

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

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16 **Abstract**

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

24 The drivers of stand biomass growth were assessed on both inter-site and inter-annual scales. Our
25 dataset included field measurements performed at 49 sites (931 site-years) and it was
26 complemented with process-based simulations when possible explanatory variables could not be
27 directly measured. Specifically, the relative influences of tree C balance (source control), direct
28 environmental control (water and temperature controls of sink activity) and allocation
29 adjustments related to age, past climate conditions, competition intensity and soil nutrient
30 availability on growth were quantified.

31 The inter-site variability in the stand C allocation to wood was predominantly driven by age-
32 related decline. The direct effects of temperature and water stress on sink activity (i.e., effects
33 independent from their effects on the C supply) exerted a strong influence on the annual stand
34 wood growth in all of the species considered, including deciduous temperate species. The lagged
35 effect of the past environmental conditions (e.g., the previous year's water stress and low C
36 uptake) significantly affected the annual C allocation to wood. The C supply appeared to strongly
37 limit growth only in temperate deciduous species.

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

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50 1 Introduction

51 Forests play a critical role in the global carbon (C) cycle. Inventory-based estimates indicate that
52 established forests have been a persistent carbon sink for decades, sequestering almost 30% of the
53 world's total anthropogenic C emissions between 1990 and 2007 (Pan et al., 2011). The fate of
54 the sequestered C is highly dependent on the C dynamic in trees, which determines the residence
55 time of C in forest ecosystems. Despite its importance for the future terrestrial C sink (Carvalhais
56 et al., 2014; Friend et al., 2013), the partitioning of C among tree organs and ecosystem
57 respiration remains poorly understood (Brüggemann et al., 2011). In particular, there has been
58 considerable amount of debate regarding the physiological mechanisms that drive the increment
59 of the forest woody biomass (Palacio et al., 2014; Wiley and Helliker, 2012). The fraction of
60 assimilated C stored in woody biomass can be inferred by combining biometric measurements
61 with estimates of the C exchange between the ecosystem and atmosphere, based on the eddy-
62 covariance (EC) technique (Babst et al., 2014; Litton et al., 2007; Wolf et al., 2011). Global
63 meta-analyses (that included data from various biomes and species) have revealed a strong
64 correlation between the observed gross primary production (GPP) and the woody biomass
65 increment (Litton et al., 2007; Zha et al., 2013). Accordingly, growth has long been thought to be
66 C limited, because of the hypothesized causal link between C supply and growth (i.e., source
67 control, Sala *et al.* 2012). The environmental factors that have been reported to affect growth
68 (soil water content, temperature, nutrient content, light and CO₂) were therefore supposed to
69 operate through their effects on photosynthesis and respiration fluxes. This C-centric paradigm
70 underlies most of the C allocation rules formalized in the terrestrial biosphere models (TBMs)
71 that are currently used to evaluate the effects of global changes on forests (Clark et al., 2011;
72 Dufrêne et al., 2005; De Kauwe et al., 2014; Krinner et al., 2005; Sitch et al., 2003).

73 Source control of wood growth is a mechanism that has been questioned by several
74 authors, who argue that cambial activity is more sensitive than C assimilation to several
75 environmental stressors (Fatichi et al., 2014). In particular, the decrease in cell turgor that occurs
76 because of water stress strongly affects cell division and expansion (Woodruff and Meinzer,
77 2011) before there is any strong reduction in the gas exchange (Muller et al., 2011; Tardieu et al.,
78 2011). Similarly, cell division is affected by low temperatures before it is affected by
79 photosynthesis (Körner, 2008). The onset of cambial activity is also known to be highly

80 responsive to temperature (Delpierre et al., 2015; Kudo et al., 2014; Lempereur et al., 2015; Rossi
81 et al., 2011) and, in turn, may partly determine annual cell production and wood growth (Lupi et
82 al., 2010; Rossi et al., 2013). Finally, the quality and quantity of available soil nutrients,
83 particularly nitrogen (N), could affect growth independently of their impacts on C assimilation,
84 because of the relatively constrained stoichiometry of tree biomass (Leuzinger and
85 Hättenschwiler, 2013). These studies suggest that growth is limited by the direct effects of
86 environmental factors (i.e., sink control). However, numerous key environmental factors (e.g.,
87 nutrients, temperature and water) affect both sink and source activities, and it is thus difficult to
88 determine whether wood growth is more related to C supply or to the intrinsic environmental
89 sensitivity of cambium functioning (Fatichi et al., 2014). The extent to which wood growth is
90 under source or sink control is of paramount importance for predicting how trees will respond to
91 global changes and specifically how increasing atmospheric CO₂ will affect forest productivity
92 and the future terrestrial C sink. The implementation of the respective roles of source and sink
93 controls on growth in TBMs is therefore a substantial challenge for modellers, because it may
94 determine our ability to project future forest C sink, diebacks and distributions (Cheaib et al.,
95 2012; Fatichi et al., 2014; Leuzinger et al., 2013).

