Jones, C. D., Gedney, N., Best, M. J., Pryor, M., Rooney, G. G., Essery, R. L. H., Blyth, E., Boucher, O., Harding, R. J., Huntingford, C. and Cox, P. M.: The Joint UK Land Environment Simulator (JULES), model description – Part 2: Carbon fluxes and vegetation dynamics, Geosci. Model Dev., 4(3), 701–722, doi:10.5194/gmd-4-701-2011, 2011.

Cluzeau, C., Ulrich, E., Lanier, M. and Garnier, F.: RENECOFOR - Interprétation des mesures dendrométriques de 1991 à 1995 des 102 peuplements du réseau, Off. Natl. des forêts, Département des Rech. Tech., 1998.

Cosgrove, D. J.: Growth of the plant cell wall., Nat. Rev. Mol. Cell Biol., 6(11), 850–61, doi:10.1038/nrm1746, 2005.

Croisé, L., Cluzeau, C., Ulrich, E., Lanier, M. and Gomez, A.: RENECOFOR - Interprétation des analyses foliaires réalisées dans les 102 peuplements du réseau de 1993 a 1997 et premières évaluations interdisciplinaires, Off. Natl. des forêts, Département des Rech. Tech., 1999.

Cuny, H. E., Rathgeber, C. B. K., Lebourgeois, F., Fortin, M. and Fournier, M.: Life strategies in intra-annual dynamics of wood formation: example of three conifer species in a temperate forest in north-east France, Tree Physiol., 32(5), 612–625, 2012.

Cutler, D. R., Edwards, T. C., Beard, K. H., Cutler, a and Hess, K. T.: Random forests for classification in ecology, Ecology, 88(11), 2783–2792, 2007.

Daudet, F.-A., Améglio, T., Cochard, H., Archilla, O. and Lacointe, A.: Experimental analysis of the role of water and carbon in tree stem diameter variations, J. Exp. Bot., 56(409), 135–144, 2005.

Davi, H., Barbaroux, C., Francois, C. and Dufrene, E.: The fundamental role of reserves and hydraulic constraints in predicting LAI and carbon allocation in forests, Agric. For. Meteorol., 149(2), 349–361, doi:10.1016/j.agrformet.2008.08.014, 2009.

Davi, H., Dufrêne, E., Granier, a., Le Dantec, V., Barbaroux, C., François, C. and Bréda, N.: Modelling carbon and water cycles in a beech forest, Ecol. Modell., 185(2-4), 387–405, doi:10.1016/j.ecolmodel.2005.01.003, 2005.

David, A.: Modélisation de la croissance ligneuse chez le Hêtre et le Chêne sessile. Master's thesis dissertation., Université Paris-Sud, Orsay., 2011.

Deleuze, C., Pain, O., Dhôte, J. F. and Hervé, J. C.: A flexible radial increment model for individual trees in pure even-aged stands, Ann. For. Sci., 61(4), 327–335, doi:10.1051/forest, 2004.

Delpierre, N., Soudani, K., François, C., Köstner, B., Pontailler, J.-Y., Nikinmaa, E., Misson, L., Aubinet, M., Bernhofer, C., Granier, a., Grünwald, T., Heinesch, B., Longdoz, B., Ourcival, J.-M., Rambal, S., Vesala, T. and Dufrêne, E.: Exceptional carbon uptake in European forests during the warm spring of 2007: a data-model analysis, Glob. Chang. Biol., 15(6), 1455–1474, doi:10.1111/j.1365-2486.2008.01835.x, 2009.

Delpierre, N., Soudani, K., François, C., Le Maire, G., Bernhofer, C., Kutsch, W., Misson, L., Rambal, S., Vesala, T. and Dufrêne, E.: Quantifying the influence of climate and biological drivers on the interannual variability of carbon exchanges in European forests through process-based modelling, Agric. For. Meteorol., 154-155, 99–112, doi:10.1016/j.agrformet.2011.10.010, 2012.

