

Environmental control of carbon allocation matters for modelling forest growth

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Summary

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- We aimed to evaluate the importance of modulations of within-tree carbon (C) allocation by water and low-temperature stress for the prediction of annual forest growth with a process-based model.
- A new C allocation scheme was implemented in the CASTANEA model that accounts for lagged and direct environmental controls of C allocation. Different approaches (static vs dynamic) to modelling C allocation were then compared in a model–data fusion procedure, using satellite-derived leaf production estimates and biometric measurements at *c.* 10⁴ sites.
- The modelling of the environmental control of C allocation significantly improved the ability of CASTANEA to predict the spatial and year-to-year variability of aboveground forest growth along regional gradients. A significant effect of the previous year's water stress on the C allocation to leaves and wood was reported. Our results also are consistent with a prominent role of the environmental modulation of sink demand in the wood growth of the studied species.
- Data available at large scales can inform forest models about the processes driving annual and seasonal C allocation. Our results call for a greater consideration of C allocation drivers, especially sink–demand fluctuations, for the simulations of current and future forest productivity with process-based models.

Introduction

Continental ecosystems play a crucial role in the global carbon (C) cycle, removing *c.* 30% of anthropogenic C emissions from the atmosphere (Le Quéré *et al.*, 2015), of which a large part is sequestered in forests (Pan *et al.*, 2011). Despite their importance for the global C budget, the mechanisms underlying the fluctuations of the forest C sink remain insufficiently understood (Luo *et al.*, 2015). Among these mechanisms, the spatial and temporal drivers of forest growth are receiving considerable attention (Fang *et al.*, 2014; Pretzsch *et al.*, 2014), especially as early signs of saturation in the C sequestration of European forests were recently reported (Nabuurs *et al.*, 2013).

In most of the process-based models (PBMs) that are used currently to study terrestrial biogeochemical cycling at large scales, the simulated forest growth is proportional to the amount of C fixed by photosynthesis over a given time period (source-driven PBM; De Kauwe *et al.*, 2014; Körner, 2015). This assumed causal link between C acquisition and growth has, however, been challenged by empirical evidence. A growing body of studies show that meristem activities are more sensitive than photosynthesis to a panel of environmental stressors (Fatichi *et al.*, 2014).

These results, along with recent modelling studies (Leuzinger *et al.*, 2013; Schiestl-Aalto *et al.*, 2015), suggest that the modulations of organ sink demands by low temperatures (Körner, 2008) or water and nutrient deficits (Lockhart, 1965; Leuzinger & Hättenschwiler, 2013; Delpierre *et al.*, 2016a) are the main drivers of daily to seasonal growth at many forest sites (Körner, 2015). Besides, structural growth and photosynthesis are likely uncoupled when assimilated C is stored as nonstructural compounds (i.e. in a reserve pool) at the expense of organ formation, as part of an active tree response to environmental stress (Wiley & Helliker, 2012; Dietze *et al.*, 2014). The actively stored C reserve pool could explain the annual time lag often observed between C acquisition and growth (Richardson *et al.*, 2013), if the C accumulated in reserve is not used until the following year.

Altogether, these lines of evidence emphasize the prominent role of the processes driving C allocation among organs, as opposed to photosynthesis, in determining the timing and intensity of forest growth. This statement is in contrast with the good performances obtained by some source-driven PBMs when predicting regional changes in forest biomass production (e.g. Zaehle *et al.*, 2006; Bellassen *et al.*, 2011b). However, environmental stress negatively affects both photosynthesis and organ sink

demands, which is consistent with the strong correlations between C inputs and forest growth observed at large scales (Litton *et al.*, 2007). Furthermore, observational studies reported that the discrepancy between photosynthesis and growth repeatedly observed at the annual scale (e.g. Richardson *et al.*, 2013), and possibly caused by active C storage, can be resolved when data are averaged in multi-year studies (Gough *et al.*, 2008; Granier *et al.*, 2008). For these reasons there is a risk of 'getting the right answers for the wrong reason' (Leuzinger & Quinn Thomas, 2011; Fatichi *et al.*, 2014) when using the current (source-driven) generation of PBMs for predicting forest growth, with important implications for forest growth projections (Lempereur *et al.*, 2015). However, this risk remains to be quantified and related to the temporal and spatial scales of the simulations. The importance of seasonal changes in C allocation for the modelling of annual forest growth with a PBM indeed remains unknown to date.

Here, we present a first attempt to implement an ensemble of environmental modulations of the allocation of C to leaves and wood in a source-driven PBM (CASTANEA; Dufrêne *et al.*, 2005). Environmental dependencies of C allocation were derived from previous observational and data-model studies. We notably built on previous work (Guillemot *et al.*, 2015) in which we demonstrated that water and low temperature stress modulates the wood sink demand of five major European species. The modelling framework of wood growth suggested in Guillemot *et al.* (2015, their Fig. 6) was complemented by current hypotheses on C allocation mechanisms, in order to introduce direct and lagged environmental control of C allocation in the CASTANEA model (Fig. 1). This new C allocation framework was compared with a classical, purely source-driven approach, using a model–data fusion procedure (MDF; Richardson *et al.*, 2010). Model–data fusion is an efficient way to compare models of various complexities (Richardson *et al.*, 2013), as it accounts for the effects of parameter uncertainties on model performances, and thus avoids overparameterization pitfalls (Van Oijen *et al.*, 2005). In this work, our general aim was to evaluate the importance of the environmental modulation of C allocation for the prediction of leaf and wood annual growth with a PBM, along large water and low temperature stress gradients.

The different versions of CASTANEA were calibrated and evaluated against leaf and wood annual growth, based on a combination of satellite-derived and aboveground biometric measurements at *c.* 10⁴ sites from throughout mainland France. Five species were considered, which are representative of the main European forest biomes: *Fagus sylvatica*, *Quercus petraea* and *Quercus robur* for temperate deciduous broadleaved forests; *Picea abies*, for high-latitude and high-altitude evergreen needleleaved forests; and *Quercus ilex*, a Mediterranean evergreen broadleaved species. For all these species, we hypothesized that: (1) the information contained in annual growth data would inform the model regarding all or part of the studied C allocation dependencies (i.e. would constrain the corresponding parameter distributions), retrieving biologically meaningful parameter values; and (2) the environmental dependencies of C allocation would improve the leaf and wood growth predictions of the CASTANEA model.