96 The allocation of assimilated C within forest ecosystems is a complex, integrative process
97 that can be described by several non-exclusive principles (Franklin et al., 2012), including i)
98 allometric scaling, ii) functional balance and iii) evolution-based optimal responses. i) The
99 allometric scaling principle is based on the assumption that biophysical laws determine C
100 partitioning among the different forest compartments. Important allocation constraints include
101 vascular network optimality (Enquist, 2002) and functional homeostasis in water transport
102 (Magnani et al., 2000). ii) The functional balance principle suggests that the organ responsible for
103 acquiring the limiting resource is preferentially allocated C. Consistent with this principle, higher
104 C allocation to fine roots at the expense of C allocation to wood growth has been reported for
105 poor or dry soils (Chen et al., 2013; Keyes and Grier, 1981). In addition, a possibly greater
106 allocation to root symbionts and exudates at the expense of biomass production has also been
107 reported (Vicca et al., 2012). iii) Finally, the optimal response principle postulates that allocation
108 maximizes fitness in a fixed environment. This hypothesis agrees with the idea that a dynamic
109 reserve pool act as temporary storage, possibly at the expense of growth, to promote long-term
110 tree survival (Chapin et al., 1990; Sala et al., 2012). Indeed, time lags between C uptake and

111 growth have been reported (Gough et al., 2009; Richardson et al., 2013). The optimal response
112 principle is consistent with several well-known life history traits, such as preferential allocation
113 to reproduction in ageing plants, which could lead to age-related declines in woody biomass
114 allocation (Genet et al., 2010; Thomas, 2011). The woody biomass increment therefore appears to
115 be under the control of multiple factors. The effects of these drivers are expected to strongly vary
116 in space and time. Consequently, studies have reported conflicting relationships between the C
117 supply and wood growth (Gielen et al., 2013; Richardson et al., 2013), ranging from no
118 significant relationships (Mund et al., 2010; Rocha et al., 2006) to close relationships on seasonal
119 (Babst et al., 2014; Granier et al., 2008; Zweifel et al., 2010) or annual (Ohtsuka et al., 2009;
120 Peichl et al., 2010; Zweifel et al., 2010) time scales. Determining the key processes that affect
121 wood growth on different spatio-temporal scales is necessary to explain these apparently
122 contradictory results using a common framework. Moreover, investigations should be conducted
123 at the species level, because phylogeny may strongly constrain forest functioning (Carnicer et al.,
124 2013; Drobyshev et al., 2013) and induce different growth determinants among taxa (Genet et al.,
125 2010).

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

142 and *Quercus ilex*, an evergreen broadleaf species from Mediterranean forests. Specifically, the
143 relative influence of annual and seasonal (from one month to the year) tree C balance (source
144 control), direct environmental control (water and temperature effects on sink activity) and
145 allocation adjustments related to age, past climate conditions, competition intensity and soil
146 nutrient availability on tree growth were considered (Fig. 1). We aimed to (1) quantify the
147 relative contributions of source and sink controls to the spatio-temporal dynamic of forest wood
148 growth across a wide range of environmental contexts and (2) provide information that can be
149 used to refine the representation of forest growth causalities in TBMs.

150

151 **2 Materials and methods**

152 We based our analyses on three complementary data sources: field measurements, climatic
153 variables from atmospheric reanalysis (Vidal et al., 2010) and process-based simulation data.
154 This hybrid approach allowed us to assess and disentangle the effects of previously reported
155 environmental and endogenous drivers of C allocation to wood growth (Fig. 1).

156

157 **2.1 Study sites and field data**

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

162

163 **2.1.1 Growth measurements and historical stand growth reconstruction**

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

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

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

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

195

196 **2.1.2 Measurements of stand characteristics**

197 The stand measurements included the soil water holding capacity (SWHC), leaf area index (LAI),
198 leaf N content (LNC) and soil nutrient availability (SNA). The SWHC was estimated via the soil
199 depth and texture measured at two soil pits per plot (Brêthes and Ulrich, 1997). The LAI was
200 estimated from litter collection (Pasquet, 2002), and the sunlit LNC was determined annually for
201 8 trees between 1993 and 1997 (Croisé et al., 1999).

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

207

208 **2.2 Climate data**

209 The following meteorological variables at the hourly temporal scale (with 8km spatial resolution)
210 were obtained from the SAFRAN atmospheric reanalysis (Vidal et al., 2010): global radiation,
211 rainfall, wind speed, air humidity and air temperature. Temperature, which was related to the
212 average altitudes of the SAFRAN cells, was corrected using plot-specific elevation measurements
213 (assuming a lapse rate of 0.6 °K per 100 m, Supplement S1). These variables were used for
214 climate forcing in the CASTANEA model (Dufrêne *et al.* 2005, see the following section). In
215 addition, two annual temperature indices were used as proxies of winter frost damage and low
216 temperature stress during the growing period (*frost* and *templim_{gp}*, respectively, Table 2).