Delpierre, N., Vitasse, Y., Chuine, I., Guillemot, J., Bazot, S., Rutishauser, T. and Rathgeber, C. B. K.: Temperate and boreal forest tree phenology: from organ-scale processes to terrestrial ecosystem models, Ann. For. Sci., doi:10.1007/s13595-015-0477-6, 2015.

Dhôte, J.-F. and Hercé, É. de: Un modèle hyperbolique pour l'ajustement de faisceaux de courbes hauteur-diamètre, Can. J. For. Res., 24(9), 1782–1790, 1994.

Dietze, M. C., Sala, A., Carbone, M. S., Czimczik, C. I., Mantooth, J. A., Richardson, A. D. and Vargas, R.: Nonstructural Carbon in Woody Plants, Annu. Rev. Plant Biol., 65(1), 667–687, doi:10.1146/annurev-arplant-050213-040054, 2014.

Dormann, C. F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J. R. G., Gruber, B., Lafourcade, B. and Leitão, P. J.: Collinearity: a review of methods to deal with it and a simulation study evaluating their performance, Ecography (Cop.)., 36(1), 27–46, 2013.

Drake, J. E., Davis, S. C., Raetz, L. M. and DeLucia, E. H.: Mechanisms of age-related changes in forest production: the influence of physiological and successional changes, Glob. Chang. Biol., 17(4), 1522–1535, doi:10.1111/j.1365-2486.2010.02342.x, 2011.

Drobyshev, I., Gewehr, S., Berninger, F. and Bergeron, Y.: Species specific growth responses of black spruce and trembling aspen may enhance resilience of boreal forest to climate change, J. Ecol., 101(1), 231–242, 2013.

Dufrêne, E., Davi, H., Francois, C., Le Maire, G., Le Dantec, V. and Granier, A.: Modelling carbon and water cycles in a Beech forest. Part I: Model description and uncertainty analysis on modelled NEE, Ecol. Modell., 185(2-4), 407–436, doi:10.1016/j.ecolmodel.2005.01.004, 2005.

Enquist, B. J.: Universal scaling in tree and vascular plant allometry: toward a general quantitative theory linking plant form and function from cells to ecosystems, Tree Physiol., 22, 1045–1064, 2002.

Fatichi, S., Leuzinger, S. and Körner, C.: Moving beyond photosynthesis: from carbon source to sink-driven vegetation modeling, New Phytol., 201(4), 1086–1095, doi:10.1111/nph.12614, 2014.

Franklin, O., Johansson, J., Dewar, R. C., Dieckmann, U., McMurtrie, R. E., Brännström, Å. and Dybzinski, R.: Modeling carbon allocation in trees: a search for principles, Tree Physiol., 32(6), 648–666, 2012.

Friend, A. D., Lucht, W., Rademacher, T. T., Keribin, R., Betts, R., Cadule, P., Ciais, P., Clark, D. B., Dankers, R., Falloon, P. D., Ito, A., Kahana, R., Kleidon, A., Lomas, M. R., Nishina, K., Ostberg, S., Pavlick, R., Peylin, P., Schaphoff, S., Vuichard, N., Warszawski, L., Wiltshire, A. and Woodward, F. I.: Carbon residence time dominates uncertainty in terrestrial vegetation responses to future climate and atmospheric CO2, Proc. Natl. Acad. Sci., doi: 10.1073/pnas.1222477110, doi:10.1073/pnas.1222477110, 2013.

Gaucherel, C., Guiot, J. and Misson, L.: Changes of the potential distribution area of French Mediterranean forests under global warming, Biogeosciences, 5(6), 1493–1504, 2008.

Genet, H., Bréda, N. and Dufrêne, E.: Age-related variation in carbon allocation at tree and stand scales in beech (Fagus sylvatica L.) and sessile oak (Quercus petraea (Matt.) Liebl.) using a chronosequence approach., Tree Physiol., 30(2), 177–92, doi:10.1093/treephys/tpp105, 2010.