Materials and Methods

Modelling of carbon allocation

For this study, we relied on the CASTANEA process-based model (Dufrêne *et al.*, 2005; Delpierre *et al.*, 2012; Guillemot *et al.*, 2014). CASTANEA simulates the water and carbon (C) budgets of an even-aged, monospecific stand. The simulated physiological processes that are of particular importance for this study include: at the hourly timescale, photosynthesis, maintenance and growth respiration (autotrophic respiration), and evapotranspiration; at the daily timescale, organ phenology, organ growth and soil water content (Fig. 1). The growth respiration is calculated after the C has been partitioned among compartments, as a function of organ-specific growth and construction costs (Dufrêne *et al.*, 2005). The values of the model parameters are species-specific. An overview of CASTANEA and a summary of the parameter values can be found in Supporting Information Notes S1.

The simulated forest stand comprises four functional compartments: foliage, woody biomass (that includes stem, branches and coarse roots), fine roots and the pool of nonstructural carbohydrates – that is, the reserve pool. Biomass growth is simulated in CASTANEA as the flow of C to an organ per unit of time (i.e. as a C flux; see Litton *et al.*, 2007). The simulated net primary productivity (NPP, photosynthesis minus autotrophic respiration) is thus partitioned among organs at the end of each day. In the original version of the model, the fraction of NPP allocated to each organ is constant over the growing season; that is, the simulated allocation coefficients are seasonally fixed (source-driven model; Dufrêne *et al.*, 2005). In the new C allocation scheme described in this paper, the partitioning of NPP is determined on a daily basis by ontogeny, allometric constraints, organ-specific phenology, direct and lagged environmental controls (Fig. 1).

Leaf compartment The dates of budburst and leaf senescence are simulated using accumulated degree-days, combined with photoperiod sensitivity for the latter (Dufrêne *et al.*, 2005; Delpierre *et al.*, 2009a). The amount of C that is allocated to the leaf compartment strongly relies on the C reserve pool because the stand C balance is negative during most of the leaf formation period. During the period of leaf formation, C is allocated to leaf until the simulated leaf area index (LAI) reaches a defined annual maximum (LAI_{max}). LAI_{max} is a prognostic variable, simulated on a yearly basis. The value of the LAI_{max} of year *y* is determined by the LAI_{max} of year *y*−1, and the water stress experienced by the stand during year *y*−1 (Eqn 1). Eqn 1 aims at simulating the reported high sensitivity of bud formation to water stress (Bréda *et al.*, 2006), which has important implications for the next year's leaf production (Nilsson & Wiklund, 1992; Le Dantec *et al.*, 2000).

$$\text{LAI}_{\text{max},y} = \min(\text{plai1}, \text{LAI}_{\text{max},y-1} + \text{plai2} + \text{plai3} \times \text{SWS}_{y-1})$$

Eqn 1

(LAI_{max,y}, maximum LAI of year *y*; SWS_{y−1}, soil water stress index of year *y*−1; plai1 (m² leaf m^{−2} soil), parameter that corresponds to the maximum value possible for LAI_{max}; plai2 (m² leaf

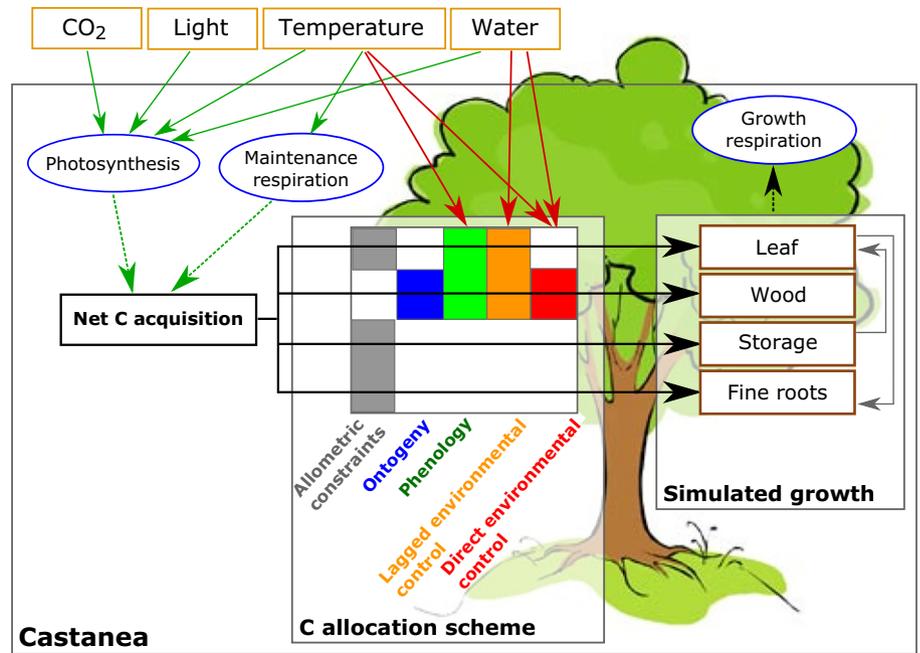


Fig. 1 Schematic diagram of the carbon (C) allocation scheme that was implemented in the CASTANEA model. Green arrows, environmental control of C acquisition; red arrows, environmental controls of C allocation; solid black arrows, within-tree C partitioning; grey arrows, allometric constraints.

m^{-2} soil) and $plai3$ (m^2 leaf m^{-2} soil), parameters associated with the effect of SWS (unitless), which is a bioclimatic index that integrates the water balance and the soil water holding capacity of the site (Notes S1).) Eqn 1 is used to describe the C allocated to the leaf compartment for all of the study species. However, in the case of the evergreen species only the most recently grown needle or leaf annual cohort (out of six and four, for *P. abies* and *Q. ilex*, respectively) is affected by the annual changes in LAImax.

Wood compartment The C allocation to aboveground wood is based on the modelling framework described in Guillemot *et al.* (2015). For comparison purposes, three versions of the C allocation submodel have been calibrated (Table 1): a null version with a constant allocation coefficient (hereafter ‘CST version’), a version that includes the age-related decline in C allocation to aboveground wood (the standard CASTANEA version, hereafter ‘STD version’) and a full version that additionally simulates the environmental controls of the C allocation to wood (hereafter ‘FULL version’; Fig. 1). Hereafter, we refer to the CST and STD versions as a ‘static’ modelling of C allocation (they correspond to typical examples of source-driven PBMs), and to the FULL version as a ‘dynamic’ modelling of C allocation.

In all three versions, wood growth is function of the NPP and of the C allocation coefficient to wood (Eqn 2).

$$AWBI_{y,d} = WAC_{y,d} \times NPP_{y,d} \quad \text{Eqn 2}$$

($AWBI_{y,d}$, simulated wood growth on day d of year y ($gC\ m^{-2}\ d^{-1}$); $WAC_{y,d}$ (unitless) and $NPP_{y,d}$ ($gC\ m^{-2}\ d^{-1}$), corresponding simulated daily wood allocation coefficient and net primary productivity, respectively.)