217

218 **2.3 Process-based simulation data**

219 We used the CASTANEA model to simulate an ensemble of diagnostic variables that are related
220 to the C source and sink activity of forest stands. The eco-physiological process-based
221 CASTANEA model aims to simulate C and water fluxes and stocks of a monospecific, same-

222 aged forest stand on a rotation time scale. The hourly stand-atmosphere C fluxes predicted by the
223 CASTANEA model have been thoroughly validated using EC data from throughout Europe
224 (Davi et al., 2005; Delpierre et al., 2009, 2012). Importantly, the biophysical hypotheses that
225 were formalized in this model are able to reproduce the interplay of the complex mechanisms that
226 lead to inter-annual variability in the stand C balance (Delpierre et al., 2012); modelling this
227 interplay has been recognized as a substantial challenge for TBMs (Keenan et al., 2012). A
228 complete description of CASTANEA is provided in Dufrêne *et al.* (2005), and subsequent
229 modifications are described in Davi *et al.* (2009) and Delpierre *et al.* (2012). For the purpose of
230 the present study, CASTANEA was parameterized with site-specific SWHC and LNC values.
231 The measured LAI and total woody biomass were used to initialize the model simulations. The
232 model's ability to reproduce the annual variability in LAI and the forest growth has been recently
233 validated (Guillemot et al., 2014). Nevertheless, the annual standing woody biomass was forced
234 to conform to the observed values, because the model was used for diagnostic purposes in this
235 study.

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

- 237 1. *The elementary components of the tree C balance.* These components included the GPP,
238 autotrophic respiration (R_a), and net balance (i.e., net primary productivity, $NPP = GPP -$
239 R_a). For a given year y , we aggregated the hourly simulated C fluxes over different
240 seasonal time periods, with starting days that ranged from 30 to 190 and ending days that
241 ranged from 190 to 350, at a 2-day resolution. The C fluxes were also summed i) for the
242 species-specific biomass growth periods reported in the literature (GPP_{gp} , $R_{a_{gp}}$ and
243 NPP_{gp} , Supplement S6) and ii) for the entire preceding year ($y-1$) as a proxy of the forest
244 C status induced by past climate conditions (lagged effect, GPP_{y-1} , $R_{a_{y-1}}$ and NPP_{y-1}).
245
- 246 2. *Bioclimatic water stress indices.* These indices included the intensity and duration of
247 water stress ($WS_{int_{gp}}$ and $WS_{per_{gp}}$, respectively, Supplement S7) during species-
248 specific growing periods that have been reported in the literature (Supplement S6). The
249 CASTANEA model simulated the daily soil water balance, based on a bucket soil sub-
250 model with 2 layers (a top soil layer and a total soil layer that includes the top soil layer,

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

253

$$254 \quad reduc_t = \max\left(0, \min\left(1, \frac{SWC_t - SWC_{wilt}}{0.4 \times (SWC_{fc} - SWC_{wilt})}\right)\right)$$

255

256 where SWC_t is the soil water content on day t (mm), SWC_{wilt} is the soil water content at
257 the wilting point (mm) and SWC_{fc} is the soil water content at field capacity (mm).

258 $WS_{per_{gp}}$ is the number of days of the current growth period during which the soil water
259 content was less than 60% of the soil water holding capacity (Table 2, modified from
260 Mund et al., (2010)). Water stress indices were also calculated for the entire preceding
261 year (lagged effect of water stress, $WS_{int_{y-1}}$ and $WS_{per_{y-1}}$).

262

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

266

267 **2.4 Statistical analyses**

268 **2.4.1 General overview**

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

278 temporally to determine the factors that were responsible for variability in the inter-annual
279 biomass growth.

280 Because many environmental factors affect both forest sink and source activities, there may be
281 strong covariance among the tree C balance and proxies of environmental stress (Fatichi et al.,
282 2014) that could hamper the inferential power of classical statistical tests (Graham, 2003).
283 However, the explanatory variables used in this study generally had correlation coefficients of
284 less than 0.7, the level above which collinearity begins to severely affect model performance
285 (Dormann et al., 2013). One exception was the correlation of components of the tree C balance
286 (because $NPP = GPP - Ra$). Consequently, the tree C balance components were introduced one at
287 a time into the models. In addition, temporal growth dependencies were evaluated using the
288 random forest (RF) learning method (Breiman, 2001). A number of studies have empirically
289 demonstrated the effectiveness of RF at identifying the “true” predictors among a large number
290 of correlated candidate predictors (e.g., Archer and Kimes, 2008; Cutler et al., 2007; Genuer et
291 al., 2010). The explanatory variables considered in our spatial and temporal analyses are
292 presented in Table 2 and Fig. 1. Analyses were conducted with the R software (R Development
293 Core Team 2013), using the packages lme4 (Bates et al., 2007), randomForest (Liaw and Wiener,
294 2002) and MuMIn (Barton and Barton, 2014). Because *Quercus petraea* and *Quercus robur* are
295 difficult to distinguish in the field and have a high hybridization rate (Abadie et al., 2012), these
296 two species were grouped in the analyses and are hereafter collectively referred to as “temperate
297 oaks”.