Genuer, R., Poggi, J.-M. and Tuleau-Malot, C.: Variable selection using random forests, Pattern Recognit. Lett., 31(14), 2225–2236, 2010.

Gielen, B., De Vos, B., Campioli, M., Neirynck, J., Papale, D., Verstraeten, a., Ceulemans, R. and Janssens, I. a.: Biometric and eddy covariance-based assessment of decadal carbon sequestration of a temperate Scots pine forest, Agric. For. Meteorol., 174-175, 135–143, doi:10.1016/j.agrformet.2013.02.008, 2013.

Gough, C. M., Flower, C. E., Vogel, C. S., Dragoni, D. and Curtis, P. S.: Whole-ecosystem labile carbon production in a north temperate deciduous forest, Agric. For. Meteorol., 149(9), 1531–1540, doi:10.1016/j.agrformet.2009.04.006, 2009.

Graham, M. H.: Confronting multicollinearity in ecological multiple regression, Ecology, 84(11), 2809–2815, 2003.

Granier, A., Bréda, N., Biron, P. and Villette, S.: A lumped water balance model to evaluate duration and intensity of drought constraints in forest stands, Ecol. Modell., 116(2), 269–283, 1999.

Granier, A., Bréda, N., Longdoz, B., Gross, P. and Ngao, J.: Ten years of fluxes and stand growth in a young beech forest at Hesse, North-eastern France, Ann. For. Sci., 64(7), 704–704 [online] Available from: http://www.springerlink.com/index/HX4J1005V68TK726.pdf, 2008.

Grote, R., Kiese, R., Grünwald, T., Ourcival, J.-M. and Granier, A.: Modelling forest carbon balances considering tree mortality and removal, Agric. For. Meteorol., 151(2), 179–190, doi:10.1016/j.agrformet.2010.10.002, 2011.

Guillemot, J., Delpierre, N., Vallet, P., François, C., Martin-StPaul, N. K., Soudani, K., Nicolas, M., Badeau, V. and Dufrêne, E.: Assessing the effects of management on forest growth across France: insights from a new functional–structural model, Ann. Bot., 114(4), 779–793, doi:10.1093/aob/mcu059, 2014.

Hicke, J. A., Allen, C. D., Desai, A. R., Dietze, M. C., Hall, R. J., Kashian, D. M., Moore, D., Raffa, K. F., Sturrock, R. N. and Vogelmann, J.: Effects of biotic disturbances on forest carbon cycling in the United States and Canada, Glob. Chang. Biol., 18(1), 7–34, 2012.

Hoch, G., Richter, A. and Körner, C.: Non-structural carbon compounds in temperate forest trees, Plant. Cell Environ., 26(7), 1067–1081, 2003.

Hoch, G., Siegwolf, R. T. W., Keel, S. G., Körner, C. and Han, Q.: Fruit production in three masting tree species does not rely on stored carbon reserves., Oecologia, 171(3), 653–62, doi:10.1007/s00442-012-2579-2, 2013.

Hölttä, T., Mäkinen, H., Nöjd, P., Mäkelä, A. and Nikinmaa, E.: A physiological model of softwood cambial growth., Tree Physiol., 30(10), 1235–52, doi:10.1093/treephys/tpq068, 2010.

De Kauwe, M. G., Medlyn, B. E., Zaehle, S., Walker, A. P., Dietze, M. C., Wang, Y., Luo, Y., Jain, A. K., El-Masri, B. and Hickler, T.: Where does the carbon go? A model–data intercomparison of vegetation carbon allocation and turnover processes at two temperate forest free-air CO2 enrichment sites, New Phytol., doi: 10.1111/nph.12847, 2014.