The allocation coefficient of the CST version is fixed to a constant value over the growing season (Eqn 3).

$$WAC_{y,d} = pwood1 \quad \text{Eqn 3}$$

($pwood1$, parameter (unitless).)

In version STD, the simulated allocation coefficient varies annually to account for the linear age-related decline in C allocation to wood (Eqn 4) that has been recently reported in the studied species (Genet *et al.*, 2010; Guillemot *et al.*, 2015).

$$WAC_{y,d} = pwood1 - pwood2 \times age \quad \text{Eqn 4}$$

($pwood2$, slope parameter (yr^{-1}).)

The FULL version also incorporates a linear age-related decline in C allocation to wood (Eqn 4). The resulting WAC value ($WAC1_{y,db}$ an intermediate value; Eqn 5) is additionally modulated on a daily basis by the following two factors.

(1) A negative effect of the previous year’s water stress on C allocation to wood (Eqn 5), assuming a logistic relationship (Guillemot *et al.*, 2015). This lagged environmental control is a proxy for both the preferential C allocation to fine roots following drought, in agreement with empirical evidence (Doughty *et al.*, 2014) and with the functional-balance theory (Chen & Reynolds, 1997); and the likely active C storage that follows a drought-induced reserve depletion (Dietze *et al.*, 2014; Klein *et al.*, 2014). It is coherent with the annual time lag often observed between C acquisition and forest growth (Richardson *et al.*, 2013).

(2) A direct environmental control on wood sink demand: when water or low temperature stress of a given day exceed a defined threshold, sink demand is assumed to temporarily stop and no C can be allocated to wood (Eqn 6). Cambial growth has been reported to be inhibited at lower water stress than

Table 1 Description of the carbon (C) allocation submodels involved in the optimization process

Submodels	Versions	Description	Related equations	Parameters to be optimized
<i>LAI</i> Simulation of the annual value of LAImax	All	There is a lagged effect of the previous year's water stress on the allocation of C to leaf (i.e. on LAImax)	Eqn 1	plai1 plai2 plai3
<i>C allocation to wood</i> Simulation of the aboveground wood biomass increment (AWBI)	CST	The wood allocation coefficient is fixed at a constant value across sites. No environmental control of C allocation	Eqn 3	pwood1
	STD	The wood allocation coefficient varies according to ontogeny (age effect). No environmental control of C allocation. It is the standard version of CASTANEA	Eqn 4	pwood1 pwood2
	FULL	The wood allocation coefficient varies according to ontogeny. There is an environmental control (direct and lagged) of C allocation to wood	Eqn 4 Eqn 5 Eqn 6	pwood1 pwood2 pwood4 pwood6 psink1 psink2

LAImax, annual maximum value of leaf area index (LAI). Units: plai1-3 (m² leaf m⁻² soil); pwood1 (unitless); pwood2 (yr⁻¹); pwood4 (unitless); pwood6 (unitless); psink1 (fraction of relative extractable soil water, unitless); psink2 (°C).

photosynthesis (Muller *et al.*, 2011; Tardieu *et al.*, 2011). Indeed, drought-induced decrease in cell turgor strongly affects cell division (Woodruff & Meinzer, 2011) and cell wall expansion (Lockhart, 1965) before leaf gas exchange modulation comes into play. There is also evidence that cell division is more sensitive than photosynthesis to low temperature (Körner, 2008).

$$WAC_{y,d} = WAC1_{y,d} - pwood3 + \frac{pwood4}{1 + \exp(pwood5 \times (SWS_{y-1} - pwood6))}$$

Eqn 5

$$\text{If}(\text{REW}_{y,d} < \text{psink1} \text{ or } T_{a,y,d} < \text{psink2}) \text{ then } WAC_{y,d} = 0$$

Eqn 6

(SWS_{y-1}, soil water stress index of year y-1 (unitless); REW_{y,d}, relative soil water content extractable by plants on day d of year y (unitless); T_{a,y,d}, air temperature on day d of year y (°C); psink1 and psink2, parameters (unitless and °C, respectively); pwood3 to pwood6, form parameters (unitless).)

The wood growth resumption of *F. sylvatica* is known to occur simultaneously with budburst (Michelot *et al.*, 2012) and consequently we simulate the day of wood growth onset for this species based on the leaf phenology submodel of CASTANEA. For the other species involved in this study, the day of growth cambial onset is simulated annually using an empirical model (N. Delpierre *et al.*, unpublished results) that is based on temperature sums (Guillemot *et al.*, 2015). The cessation of the period with possible C allocation to wood growth is based on published results (Bouriaud *et al.*, 2005; Michelot *et al.*, 2012; Lempereur *et al.*, 2015) and fixed to the day of year 230, 240 and 300 for deciduous species, *P. abies* and *Q. ilex*, respectively. The phenology of wood growth is simulated in all three versions of the model (i.e. WAC=0 outside growing season). In the FULL

version, the phenology and duration of wood growth is additionally modulated by the environmental control of sink demand.

Reserve and fine root compartments, interactions with other pools The highest C allocation priority is given to the leaves; followed by C allocation to wood. Under nonstressed conditions (i.e. when the reserve pool is not depleted), allocation to reserve and fine roots have the lowest priority. The competition abilities of reserve and fine root compartments depend on their C stocks and are ruled by allometric constraints (i.e. developmental constraints imposed by plant architecture, see Franklin *et al.*, 2012). The allocation to fine roots is based on the hypothesis of a functional homeostasis in water transport within trees (Magnani *et al.*, 2000): the fine root pool is given an annual objective in terms of C stock, which is deduced from the simulated LAImax by using the implementation described in Davi *et al.* (2009). The competition ability of the fine root pool is modulated as its stock diverges from its annual objective. The competition ability of the reserve pool increases when its stock becomes too low (i.e. between 75 and 100 gC m⁻² soil, see Notes S1), in an attempt to avoid complete C depletion. In case of extremely low C reserve stock during the C-demanding leaf formation period, the reserve pool interacts with the leaf compartment: the daily LAI increase is stopped if the reserve pool drops below 20 gC m⁻² soil. The allocation to reserve and fine roots can occur throughout the year (i.e. as soon as NPP > 0) but it is strongly impacted by the C allocation to leaves and wood. More details about the C allocation to reserve and fine roots and the interactions among pools can be found in Notes S1.

Measurements

A complete description of the field measurements, satellite-derived data and historical climate used in this study is provided in Notes S2. We provide here a brief description of the datasets.