298

299 **2.4.2 Correlations between growth and C fluxes**

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

306

307 **2.4.3 Drivers of spatial variations in biomass growth**

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

327

328 **2.4.4 Drivers of temporal variations in biomass growth**

329 A temporal analysis was conducted on the standardized AWBI series: a double-detrending
330 process was applied to each series based on an initial linear regression model, followed by fitting
331 a cubic smoothing spline with a 50% frequency response cut-off (Mérian et al., 2011). For
332 analysing the temporal variations in biomass growth we used an RF learning method (Breiman,
333 2001), which was possible because of the large sample size (n = 931 site-years). The RF learning

334 method is a non-parametric method that is used to rank the contribution of different explanatory
335 variables and evaluate their marginal effects on a variable of interest without assuming an *a*
336 *priori* dependence. The RF method combined 500 binary decision trees that were built using
337 bootstrap samples from the initial dataset. The decisions trees aimed to reduce the heterogeneity
338 of the explained variable in the resulting branches. For each of the 500 trees, the data that were
339 not involved in the tree construction were used for validation. The tree predictions and errors
340 were then averaged to provide the final RF results. The RF method does not overfit or require
341 cross-validation (Cutler et al., 2007). A subset of explanatory variables was randomly chosen at
342 each node, thus reducing the effect of collinear variables on the output. The RF method was used
343 to select variables that explained the temporal variability in biomass growth (Genuer et al., 2010).
344 Variable selection relied on permutation importance, i.e., the existence of an increase in the
345 global mean square error when a given variable was randomized in the validation subsamples.
346 The forms of the dependences were illustrated by partial dependence plots (graphical depiction of
347 the marginal effect of a given variable, Cutler *et al.* 2007). We used this information (variable
348 selection and dependence forms) to test for the significance of the temporal AWBI dependences
349 within the linear model. The uncertainty in the simulated C fluxes was considered in the linear
350 models, following the procedure described in the spatial analysis section.

351

352 **3 Results**

353 **3.1 Relationship between woody biomass growth and C fluxes**

354 The elementary components of the simulated seasonal tree C balance differed in terms of their
355 relationships with the inter-annual variability of the AWBI (Table 3). The simulated seasonal
356 GPP and NPP were linked to AWBIs with a comparable agreement between species. However,
357 the simulated Ra had weak and often non-significant relationships with the AWBIs across the 49
358 studied plots. The strongest correlations were obtained for flux aggregation periods that i) were
359 generally consistent within a species for GPP and NPP but different for Ra and ii) strongly
360 differed among species (Table 3). The coefficients of variation of the simulated annual NPP, GPP
361 and Ra across the 49 studied sites were $10.8\% \pm 3$, $7.4\% \pm 2$, and $6.8\% \pm 3$, respectively. GPP
362 and NPP were summed from the beginning of May to the beginning of August and September, in

363 temperate oaks and *F. sylvatica*, respectively. The longest GPP and NPP aggregation periods
364 were obtained for *P. abies* (from the beginning of February to mid-September), and the shortest
365 period were found for *Q. ilex* (from the beginning of July to mid-August). Minor (less than 20
366 days) changes in the flux aggregation period associated with the maximum simulated flux-AWBI
367 correlation usually marginally affected the correlation values (Supplement S10). Consequently,
368 aggregation periods that were less than 13 days different (either in terms of their starting or
369 ending dates) from the values reported in Table 3 were generally not significantly lower than the
370 maximum values (see the critical values presented in Supplement S10).

371 **3.2 Spatial dynamic of C allocation to woody biomass growth**

372 The inter-site variability in biomass growth was well explained by the selected multiple
373 regression models ($R^2 \geq 0.6$). We highlighted that species varied in terms of their inter-site
374 dependences (Table 4). The simulated C supply during the growth period (GPP_{gp} , Table 2) was
375 positively correlated with biomass growth in *F. sylvatica* and *P. abies*, whereas there was no
376 significant relationship between the average AWBI and photosynthesis among sites for temperate
377 oaks (Fig. 3A). Notably, the final models did not include NPP_{gp} or Ra_{gp} for any species. The stand
378 age was an important driver of biomass growth in temperate oaks and *F. sylvatica*. The stand age
379 explained a substantial portion of the AWBI:C supply ratio in all species, although the
380 relationship was not significant for *P. abies* (Fig. 3B). The fraction of C sequestered in woody
381 biomass decreased with stand age (Table 4, Fig. 3B) and was reduced by half in temperate oaks
382 and *F. sylvatica* stands that were between 50 and 150 years of age (from 0.3 to 0.13 and from
383 0.25 to 0.1, respectively). Additionally, we identified a significant and positive effect of stand
384 basal area on both AWBI (Table 4) and the AWBI: GPP_{gp} ratio (*data not shown*) in temperate
385 oaks.

386

387 **3.3 Temporal dynamic of carbon allocation to woody biomass growth**

388 The ranking of the drivers of biomass growth obtained using the RF algorithm indicated that the
389 temporal AWBI dependences varied among species (Fig. 4). The growth of temperate deciduous
390 species was under a more complex environmental control than the growth of *P. abies* and *Q. ilex*,