Keenan, T. F., Baker, I., Barr, A., Ciais, P., Davis, K., Dietze, M., Dragoni, D., Gough, C. M., Grant, R. and Hollinger, D.: Terrestrial biosphere model performance for inter-annual variability of land-atmosphere CO2 exchange, Glob. Chang. Biol., 18(6), 1971–1987, 2012.

Keyes, M. R. and Grier, C. C.: Above- and below-ground net production in 40-year-old Douglas-fir stands on low and high productivity sites, Can. J. For. Res., 11(3), 599–605, doi:10.1139/x81-082, 1981.

Körner, C.: Carbon limitation in trees, J. Ecol., 91(1), 4–17 [online] Available from: http://www.blackwell-synergy.com/links/doi/10.1046%2Fj.1365-2745.2003.00742.x, 2003.

Körner, C.: Winter crop growth at low temperature may hold the answer for alpine treeline formation, Plant Ecol. Divers., 1(1), 3–11, doi:10.1080/17550870802273411, 2008.

Krinner, G., Viovy, N., de Noblet-Ducoudré, N., Ogée, J., Polcher, J., Friedlingstein, P., Ciais, P., Sitch, S. and Prentice, I. C.: A dynamic global vegetation model for studies of the coupled atmosphere-biosphere system, Global Biogeochem. Cycles, 19(1), 2005.

Kudo, K., Nabeshima, E., Begum, S., Yamagishi, Y., Nakaba, S., Oribe, Y., Yasue, K. and Funada, R.: The effects of localized heating and disbudding on cambial reactivation and formation of earlywood vessels in seedlings of the deciduous ring-porous hardwood, Quercus serrata, Ann. Bot. , 113 (6), 1021–1027 [online] Available from: http://aob.oxfordjournals.org/content/113/6/1021.abstract, 2014.

Kunstler, G., Albert, C. H., Courbaud, B., Lavergne, S., Thuiller, W., Vieilledent, G., Zimmermann, N. E. and Coomes, D. a.: Effects of competition on tree radial-growth vary in importance but not in intensity along climatic gradients, J. Ecol., 99(1), 300–312, doi:10.1111/j.1365-2745.2010.01751.x, 2011.

Lebourgeois, F.: RENECOFOR - Etude dendrochronologique des 102 peuplements du réseau, Off. Natl. des forêts, Département des Rech. Tech., 1997.

Lebourgeois, F., Bréda, N., Ulrich, E. and Granier, A.: Climate-tree-growth relationships of European beech (Fagus sylvatica L.) in the French Permanent Plot Network (RENECOFOR), Trees, 19(4), 385–401, doi:10.1007/s00468-004-0397-9, 2005.

Lempereur, M., Martin-StPaul, N. K., Damesin, C., Joffre, R., Ourcival, J. M., Rocheteau, A. and Rambal, S.: Growth duration is a better predictor of stem increment than carbon supply in a Mediterranean oak forest: implications for assessing forest productivity under climate change, New Phytol., In press, doi:10.1111/nph.13400, 2015.

Leuschner, C., Backes, K., Hertel, D., Schipka, F., Schmitt, U., Terborg, O. and Runge, M.: Drought responses at leaf, stem and fine root levels of competitive Fagus sylvatica L. and Quercus petraea (Matt.) Liebl. trees in dry and wet years, For. Ecol. Manage., 149(1), 33–46, 2001.

Leuzinger, S. and Hättenschwiler, S.: Beyond global change: lessons from 25 years of CO2 research., Oecologia, 171(3), 639–51, doi:10.1007/s00442-012-2584-5, 2013.

Leuzinger, S., Manusch, C., Bugmann, H. and Wolf, A.: A sink-limited growth model improves biomass estimation along boreal and alpine tree lines, Glob. Ecol. Biogeogr., 22(8), 924–932, doi:10.1111/geb.12047, 2013.

Liaw, A. and Wiener, M.: The randomforest package, R News, 2(3), 18–22, 2002.