Biometric measurements were obtained from two complementary sources: the French national forest inventory (NFI; Charru *et al.*, 2010; Vallet & Pérot, 2011) and a permanent forest plot network (RENECOFOR; Ulrich, 1997). Because the RENECOFOR network does not include *Q. ilex* plots, it was completed with measurements from the Puéchabon site (Rambal *et al.*, 2014). The NFI dataset comprised 6204, 2050, 1424 and 228 plots of temperate oak (*Q. petraea* and *Q. robur*), *F. sylvatica*, *P. abies* and *Q. ilex* stands, respectively, spread over mainland France (Notes S3). Because *Quercus petraea* and *Q. robur* are difficult to distinguish in the field and have a high hybridization rate (Abadie *et al.*, 2012), these two species were grouped in the analyses and are hereafter referred to collectively as 'temperate oaks'. The NFI dataset contained one record of 5-yr aboveground wood biomass increment (AWBI) per site (collected over the 2005–2012 period; Notes S2). The RENECOFOR network included measurements from 26, 16 and six plots of temperate oak, *F. sylvatica* and *P. abies* stands, respectively. Biometric measurements in the RENECOFOR and at the Puéchabon site consisted of dendrochronological sampling conducted in 1994 (2008 for the Puéchabon site) and extensive circumference surveys that were combined to calculate annually resolved AWBIs at each plot (over the 1980–1994 period for the RENECOFOR sites and 1966–2008 at the Puéchabon site). Soil texture and soil depth estimates were used to infer soil water holding capacities at all the study sites.

The normalized difference vegetation index (NDVI) estimates of the MODIS/TERRA surface reflectance product at a 250-m resolution (MOD09GQK, Earth Observing System Data Gateway) were extracted on a daily basis over the 2001–2012 period for each NFI site. Following the procedure proposed by Hmimina *et al.* (2013), we retrieved the annual maximum NDVI value (NDVImax) observed at each NFI sites over the 2001–2012 period. NDVImax values were converted to the maximum fraction of absorbed photosynthetically active radiation (FAPARmax, Notes S3) and then to LAImax (annual maximum LAI value), using the equations of Knyazikhin *et al.* (1999). In order to characterize the factors driving the spatial changes in FAPARmax, the correlations between FAPARmax and a panel of bioclimatic variables observed or simulated at the NFI sites were evaluated (Notes S3). For this step, satellite-derived FAPARmax was used instead of the LAImax products, which are more prone to saturation effects (Seixas *et al.*, 2009; McCallum *et al.*, 2010).

Model calibration and evaluation

We used a two-step calibration procedure: the LAImax submodel was first calibrated and evaluated, and was subsequently used during the wood growth submodel calibration and evaluations (Table 1). We selected half of the NFI sites using a random sampling stratified by species, age, water stress and low temperature stress for the calibration process (calibration dataset). The remaining NFI sites, as well as the RENECOFOR and Puéchabon sites were used to evaluate the model (evaluation dataset). The three versions of the wood growth submodels were calibrated independently. In order to avoid high correlation among parameter distributions, only a subset of parameters of

Eqn 5 was involved in the calibration of the FULL version (Table 1). These correspond to the parameters with greatest impact on the model predictions in a preliminary sensitivity analysis (data not shown). The values of the parameters that were not involved in the optimization procedure were based on Guillemot *et al.* (2014) (Notes S1). The model was initialized using the aboveground standing biomass and the LAImax value observed at each site. More details about the calibration procedure can be found in Notes S4.

The parameter optimizations of the LAImax and wood allocation submodels were based on a model–data fusion (MDF) procedure, using the MCMC Metropolis–Hastings algorithm (Metropolis *et al.*, 1953; Van Oijen *et al.*, 2005). A MDF comparison of the different model versions was required to ensure that the more complex model (i.e. the FULL version) did not obtain better fit merely as a result of overparameterization. The cost function was defined as the averaged squared data–model mismatch ('least-squares optimization'; Richardson *et al.*, 2010). Prior distributions for each parameter were assumed to be normal with large SD (Notes S5). For each species, the parameter space of the LAImax and wood submodels were explored for at least 25 000 iterations. The resulting posterior distributions were constituted by the 1000 parameter sets that best matched to the data. The presented submodel performances are averages of 2000 runs using the final posterior parameter distribution and tested against the evaluation dataset (Fu *et al.*, 2012). The optimization procedure relied on an *ad hoc* routine coded in R (N. Delpierre & N. K. Martin-StPaul, unpublished routine) using the snow package (Tierney *et al.*, 2008).

The evaluation of the model performances included:

- *AN intersite evaluation* using the NFI evaluation dataset (evaluation of both the LAImax and wood allocation submodels). In this case, 'simulations' and 'observations' refer to annual averages of AWBIs over 5 yr, and average FAPARmax over the 2011–2012 period, for wood and LAImax submodels, respectively.
- *An interannual evaluation* (evaluation of the wood allocation submodel). The model versions were evaluated using annual AWBIs from the RENECOFOR network. The RENECOFOR dataset includes both intersite variability (related, e.g., to site fertility and stand age) and interannual variability (related to weather fluctuations). Observations and simulations were therefore preliminarily standardized following the methodology described in Mérian & Lebourgeois (2011), in order to isolate the interannual AWBI variability. In this case, 'simulations' and 'observations' of aboveground wood growth refer to annual AWBI.

The performance of the model was assessed using Pearson correlation coefficient (r), the average bias (AB), the root mean square error (RMSE) and relative root mean square error (RMSE divided by the mean of the observations, rRMSE). Performance criteria are further described in Notes S6.

Results

Model calibration

The optimization process retrieved parameter values that correspond to a decline of LAImax following drought years in

temperate oaks, *F. sylvatica* and *P. abies* (Table 2). The posterior distributions of the parameters of the LAI submodel, as well as the parameter of the CST and STD wood growth submodels, were well constrained by the data (Table 2; Notes S5). By contrast, the identification of parameters of the FULL wood growth submodel by the MCMC procedure strongly varied among parameters and species. The ontogenetic decline of the C allocation to wood (Eqn 4, pwood1 and pwood2) was well constrained by the data and more pronounced for the evergreen species (Table 2). With regards to the lagged effect of water stress on C allocation to wood growth (Eqn 5), only one (pwood4) of two parameters involved in the calibration process yielded moderately constrained posterior distributions (Notes S5), with consistent average values among species. The modelling of the direct modulation of C allocation to wood by water stress (Eqn 6, psink1; Table 2) was reasonably constrained by the data in all the species, but the shrinkage in the posterior distributions was more pronounced for species often found in drought prone areas (*Q. petraea/Q. robur* and *Q. ilex*; Notes S5). The modelling of the direct modulation of C allocation to wood by low temperature (Eqn 6, psink2; Table 2), was only significantly constrained in the mountainous species *P. abies*, and to a lesser extent in temperate oaks (*Q. petraea/Q. robur*).