391 with several variables explaining a substantial portion of the annual variability in AWBI (Fig.
392 4A, B). Simulated C supply (GPP_{gp}) was strongly related to the AWBI of temperate oaks and *F.*
393 *sylvatica* and, to a lesser extent, *P. abies* (Fig. 4A, B, C), with positive marginal effects (Fig. 5 a,
394 e, h). The duration of water stress during the growth period ($WS_{per_{gp}}$) was the predominant
395 driver of the AWBI variability of *Q. ilex*, and was also strongly related to growth in temperate
396 deciduous species. Low temperatures during the growth period ($templim_{gp}$) most substantially
397 affected *P. abies* and also explained a portion of the variability in AWBI of temperate oaks. The
398 simulated water and temperature stress indices had negative and quasi-linear marginal effects on
399 the AWBI (Fig 5). Finally, environmental lagged effects contributed substantially to the AWBI
400 variability in all species: the water stress intensity of the previous year ($WS_{int_{y-1}}$) affected the
401 growth of *F. sylvatica* and *Q. ilex*, whereas the simulated C supply of the previous year (GPP_{y-1})
402 affected temperate oaks and *P. abies*. Lagged effects generally revealed threshold in marginal
403 dependences, with a significant negative effect on AWBI only under high water stress or low C
404 supply (Fig. 5). The effects of the retained variables (Fig. 4) were evaluated via multiple
405 regression models that used dummy variables to test for the significance of slope changes when
406 thresholds appeared on partial plots (Fig. 5). The models explained approximately 20% of the
407 variability in the AWBI for temperate oaks and *P. abies*, and approximately 40% of the
408 variability for *F. sylvatica* and *Q. ilex* (Table 5). All of the explanatory variables had significant
409 effects, but $templim$ was not retained in the models for temperate oaks after the bootstrap
410 procedure that accounted for the uncertainty of the C flux simulations. We observed significant
411 changes in the slopes of the effect of GPP_{y-1} on temperate oaks and the effect of GPP_{gp} on *P.*
412 *abies* (Table 5). The models with NPP_{gp} and NPP_{y-1} variables revealed the same AWBI
413 dependences as the models described above, but with reduced explanatory power. The models
414 with Ra_{gp} and Ra_{y-1} variables were not significant (*data not shown*).

415

416 **4 Discussion**

417 This study quantified the C that is allocated annually to the woody biomass increment for five
418 species that are representative of the main European forest biomes. By complementing field
419 measurements from a permanent plot network with process-based modelling, our approach
420 circumvented the limitation of EC data scarcity and characterized the annual partitioning of C

421 into woody biomass at 49 sites (931 site-years). We were thus able to identify the species-
422 specific drivers of the spatiotemporal dynamics of the allocation of C to wood growth along
423 ecological gradients.

424

425 **4.1 The correlation between the tree C balance and woody biomass growth**

426 Relating EC-based estimates of forest C balance and biometric measurements of woody biomass
427 growth has been the focus of an increasing number of studies. These studies can enhance our
428 understanding of ecosystem C dynamics but have so far provided conflicting conclusions. Indeed,
429 the correlation between woody biomass growth and forest C gain has been reported as both non-
430 significant (Mund et al., 2010; Richardson et al., 2013; Rocha et al., 2006) and highly significant
431 (Babst et al., 2014; Ohtsuka et al., 2009; Peichl et al., 2010; Zweifel et al., 2010). Accordingly,
432 the relationships between AWBI and C fluxes reported in this study strongly varied among sites
433 for each of the species studied (Table 3). Nevertheless, the annual woody biomass increment was
434 consistently related to GPP_{gp} and NPP_{gp} , and only marginally to Ra_{gp} for the majority of sites
435 (Table 3). Babst et al. (2014) reported a similar dependence of biomass growth on C fluxes at 5
436 sites that spanned a wide range of latitude in Europe. The authors attributed this result to a
437 common sensitivity of C assimilation and biomass growth to the water balance. Our results also
438 support the view that biomass growth and tree C balance are under the control of distinct but
439 partially correlated processes (Beer et al., 2007; Fatichi et al., 2014); these processes may or may
440 not induce consistent annual changes, depending on the environmental conditions faced by trees.
441 For *F. sylvatica* and temperate oaks, maximum correlation values corresponded to flux
442 aggregation periods that were consistent with the previously reported phenology of the woody
443 biomass increment (Table 3, Michelot *et al.* 2012, Supplement S10). Babst et al. (2014) and
444 Granier et al. (2008) similarly reported close relationships between the AWBI and forest C fluxes
445 that were summed until cessation of growth (August/September). The flux aggregation periods
446 were, however, not related to the timing of wood growth in *Q. ilex* or *P. abies* (Cuny et al., 2012;
447 Lempereur et al., 2015), which indicates that inter-annual variation in the AWBI is not always
448 solely (or even primarily, e.g., *Q. ilex* and *P. abies*) dependent on the C derived from
449 photosynthesis. Specifically, the agreement between the observed annual growth and a short
450 period of C flux aggregation in early summer that was reported for *Q. ilex* corresponds to the

451 effect of growth cessation on the annual biomass increment, which has been attributed to a
452 drought-induced limitation of cambial activity at the Puéchabon site (Lempereur et al., 2015).
453 The processes that underlie the relationship of the long flux aggregation period and the annual
454 biomass increment of *P. abies* may include the effect of late winter temperature on cambium
455 phenology (Rossi et al., 2011). Overall, our results suggest that using growth-flux correlation
456 coefficients when investigating either source limitation of growth or the seasonality of C
457 allocation to woody biomass can lead to misleading conclusions.