Litton, C. M., Raich, J. W. and Ryan, M. G.: Carbon allocation in forest ecosystems, Glob. Chang. Biol., 13(10), 2089–2109, doi:10.1111/j.1365-2486.2007.01420.x, 2007.

Lockhart, J. A.: An analysis of irreversible plant cell elongation, J. Theor. Biol., 8(2), 264–275, 1965.

López, B. C., Sabate, S. and Gracia, C. A.: Thinning effects on carbon allocation to fine roots in a Quercus ilex forest, Tree Physiol. , 23 (17), 1217–1224, doi:10.1093/treephys/23.17.1217, 2003.

Lupi, C., Morin, H., Deslauriers, A. and Rossi, S.: Xylem phenology and wood production: resolving the chicken-or-egg dilemma., Plant. Cell Environ., 33(10), 1721–30, doi:10.1111/j.1365-3040.2010.02176.x, 2010.

Luyssaert, S., Inglima, I., Jung, M., Richardson, a. D., Reichstein, M., Papale, D., Piao, S. L., Schulze, E.-D., Wingate, L., Matteucci, G., Aragao, L., Aubinet, M., Beer, C., Bernhofer, C., Black, K. G., Bonal, D., Bonnefond, J.-M., Chambers, J., Ciais, P., Cook, B., Davis, K. J., Dolman, a. J., Gielen, B., Goulden, M., Grace, J., Granier, A., Grelle, A., Griffis, T., Grünwald, T., Guidolotti, G., Hanson, P. J., Harding, R., Hollinger, D. Y., Hutyra, L. R., Kolari, P., Kruijt, B., Kutsch, W., Lagergren, F., Laurila, T., Law, B. E., Le Maire, G., Lindroth, A., Loustau, D., Malhi, Y., Mateus, J., Migliavacca, M., Misson, L., Montagnani, L., Moncrieff, J., Moors, E., Munger, J.

W., Nikinmaa, E., Ollinger, S. V., Pita, G., Rebmann, C., Roupsard, O., Saigusa, N., Sanz, M. J., Seufert, G., Sierra, C., Smith, M.-L., Tang, J., Valentini, R., Vesala, T. and Janssens, I. A.: CO2 balance of boreal, temperate, and tropical forests derived from a global database, Glob. Chang. Biol., 13(12), 2509–2537, doi:10.1111/j.1365-2486.2007.01439.x, 2007.

Magnani, F., Mencuccini, M. and Grace, J.: Age-related decline in stand productivity: the role of structural acclimation under hydraulic constraints, Plant. Cell Environ., 23(3), 251–263, 2000.

Martin-StPaul, N. K., Limousin, J.-M., Vogt-Schilb, H., Rodríguez-Calcerrada, J., Rambal, S., Longepierre, D. and Misson, L.: The temporal response to drought in a Mediterranean evergreen tree: comparing a regional precipitation gradient and a throughfall exclusion experiment., Glob. Chang. Biol., 19(8), 2413–26, doi:10.1111/gcb.12215, 2013.

Mérian, P., Bontemps, J.-D., Bergès, L. and Lebourgeois, F.: Spatial variation and temporal instability in climate-growth relationships of sessile oak (Quercus petraea [Matt.] Liebl.) under temperate conditions, Plant Ecol., 212(11), 1855–1871, doi:10.1007/s11258-011-9959-2, 2011.

Michelot, A., Simard, S., Rathgeber, C., Dufrêne, E. and Damesin, C.: Comparing the intra-annual wood formation of three European species (Fagus sylvatica, Quercus petraea and Pinus sylvestris) as related to leaf phenology and non-structural carbohydrate dynamics., Tree Physiol., 32(8), 1033–45, doi:10.1093/treephys/tps052, 2012.

Millard, P. and Grelet, G.-A.: Nitrogen storage and remobilization by trees: ecophysiological relevance in a changing world., Tree Physiol., 30(9), 1083–95, doi:10.1093/treephys/tpq042, 2010.