Prediction of the LAI

The satellite-derived FAPARmax retrieved at the NFI plots was significantly linked to an aridity index (P-PET summed from April to August; Fig. 2) in *F. sylvatica*, *Q. petraea/robur* and *P. abies*. Among these three species, the reported decline in FAPARmax at dry sites was more pronounced in *Q. petraea* and reduced in *P. abies*. Aridity (P-PET) explained a moderate part of the overall FAPARmax spatial variability ($R^2 < 0.15$ in all three species); however, no other explanatory variables, including biometric and site fertility data, were found to be linked to the FAPARmax for these three species. No significant dependences were found in *Q. ilex* and this species was therefore not included in the calibration procedure described in the previous section.

The FAPARmax simulated with the CASTANEA model at the NFI evaluation sites showed a decline with aridity that was consistent with the observations (Fig. 2) in *F. sylvatica*, *Q. petraea/robur* and *P. abies*. This simulated drought-related decline of LAI_{max} and FAPARmax values was a direct consequence of the dependency of LAI_{max} on the soil water stress index of the previous year (SWS_{y-1} ; Eqn 1) – that is, the negative impact of low reserve on LAI_{max} (see model description) was negligible (result not shown).

Prediction of the aboveground wood growth

The FULL version of CASTANEA was able to capture the changes in 5-yr wood growth (AWBI) across a large number of sites ($n = 3102, 1025, 712, 114$ in *Q. petraea/robur*, *F. sylvatica*, *P. abies* and *Q. ilex*, respectively) in the four study species (Fig. 3).

Interestingly, the CASTANEA performances (FULL version) were satisfactory in all of the age classes of the NFI chronosequence (Notes S7). In particular, the observed age-related decline in AWBIs was well predicted at evaluation plots in the four study species, in accordance with the age-related decline in the allocation to wood that was formalized in Eqn 4. The model also was able to predict a significant part of the interannual variability of AWBIs in 763 site-years (Fig. 4; the evaluation using the non-standardized RENECOFOR dataset is provided in Notes S8). The wood growth of deciduous temperate species (*Q. petraea/robur* and *F. sylvatica*) was generally better predicted by the model, both spatially (Fig. 3) and temporally (Fig. 4), than the wood growth of evergreen species (*P. abies* and *Q. ilex*). We acknowledge, however, that a large part of the spatial and temporal variability of wood growth (i.e. half or more of the total growth variability) remains unexplained by the different model versions in all the studied species.

Overall, we observed that the representation of the environmental dependencies of C allocation substantially increased the ability of the CASTANEA model to simulate the spatial and temporal variations affecting the AWBIs at the regional scale (Fig. 5). The root mean square error (RMSE) obtained when predicting 5-yr

Table 2 Optimized parameter values of the FULL version of the carbon (C) allocation scheme

Submodel	Species	Parameters					
LAI _{max}		plai1	plai2	plai3			
	<i>Q. petraea/robur</i>	5.22**	1.52*	−0.058*			
	<i>F. sylvatica</i>	5.31**	2.66*	−0.059**			
	<i>P. abies</i>	6.26**	2.03*	−0.081**			
Wood growth		pwood1	pwood2	pwood4	pwood6	psink1	psink2
	<i>Q. petraea/robur</i>	0.54**	−0.0015*	−0.11	50.7*	0.31**	5.5**
	<i>F. sylvatica</i>	0.62**	−0.0013*	−0.11	50.9*	0.28*	5.6*
	<i>P. abies</i>	0.69**	−0.0024	−0.12	50.4*	0.26*	6.2**
	<i>Q. ilex</i>	0.55**	−0.0025	−0.12	52.9	0.28*	6.1*

The presented values are the averages of the posterior distributions. The star marks indicate the confidence range of each parameter, that is, the SD of the posterior distribution divided by its average (**, $\leq 20\%$; *, $> 20\%$ and $\leq 50\%$; no asterisk, $> 50\%$). The parameters that obtained posterior distributions with a SD reduced more than two-fold compared with the corresponding priors are marked in grey.