458

459 **4.2 Between-site variability in the C allocation to woody biomass growth is** 460 **related to ontogeny and competition intensity**

461 We highlighted an age-related decline in the C partitioning to woody biomass in all three species
462 (Fig. 3B). This result had previously been observed in *F. sylvatica* stands using measurements of
463 the main C compartments along a chronosequence (Genet et al., 2010). Several non-exclusive
464 processes can explain this age-related trend. Increases in tree height are associated with increases
465 in the hydraulic resistance of xylem, which may lead to declines in the turgor of living cells and
466 result in potentially negative consequences on cambial activity (Woodruff et al., 2004). This
467 constraint may result in a height-related sink-limitation of growth (Woodruff and Meinzer, 2011),
468 which is consistent with our results. Additionally, life-history traits, such as a greater emphasis on
469 reproduction in older stands, could also be involved. However, the interactions of growth and
470 reproductive mechanisms are still under debate (Hoch et al., 2013; Thomas, 2011) and have yet
471 to be properly represented in TBMs. Only the GPP component of the simulated tree C balance
472 was retained in the final models (Table 4), thereby indicating that an increase in maintenance
473 respiration with greater stand biomass most likely did not contribute to the age-related decline in
474 biomass growth (Drake et al., 2011; Tang et al., 2014). Although height-related hydraulic
475 constraints on C assimilation have been suggested to be an important driver (Ryan et al., 2006;
476 Tang et al., 2014), recent studies have suggested that changes in demography and stand structure
477 may primarily explain the age-related decline observed in stand wood growth (Binkley et al.,
478 2002; Xu et al., 2012). Our results suggest that changes in the C allocation should also be
479 considered, because no mortality occurred in our plots during the measurement period (*data not*
480 *shown*). We additionally identified a significantly higher C partitioning to woody biomass in

481 temperate oak stands with greater competition intensity (i.e., high stand basal area, Table 3). To
482 date, reports regarding the effect of competition on C allocation dynamics are conflicting (Litton
483 et al., 2007) and suggest no significant or consistent effect. Moreover, we found no significant
484 effect of soil nutrient availability on the C allocation dynamics along the studied ecological
485 gradient whereas a recent meta-analysis reported that this factor positively affects C partitioning
486 to forest biomass on the global scale (Vicca et al., 2012). The RENECOFOR network only
487 includes relatively fertile sites (Supplement S5), which could putatively explain the apparent
488 tension between our results and the conclusions of the meta-analysis. Therefore, more studies are
489 required to elucidate the contributions of the various drivers to the variation in C partitioning to
490 woody biomass on scales that range from local to global.

491

492 **4.3 Inter-annual variability in woody biomass growth is consistent with** 493 **combined source-sink limitations**

494 Water and temperature stress exerted significant direct control on the inter-annual variation of
495 woody biomass growth (i.e., independently from their effects on C assimilation) for every species
496 and biome (Table 5 and Fig. 4 and 5). Cambial growth has been reported to be inhibited at lower
497 water stress levels than photosynthesis (Muller et al., 2011; Tardieu et al., 2011). Indeed,
498 drought-induced decrease in cell turgor strongly affects cell divisions (Woodruff and Meinzer,
499 2011) and cell wall expansion (Cosgrove, 2005; Lockhart, 1965) before gas exchange modulation
500 comes into play. Similarly, there is evidence that cell growth processes, such as cell division, are
501 more sensitive than photosynthesis to low temperatures (Körner, 2008). Although these findings
502 documented the plausible mechanisms of sink control of biomass growth at the cellular scale,
503 there is still considerable debate regarding whether the sink or the C source actually limit the
504 growth of the world's forests (Palacio et al., 2014; Wiley and Helliker, 2012). The typically
505 observed large C reserve pools (Hoch et al., 2003; Würth et al., 2005) have been interpreted as a
506 consequence of an overabundant C supply and thus evidence of sink control of tree growth
507 (Körner, 2003). However, recent works have suggested that a source limitation of growth may be
508 compatible with large C reserve pools if part of this mobile C is sequestered rather than stored
509 (Millard and Grelet, 2010) or if C storage is an active tree response to environmental stress
510 (Dietze et al., 2014; Wiley and Helliker, 2012). Using an alternative methodology (i.e. a

511 methodology that is not based on C storage measurement) our results suggest that sink limitation
512 has a significant effect on the annual woody biomass growth of five species that are
513 representative of different European biomes, including deciduous temperate forests. Because sink
514 limitation implies that there are periods with significant C supply but no growth, our results also
515 corroborate recent empirical studies that reported a significant role of growth duration in the
516 annual variability of tree radial increment (Brzostek et al., 2014; Cuny et al., 2012; Lempereur et
517 al., 2015). Additionally, we observed that past environmental constraints significantly affected C
518 partitioning to wood growth for each species and biome (Table 5 and Fig. 4 and 5). The lagged
519 effect of the previous year's low C supply (GPP_{y-1}) possibly indicates a preferential C allocation
520 to storage at the expense of growth in trees that face C reserve pool depletion (Bansal and
521 Germino, 2008; Wiley et al., 2013). In support of this finding, Richardson *et al.* (2012) reported a
522 strong relationship between the AWBI and the EC-based estimate of the previous year's C supply
523 in a mature maple stand. The detrimental effect of a previous year's low C supply on temperate
524 oak wood growth (Fig. 4) may be related to growth phenology, because this species relies on C
525 reserves to achieve a large part of its annual biomass growth prior to leaf expansion in the spring
526 (Barbaroux et al., 2003). The lagged effect of high water stress intensity on *F. sylvatica* and *Q.*
527 *ilex* (Fig. 4) may be linked to previous drought-induced mortalities of buds or fine roots
528 (Leuschner et al., 2001; López et al., 2003). Indeed, pre-built buds are thought to strongly
529 regulate the following year's cambial activity (Delpierre et al., 2015; Palacio et al., 2012; Zweifel
530 et al., 2006) and a recent meta-analysis concluded that C is preferentially allocated to fine roots at
531 the expense of wood growth in stands that face constraining environments (Chen et al., 2013).
532 Finally, our results suggest that C supply (GPP_{gp}) is an important driver of the annual woody
533 biomass growth in temperate deciduous forests (Daudet et al., 2005). GPP was the component of
534 the simulated tree C balance that was most closely related to the annual variability in growth; this
535 result indicates GPP's important role in explaining the annual variability in the net ecosystem
536 productivity of European forests (Delpierre et al., 2012). Overall, our findings support the
537 premise that forest woody biomass growth is subject to complex control processes that include
538 both source and sink limitations, following Liebig's law: although numerous processes
539 potentially influence wood growth, stand growth at a given site and a given year is predominantly
540 limited by the most constraining factor. C (source) limitation of growth can thus only occur when