Muller, B., Pantin, F., Génard, M., Turc, O., Freixes, S., Piques, M. and Gibon, Y.: Water deficits uncouple growth from photosynthesis, increase C content, and modify the relationships between C and growth in sink organs., J. Exp. Bot., 62(6), 1715–29, doi:10.1093/jxb/erq438, 2011.

Mund, M., Kutsch, W. L., Wirth, C., Kahl, T., Knohl, a, Skomarkova, M. V and Schulze, E.-D.: The influence of climate and fructification on the inter-annual variability of stem growth and net primary productivity in an old-growth, mixed beech forest., Tree Physiol., 30(6), 689–704, doi:10.1093/treephys/tpq027, 2010.

Ohtsuka, T., Saigusa, N. and Koizumi, H.: On linking multiyear biometric measurements of tree growth with eddy covariance-based net ecosystem production, Glob. Chang. Biol., 15(4), 1015–1024, 2009.

Palacio, S., Hernández, R., Maestro-Martínez, M. and Camarero, J. J.: Fast replenishment of initial carbon stores after defoliation by the pine processionary moth and its relationship to the re-growth ability of trees, Trees, 26(5), 1627–1640, 2012.

Palacio, S., Hoch, G., Sala, A., Körner, C. and Millard, P.: Does carbon storage limit tree growth?, New Phytol., 201(4), 1096–1100, doi:10.1111/nph.12602, 2014.

Pan, Y., Birdsey, R. a, Fang, J., Houghton, R., Kauppi, P. E., Kurz, W. a, Phillips, O. L., Shvidenko, A., Lewis, S. L., Canadell, J. G., Ciais, P., Jackson, R. B., Pacala, S. W., McGuire, a D., Piao, S., Rautiainen, A., Sitch, S. and Hayes, D.: A large and persistent carbon sink in the world’s forests., Science, 333(6045), 988–93, doi:10.1126/science.1201609, 2011.

Pasquet, K.: Determination des chuttes de littières sur le réseau RENECOFOR de 1995 à 2002, Off. Natl. des forêts, Département des Rech. Tech., 2002.

Peichl, M., Brodeur, J. J., Khomik, M. and Arain, M. A.: Biometric and eddy-covariance based estimates of carbon fluxes in an age-sequence of temperate pine forests, Agric. For. Meteorol., 150(7-8), 952–965, doi:10.1016/j.agrformet.2010.03.002, 2010.

Ponette, Q.: Chimie des sols dans les 102 peuplements du réseau, Office National des Forêts-Direction Technique., 1997.

Rambal, S., Joffre, R., Ourcival, J. M., Cavender-Bares, J. and Rocheteau, A.: The growth respiration component in eddy CO2 flux from a Quercus ilex mediterranean forest, Glob. Chang. Biol., 10(9), 1460–1469, 2004.

Richardson, A. D., Carbone, M. S., Keenan, T. F., Czimczik, C. I., Hollinger, D. Y., Murakami, P., Schaberg, P. G. and Xu, X.: Seasonal dynamics and age of stemwood nonstructural carbohydrates in temperate forest trees, New Phytol., 197(3), 850–861, 2013.

Rocha, A. V., Goulden, M. L., Dunn, A. L. and Wofsy, S. C.: On linking interannual tree ring variability with observations of whole-forest CO2 flux, Glob. Chang. Biol., 12(8), 1378–1389, doi:10.1111/j.1365-2486.2006.01179.x, 2006.

Rossi, S., Anfodillo, T., Cufar, K., Cuny, H. E., Deslauriers, A., Fonti, P., Frank, D., Gricar, J., Gruber, A., King, G. M., Krause, C., Morin, H., Oberhuber, W., Prislan, P. and Rathgeber, C. B. K.: A meta-analysis of cambium phenology and growth: linear and non-linear patterns in conifers of the northern hemisphere., Ann. Bot., 112(9), 1911–20, doi:10.1093/aob/mct243, 2013.