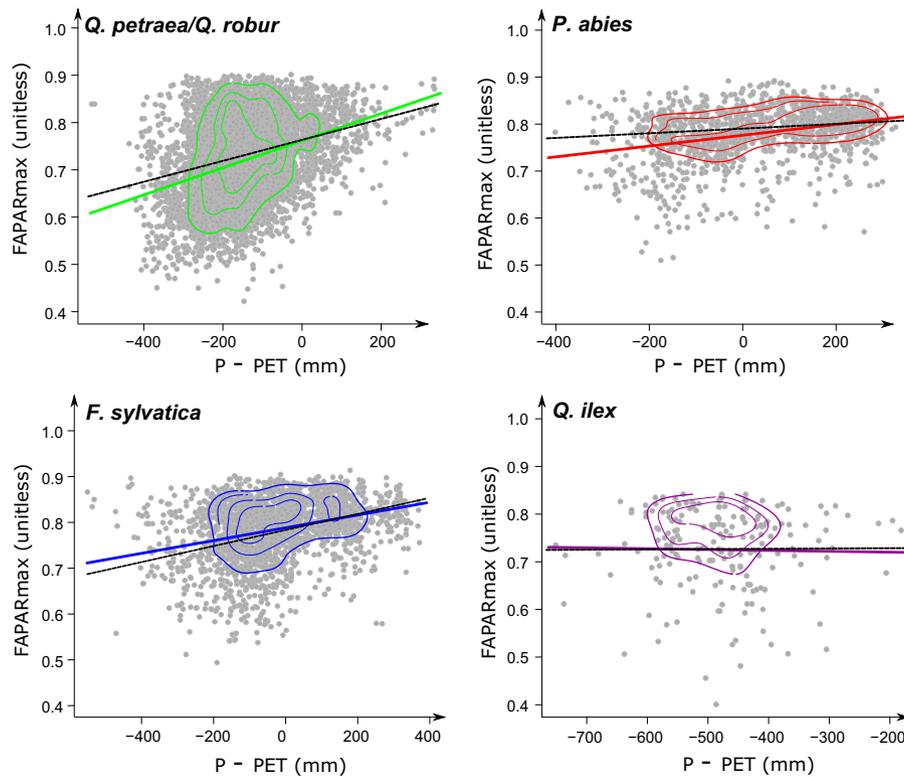


Fig. 2 Relationship between the maximum fraction of absorbed photosynthetically active radiation (FAPARmax) values (observed and simulated) and the aridity of the national forest inventory (NFI) sites. FAPARmax is the annual maximum FAPAR value observed at each site over the 2001–2012 period. CASTANEA simulates the annual maximum leaf area index (LAI_{max}) values, which were then converted to FAPARmax values using the equations from Knyazikhin *et al.* (1999). P-PET is the daily difference between rainfall and forest potential evapotranspiration. P-PET was summed from April to August and averaged over the 2001–2012 period. Dots are the observed FAPARmax at all the NFI sites. Solid coloured lines are the observed FAPARmax vs aridity regression lines, at all the NFI sites (*Quercus petraea*/*Q. robur*: $n = 6204$, $P < 0.01$; *Fagus sylvatica*: $n = 2050$, $P < 0.01$; *Picea abies*: $n = 1424$, $P < 0.01$; *Quercus ilex*: $n = 228$, $P = 0.4$). Dashed black lines are the simulated FAPARmax vs aridity regression lines, at the NFI evaluation sites (*Q. petraea*/*Q. robur*: $n = 3102$, $P < 0.01$; *F. sylvatica*: $n = 1025$, $P < 0.01$; *P. abies*: $n = 712$, $P = 0.02$; *Q. ilex*: $n = 114$, $P = 0.5$). Line levels are 0.75, 0.5 and 0.25 quartiles.

wood growth increments at the 4093 sites of the NFI evaluation dataset indeed decreased by 35.7% on average when using the FULL instead of the STD version, resulting in an average error decrease of $32.6 \text{ gC m}^{-2} \text{ yr}^{-1}$. The year-to-year wood growth variation was also better predicted with the FULL version, as it obtained a 15.2% decrease of RMSE compared with the STD version.

A comprehensive analysis of the error affecting the predictions of CASTANEA for the NFI evaluation dataset (Fig. 6) revealed that the modelling of the environmental dependencies of C allocation in the FULL version reduced the bias affecting the STD version at sites with no environmental stress (where STD underestimates AWBIs) and at sites with high environmental stress (where STD overestimates AWBIs).

Last, in an attempt to further evaluate the biological plausibility of the parameter values retrieved by the MDF procedure, we compared the seasonal wood growth patterns simulated by the STD and FULL versions of CASTANEA (Fig. 7). The FULL version noticeably simulates earlier growth cessation in temperate species and later growth onset in *P. abies* than the STD version, and was the only version predicting a growth cessation during summer in *Q. ilex*.

Discussion

Changes in carbon allocation to leaves are needed to predict leaf area index decline along regional water stress gradients with CASTANEA

In agreement with observations, CASTANEA simulated a significant adjustment of annual maximum leaf area index (LAI_{max}) to water stress in species from temperate (*Fagus sylvatica*, *Quercus petraea/robur*) and high-latitude and high-altitude forests (*Picea abies*) – that is, at sites that were not expected to be strongly water-limited (Fig. 2). Modulation of carbon (C) allocation to leaves by the previous year's water stress (Eqn 1) was required in CASTANEA to predict the corresponding LAI_{max} decline. In all of the species studied, leaf formation is a 2-yr process that involves leaf bud development in summer and leaf growth during the next spring (Delpierre *et al.*, 2016a). Our result is thus in agreement with empirical studies reporting the high sensitivity of buds (notably the number of prebuilt leaves) to water stress (Bréda *et al.*, 2006), with important implications for the next year's leaf production (Nilsson & Wiklund, 1992; Le Dantec *et al.*, 2000). Alternatively, this lagged environmental

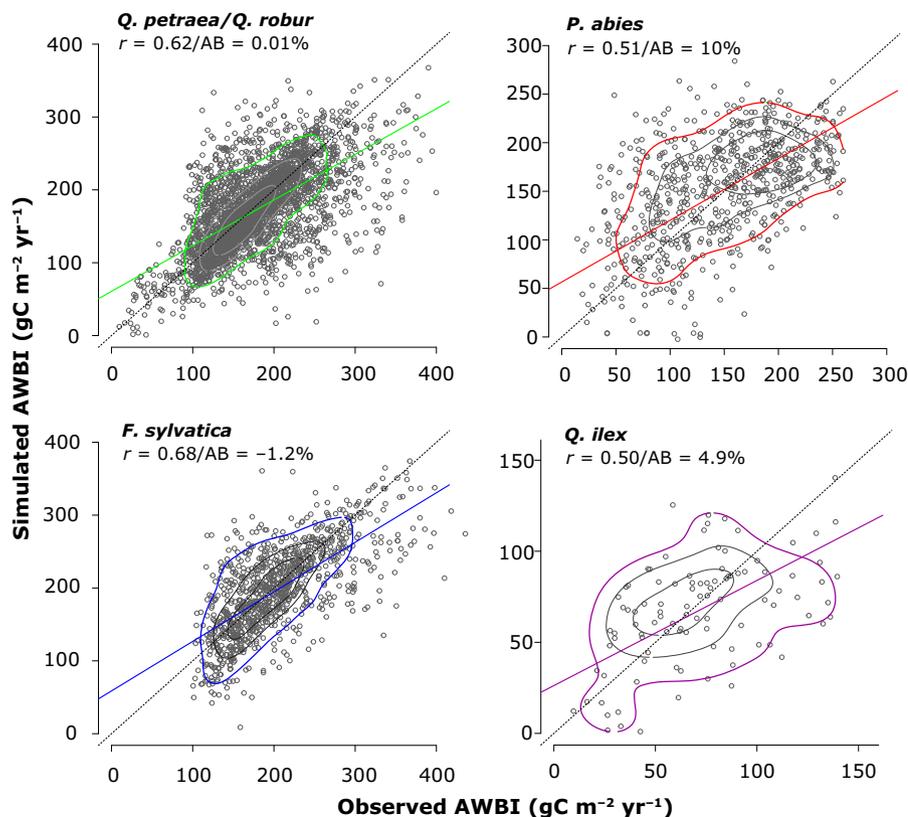


Fig. 3 Spatial evaluation (site to site) of the CASTANEA model (FULL version) using the national forest inventory (NFI) aboveground wood growth measurements (NFI evaluation dataset). AWBI, aboveground wood biomass increment. Each dot corresponds to the average annual AWBI over 5 yr at a NFI site (*Quercus petraea*/*Q. robur*: $n = 3102$; *Fagus sylvatica*: $n = 1025$; *Picea abies*: $n = 712$; *Quercus ilex*: $n = 114$). Coloured lines are observation vs simulation regression lines. Black lines are 1 : 1 lines. r and AB are Pearson correlation coefficient and average bias, respectively. Line levels are 0.75, 0.5 and 0.25 quartiles. C, carbon.

control on C allocation could also be explained by an active prioritization of the C reserve pool at the expense of leaves following drought years (Richardson *et al.*, 2013). The studied species indeed rely importantly on C reserves to build new leaves in spring (Barbaroux *et al.*, 2003), which could compromise survival in case of depleted C reserves caused by a low C accumulation during the preceding year.