541 other factors are non-limiting (Fatichi et al., 2014), a situation that is expected to be rare in
542 strongly constrained environment such as Mediterranean or mountainous areas (Fig. 4).

543

544 **4.4 Toward an integrated modelling framework**

545 Most models that are currently used to project the outcome of global changes on forests represent
546 wood growth as a fraction of the total C uptake (i.e., source control of growth, De Kauwe *et al.*
547 2014). This C-centric perspective overlooks the possibility of sink control of growth and thus
548 ignores results such as those presented in this study and those of earlier local studies (reviewed
549 by Fatichi *et al.* 2014). Consequently, this perspective possibly hampers the ability of TBMs to
550 project future forest productivity (Fatichi *et al.* 2014). On the basis of our analysis of the
551 spatiotemporal dynamics of C allocation to wood growth on a regional scale, we suggest a
552 straightforward, combined source- and sink-driven forest growth modelling framework (Fig. 6).
553 In this framework, a potential site-specific allocation coefficient is first defined to represent the
554 effect of soil fertility on the C allocation to wood (Vicca et al., 2012). In a second step, this
555 coefficient is adjusted to the physiological state of the stand by accounting for the dependences of
556 the C allocation on ontogeny, competition intensity and lagged environmental stressors. Lagged
557 environmental stressors are represented by a negative effect on the previous year's water stress
558 index and low C uptake on the allocation coefficient. Inclusion of the age-related decline in forest
559 growth has been highlighted as an important modelling goal (Magnani et al., 2000; Zaehle et al.,
560 2006). However, this effect has thus far been incorporated in models by including a negative
561 effect of the increasing stand respiration on the tree C balance, which contradicts current
562 knowledge (Ryan et al., 2006). The resulting annual allocation coefficient is finally modulated by
563 the direct water and temperature constraints on growth. In a similar fashion, Leuzinger *et al.*
564 (2013) improved the Lund-Potsdam-Jena (LPJ) terrestrial biosphere model predictions for the
565 cold tree-line by accounting for the direct temperature limitation of growth. Our approach can be
566 seen as an intermediate step toward a more mechanistic representation of C allocation to woody
567 biomass (Hölttä et al., 2010; Schiestl-Aalto et al., 2015). It synthesizes the current knowledge
568 regarding forest growth dependences and has the potential to unify seemingly contradictory
569 observations within a single modelling framework. The simulated growth is indeed subject to the
570 combined controls of C supply and changes in C allocation due to endogenous adjustments

571 and/or modulations of sink activity (Fig. 6). These controls result from distinct processes, which
572 are independently represented in the modelling framework. The relative influences of the various
573 processes, i.e., the simulated growth causalities, are thus likely to vary both spatially and
574 temporally, depending on the environmental conditions faced by trees. Our approach has
575 therefore the potential to shed light on the contrasted results reported by correlative studies.
576 Although the value is comparable to those of previous studies (Lebourgeois et al., 2005; Mérian
577 et al., 2011), the proportion of the annual growth variability that was explained by our approach
578 was moderate (Table 5). Plausible explanations of this result include: i) unreported management
579 interventions that may have skewed the historical stand growth reconstruction and ii) potentially
580 important growth drivers that were not considered here, such as changes in C partitioning due to
581 mast seeding (Mund et al., 2010), genetic differentiation among tree populations (Vitasse et al.,
582 2014) or allometry-mediated tree acclimation to drought (Martin-StPaul et al., 2013). A third
583 factor that hampered the ability of our empirical models to explain the annual growth variability
584 is the potential disagreement between the CASTANEA outputs that were used as explanatory
585 variables and the corresponding actual drivers. Although we argued that i) the CASTANEA
586 model has been thoroughly validated at many EC sites from throughout Europe and ii) the
587 presented growth dependences demonstrated their robustness against the reported uncertainties of
588 the CASTANEA simulations, the quality of the simulations was limited by the idiosyncrasies of
589 the sites we examined in this study. In particular, a number of past disturbances such as insect
590 outbreaks, windthrow or unreported commercial thinning could have temporarily induced large
591 discrepancies between the actual and simulated C fluxes (Grote et al., 2011; Hicke et al., 2012).
592 The error that is attributable to model performance unfortunately remains unknown because of
593 the absence of EC measurements at our study sites (except for the Puéchabon site, see Delpierre
594 et al., 2012). Despite this additional uncertainty, the combined use of field measurements and
595 process-based modelling allowed us to present the first species-specific evaluation of annual C
596 allocation to growth along regional environmental gradients. Our results suggest that
597 implementing the presented C allocation dependences in TBMs will refine the projections of the
598 outcome of global changes on forest growth, and have implications for the predicted evolution of
599 forest C sink, forest diebacks and tree species distributions (Cheaib et al., 2012).