Rossi, S., Morin, H., Deslauriers, A. and Plourde, P.-Y.: Predicting xylem phenology in black spruce under climate warming, Glob. Chang. Biol., 17(1), 614–625, 2011.

Ryan, M. G., Phillips, N. and Bond, B. J.: The hydraulic limitation hypothesis revisited, Plant Cell Environ., 29(3), 367–81, doi:10.1111/j.1365-3040.2005.01478.x, 2006.

Sala, A., Woodruff, D. R. and Meinzer, F. C.: Carbon dynamics in trees: feast or famine?, Tree Physiol., 32(6), 1–12, doi:10.1093/treephys/tpr143, 2012.

Schiestl-Aalto, P., Kulmala, L., Mäkinen, H., Nikinmaa, E. and Mäkelä, A.: CASSIA–a dynamic model for predicting intra-annual sink demand and interannual growth variation in Scots pine, New Phytol., doi:10.1111/nph.13275, 2015.

Seynave, I., Gégout, J., Hervé, J., Drapier, J., Bruno, É. and Dumé, G.: Picea abies site index prediction by environmental factors and understorey vegetation : a two-scale approach based on survey databases, , 1678, 1669–1678, doi:10.1139/X05-088, 2005.

Sitch, S., Smith, B., Prentice, I. C., Arneth, A., Bondeau, A., Cramer, W., Kaplan, J. O., Levis, S., Lucht, W. and Sykes, M. T.: Evaluation of ecosystem dynamics, plant geography and terrestrial carbon cycling in the LPJ dynamic global vegetation model, Glob. Chang. Biol., 9(2), 161–185, 2003.

Tang, J., Luyssaert, S., Richardson, A. D., Kutsch, W. and Janssens, I. A.: Steeper declines in forest photosynthesis than respiration explain age-driven decreases in forest growth, Proc. Natl. Acad. Sci., doi: 10.1073/pnas.1320761111, 2014.

Tardieu, F., Granier, C. and Muller, B.: Water deficit and growth. Co-ordinating processes without an orchestrator?, Curr. Opin. Plant Biol., 14(3), 283–289, 2011.

Thomas, S. C.: Age-related changes in tree growth and functional biology: the role of reproduction, in Size-and age-related changes in tree structure and function, pp. 33–64, Springer., 2011.

Ulrich, E.: Organization of forest system monitoring in France-the RENECOFOR network, in World Forestry Congress, Antalya, TR., 1997.

Vallet, P., Dhôte, J.-F., Moguédec, G. Le, Ravart, M. and Pignard, G.: Development of total aboveground volume equations for seven important forest tree species in France, For. Ecol. Manage., 229(1-3), 98–110, doi:10.1016/j.foreco.2006.03.013, 2006.

Vicca, S., Luyssaert, S., Peñuelas, J., Campioli, M., Chapin, F. S., Ciais, P., Heinemeyer, a, Högberg, P., Kutsch, W. L., Law, B. E., Malhi, Y., Papale, D., Piao, S. L., Reichstein, M., Schulze, E. D. and Janssens, I. a: Fertile forests produce biomass more efficiently., Ecol. Lett., 15(6), 520–6, doi:10.1111/j.1461-0248.2012.01775.x, 2012.

Vidal, J.-P., Martin, E., Franchistéguy, L., Baillon, M. and Soubeyroux, J.-M.: A 50-year high-resolution atmospheric reanalysis over France with the Safran system, Int. J. Climatol., 30(11), 1627–1644, doi:10.1002/joc.2003, 2010.

Vitasse, Y., Lenz, A., Kollas, C., Randin, C. F., Hoch, G. and Körner, C.: Genetic vs. non-genetic responses of leaf morphology and growth to elevation in temperate tree species, Funct. Ecol., 28(1), 243–252, 2014.

Wiley, E. and Helliker, B.: A re-evaluation of carbon storage in trees lends greater support for carbon limitation to growth, New Phytol., 195(2), 285–289, 2012.