Furthermore, the drought-related LAImax decline observed at the French national forest inventory (NFI) sites is consistent with the ecohydrological equilibrium hypothesis (Eagleson, 1982), which states that ecosystems develop a vegetation density maximizing C sequestration and minimizing water loss. The canopy density is therefore expected to decline with aridity because the development of the plant canopy increases the quantity of water that is lost by transpiration. The ecohydrological equilibrium of LAImax has for a long time been implemented in models by assuming an optimal canopy-scale water use efficiency (WUE) in plants (Kergoat, 1998; Mouillot *et al.*, 2001). Here, we show that the modelling of the environmental control of C allocation allows predicting the decline of canopy density at dry sites, in line with the prediction of the WUE optimality theory.

Pluri-annual biometric data can inform process-based models about the environmental dependencies of C allocation to wood

Forest growth inventories were able to inform CASTANEA regarding the environmental dependencies of C allocation to wood: in all studied species, most parameters of the dynamic C

allocation scheme (FULL version) were well constrained by the model–data fusion procedure (MDF).

The modelling of the environmental control on C allocation leads to an early growth cessation in temperate species (Fig. 7). This is in agreement with a number of empirical studies showing that wood growth cessation is more sensitive than gas exchanges to summer water stress (Mund *et al.*, 2010; Delpierre *et al.*, 2016a) and that phenology, not C supply, is a key driver of temperate forest growth (Delpierre *et al.*, 2016b). The direct comparison of soil water content thresholds for growth cessation among studies is made difficult by methodological differences. The threshold for growth cessation of 0.28 and 0.31 (unitless) that we found in *F. sylvatica* and temperate oaks (psink1 parameter; Table 2, corresponding to 28% and 31% of the relative extractable water, REW), respectively, are low compared with results previously obtained in deciduous forests (50% of REW in Delpierre *et al.*, 2016a; 60% of REW in Mund *et al.*, 2010). However, these empirical studies evaluate the REWs from measurements of the water content in the shallow layers of the soil, whereas our modelling study considers soil water-holding capacities that presumably are closer to the total amounts of water potentially available for trees (Notes S2).

The summer drought-induced cessation of wood growth that is observed in *Q. ilex* (Mediterranean species) at the Puéchabon site (Lempereur *et al.*, 2015) is only predicted by the FULL version of CASTANEA. This is in line with a recent study reporting that this seasonal pattern is most likely induced by a negative drought effect on wood sink demand

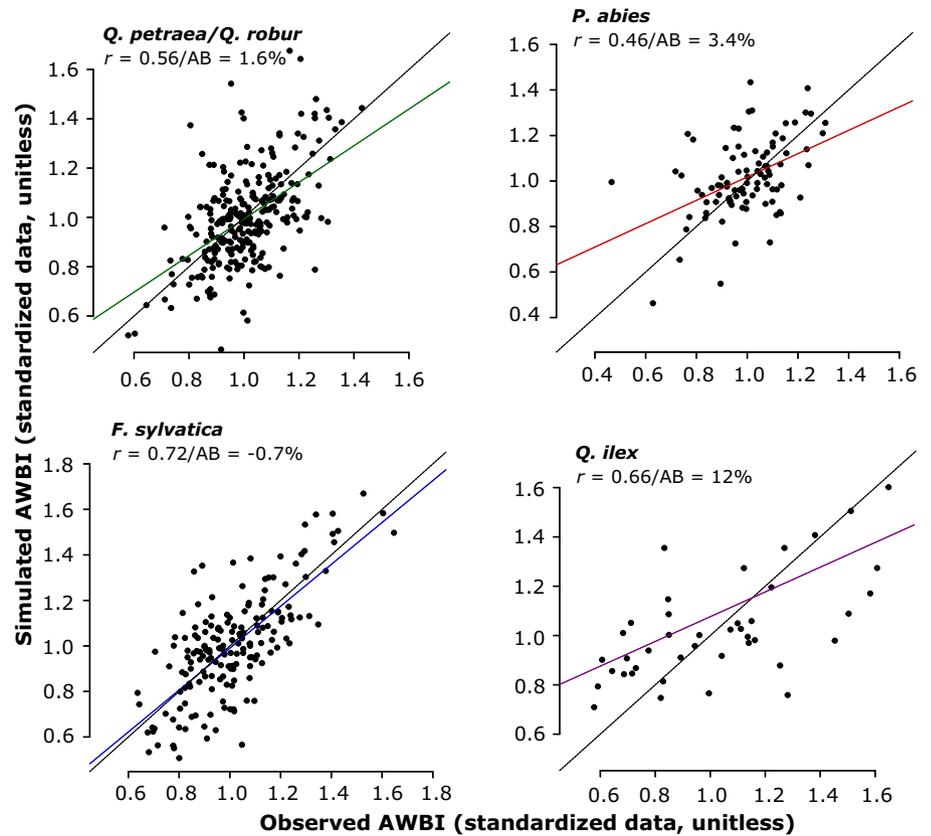


Fig. 4 Temporal evaluation (year to year) of the CASTANEA model (FULL version) using the RENECOFOR and Puéchabon aboveground wood growth measurements. AWBI, aboveground wood biomass increment. Each dot corresponds to the AWBI at a particular site-year, standardized per site (*Quercus petraea*/*Q. robur*: $n = 390$; *Fagus sylvatica*: $n = 240$; *Picea abies*: $n = 90$; *Quercus ilex*: $n = 43$). Coloured lines are observation vs simulation regression lines. Dotted black lines are 1 : 1 lines. r and AB are Pearson correlation coefficient and average bias, respectively.

rather than by a shortage of C supply (Lempereur *et al.*, 2015). Moreover, the threshold for growth cessation at the Puéchabon site is 31% of REW (calculated from Rambal *et al.*, 2003; Lempereur *et al.*, 2015), which compares well with the value of 28% that we found by calibrating our C allocation scheme using the NFI dataset (Table 2).

The modelling of the environmental control of C allocation leads to a delayed growth onset in *P. abies* (mountainous species), which we interpreted as a direct control of spring low temperature on wood phenology. In line with this result, growth resumption in trees has been shown to be affected strongly by temperature (Begum *et al.*, 2013): the onset of cambium activity seems to be triggered by the increase of daily minimum air temperature in spring. In addition, Rossi *et al.* (2008) reported that although daily temperatures below 4–5°C are still favourable for photosynthesis, thermal conditions below these values inhibit cambial activity, also with strong implications for the wood growth phenology. The temperature threshold for growth cessation that we obtained for *P. abies* (6.2°C, Table 2) is in fair agreement with these reported values.