600

601

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612

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

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

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

IDs	Description	Unit	Type	Scale
<i>age</i>	Stand age	years	M	S
<i>AWBI</i>	Annual woody biomass increment	gC.m ⁻²	M	ST
<i>SBA</i>	Stand basal area	m ²	M	S
<i>camb_onset</i>	Onset of the cambial activity	day of the year	S	T
<i>GPP_{gp}</i>	Gross primary production of the current (y) growth period	gC.m ⁻²	S	ST
<i>GPP_{y-1}</i>	Gross primary production of the previous (y-1) year	gC.m ⁻²	S	T
<i>frost</i>	Sum of the average daily temperatures below -2°C during the last winter (year y-1 and y)	°C	C	ST
<i>LNC</i>	Leaf nitrogen content	gN.gDM ⁻¹	M	S
<i>NPP_{gp}</i>	Net primary production of the current (y) growth period	gC.m ⁻²	S	ST
<i>NPP_{y-1}</i>	Net primary production of the previous (y-1) year	gC.m ⁻²	S	T
<i>numstem</i>	Stem density	number.ha ⁻¹	M	S
<i>SNA</i>	Class of soil nutrient availability (1: low, 2: medium, 3: high)	unitless	M	S
<i>SWHC</i>	Soil water holding capacity	mm	M	S
<i>templim_{gp}</i>	Number of days of the current (y) growth period with an average temperature below 6°C	number of days	C	ST
<i>Ra_{gp}</i>	Autotrophic respiration of the current (y) growth period	gC.m ⁻²	S	ST
<i>Ra_{y-1}</i>	Autotrophic respiration of the previous (y-1) year	gC.m ⁻²	S	T
<i>WS_{per_{gp}}</i>	Number of days of the current (y) growth period with soil water content below 60% of the soil water holding capacity	number of days	S	ST
<i>WS_{per_{y-1}}</i>	Number of days of the previous (y-1) year with soil water content below 60% of the soil water holding capacity	number of days	S	T
<i>WS_{int_{gp}}</i>	Water stress intensity index over the current (y) growth period	unitless	S	ST
<i>WS_{int_{y-1}}</i>	Water stress intensity index of the previous (y-1) year	unitless	S	T

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

Species	GPP				Ra				NPP			
	<i>start</i>	<i>end</i>	<i>r</i>	σ	<i>start</i>	<i>end</i>	<i>r</i>	σ	<i>start</i>	<i>end</i>	<i>r</i>	σ
<i>F. sylvatica</i>	124	258	0.62**	0.18	96	200	-0.29*	0.33	126	262	0.58**	0.24
<i>Q. petraea</i> / <i>Q. robur</i>	136	214	0.59**	0.25	98	192	0.31*	0.24	130	214	0.50**	0.28
<i>P. abies</i>	32	262	0.52**	0.38	78	348	0.11	0.52	32	200	0.49**	0.29
<i>Q. ilex</i>	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			P	adj. R ²
	GPP_{gp}	age	SBA		
<i>Q. petraea</i> / <i>Q. robur</i>		-8.88×10^{-1} [39.5]	4.27×10^{-1} [19.5]	$<10^{-4}$	0.69
<i>F. sylvatica</i>	5.07×10^{-1} [59.4]	-6.96×10^{-1} [61.6]		$<10^{-4}$	0.88
<i>P. abies</i>	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 $GPP_{gp} < 1400 \text{ gC m}^{-2}$; otherwise, D1 = 1. D2 = 0 if $GPP_{y-1} < 1550 \text{ gC m}^{-2}$; 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			
	<i>Q. petraea</i> / <i>Q. robur</i>	<i>F. sylvatica</i>	<i>P. abies</i>	<i>Q. ilex</i>
GPP_{gp}	3.26×10^{-1} ***	4.87×10^{-1} ***	2.4×10^{-1} * [3.5]	
$WS_{per_{gp}}$	-1.09×10^{-1} **	-2.04×10^{-1} ***		-5.8×10^{-1} ***
$WS_{int_{y-1}}$		-2.37×10^{-1} ***		-2.2×10^{-1} * [6.3]
GPP_{y-1}	3.82×10^{-1} * [3.3]		-4×10^{-1} ** [3.2]	
$templim_{gp}$	-9.60×10^{-2} ** Δ		-1.26 *** [3.5]	
D1			-2.4×10^{-1} ***	
D2	-3.9×10^{-1} ** [0.8]			
D1 * GPP_{gp}			1.33 ** [8.2]	
D2 * GPP_{y-1}	-4×10^{-1} ** [6.4]			
ρ	0.61	0.68	0.52	0.44
P	$<10^{-4}$	$<10^{-4}$	$7.7 \cdot 10^{-3}$	$<10^{-4}$
adj. R²	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.**