Wiley, E., Huepenbecker, S., Casper, B. B. and Helliker, B. R.: The effects of defoliation on carbon allocation: can carbon limitation reduce growth in favour of storage?, Tree Physiol., 33(11), 1216–1228, 2013.

Wilhelmsson, L., Arlinger, J., Spångberg, K., Lundqvist, S.-O., Grahn, T., Hedenberg, Ö. and Olsson, L.: Models for Predicting Wood Properties in Stems of Picea abies and Pinus sylvestris in Sweden, Scand. J. For. Res., 17(4), 330–350, doi:10.1080/02827580260138080, 2002.

Wolf, A., Field, C. B. and Berry, J. A.: Allometric growth and allocation in forests: a perspective from FLUXNET, Ecol. Appl., 21(5), 1546–1556, 2011.

Woodruff, D. R., Bond, B. J. and Meinzer, F. C.: Does turgor limit growth in tall trees?, Plant. Cell Environ., 27(2), 229–236, 2004.

Woodruff, D. R. and Meinzer, F. C.: Size-dependent changes in biophysical control of tree growth: the role of turgor, in Size-and age-related changes in tree structure and function, pp. 363–384, Springer., 2011.

Würth, M. K. R., Peláez-Riedl, S., Wright, S. J. and Körner, C.: Non-structural carbohydrate pools in a tropical forest., Oecologia, 143(1), 11–24, doi:10.1007/s00442-004-1773-2, 2005.

Xu, C., Turnbull, M. H., Tissue, D. T., Lewis, J. D., Carson, R., Schuster, W. S. F., Whitehead, D., Walcroft, A. S., Li, J. and Griffin, K. L.: Age-related decline of stand biomass accumulation is primarily due to mortality and not to reduction in NPP associated with individual tree physiology, tree growth or stand structure in a Quercus-dominated forest, J. Ecol., 100(2), 428–440, 2012.

Zaehle, S., Sitch, S., Prentice, I. C., Liski, J., Cramer, W., Erhard, M., Hickler, T. and Smith, B.: The importance of age-related decline in forest NPP for modeling regional carbon balances, Ecol. Appl., 16(4), 1555–1574, 2006.

Zha, T. S., Barr, a. G., Bernier, P.-Y., Lavigne, M. B., Trofymow, J. a., Amiro, B. D., Arain, M. a., Bhatti, J. S., Black, T. a., Margolis, H. a., McCaughey, J. H., Xing, Z. S., Van Rees, K. C. J. and Coursolle, C.: Gross and aboveground net primary production at Canadian forest carbon flux sites, Agric. For. Meteorol., 174-175, 54–64, doi:10.1016/j.agrformet.2013.02.004, 2013.

Zhang, S.-Y., Owoundi, R. E., Nepveu, G., Mothe, F. and Dhôte, J.-F.: Modelling wood density in European oak (Quercuspetraea and Quercusrobur) and simulating the silvicultural influence, Can. J. For. Res., 23(12), 2587–2593, doi:10.1139/x93-320, 1993.

Zweifel, R., Eugster, W., Etzold, S., Dobbertin, M., Buchmann, N. and Häsler, R.: Link between continuous stem radius changes and net ecosystem productivity of a subalpine Norway spruce forest in the Swiss Alps, New Phytol., 187(3), 819–830, 2010.

Zweifel, R., Zimmermann, L., Zeugin, F. and Newbery, D. M.: Intra-annual radial growth and water relations of trees: implications towards a growth mechanism., J. Exp. Bot., 57(6), 1445–59, doi:10.1093/jxb/erj125, 2006.

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.

~~**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 ± 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.

~~**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)~~

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	m²	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 ~~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_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

Mis en forme : Police :11 pt, Italique

Mis en forme : Indice

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

~~Figure 2. **Location of the studied sites**.~~

~~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}).~~

~~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.~~

~~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.~~

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