The direct environmental control of C allocation that was evidenced in this study is therefore in line with a prominent role of the modulation of sink demand (i.e. cambial activity) by water and low temperature stress in the wood growth of the studied species. We additionally report a significant decrease of C allocation to wood following drought years. This lagged environmental control may be a consequence of an active replenishment of the depleted reserve pool following periods of low leaf gas exchanges,

at the expense of other organ growth (Wiley & Helliker, 2012). It is also consistent with the functional-balance theory (Chen & Reynolds, 1997) that predicts a preferential allocation to fine roots in trees growing in water-limited areas (Doughty *et al.*, 2014).

The modelling of the environmental dependencies of C allocation reduces the bias affecting CASTANEA wood growth predictions

To the best of our knowledge, this study is the first to quantify how the modelling of the environmental control of C allocation affects the wood growth predictions of a process-based model (PBM). Although it was based on a simple modelling framework (Guillemot *et al.*, 2015), our dynamic modelling of C allocation to wood increased substantially the ability of CASTANEA to simulate the spatial (site-to-site) and temporal (year-to-year) variations of wood growth (Fig. 5). The simulated variability in source-related processes (i.e. photosynthesis and maintenance respiration) was indeed unable to explain the sharp decrease of wood growth at sites experiencing strong environmental constraints, where the standard CASTANEA version (STD) clearly overestimated aboveground wood biomass increments (AWBIs) (Fig. 6). As a consequence, the MDF procedure retrieved low wood allocation coefficients in STD in order to improve the overall model performance, which translated into the STD version underestimating growth at low-constraint sites. This bias did not appear in the FULL version, which represented site-wise variations in wood allocation coefficients in response to environmental stress.

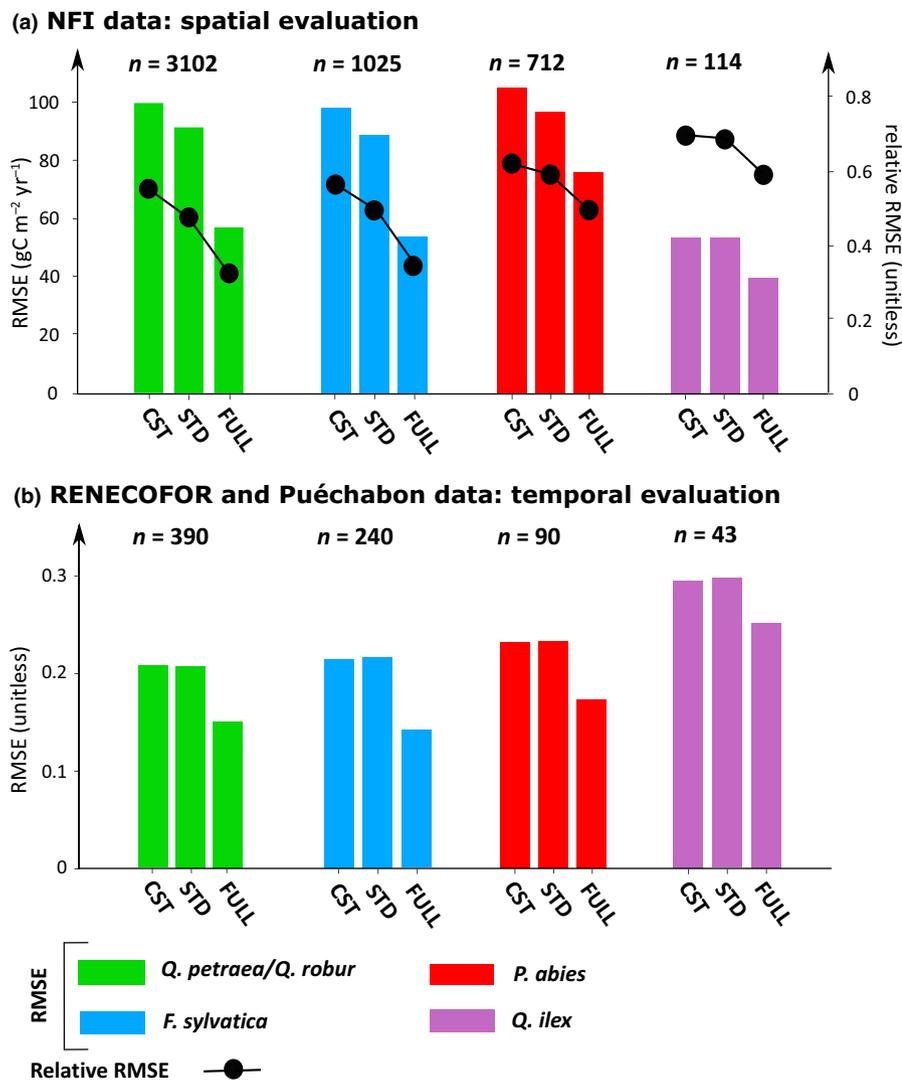


Fig. 5 Comparison of the performances of the CST, STD and FULL versions of CASTANEA using aboveground wood growth (AWBI) evaluation datasets. (a) National forest inventory (NFI) data: average woody biomass increments over 5 yr. (b) RENECOFOR and Puéchabon data: standardized annual woody biomass increments. The relationships embedded in the carbon (C) allocation scheme of the different model versions are described in Table 1.

Importantly, we used an MDF procedure to calibrate the parameters of both ‘static’ and ‘dynamic’ C allocation schemes and to quantify the associated parameter uncertainties (Van Oijen *et al.*, 2005). We therefore ensured that the dynamic simulation of C allocation does not improve CASTANEA performance because of overparameterization, but instead because it represents more accurately those fundamental processes driving annual forest growth. Hence, our results demonstrated that the modelling of the environmental control of C allocation improves the ability of CASTANEA to predict both the spatial and the year-to-year variability of wood growth induced by water and low-temperature stress gradients (Fig. 6). If confirmed by other modelling studies, our finding may explain partly why most PBMs currently used at the regional and global scales obtain inaccurate predictions of C allocation (De Kauwe *et al.*, 2014) and annual wood growth variability (e.g. Babst *et al.*, 2013) when run at particular sites. Moreover, it implies that the modelling of sink demand, by its impact on C allocation, is likely to impact the PBM projections of forest growth, as suggested recently by Lempereur *et al.* (2015) for a Mediterranean *Q. ilex* forest.

Limitations of our modelling approach and need for further research

The results that we present are contingent on the structure and hypotheses formalized in CASTANEA. In particular, the version of CASTANEA used in this study does not include an explicit representation of nutrient cycling and plant–nutrient interactions, which likely impacts forest C budgets (Fernández-Martínez *et al.*, 2014), sink demands and within-tree C allocation (Leuzinger & Hättenschwiler, 2013; Hofhansl *et al.*, 2015). The decrease of leaf expansion during springtime water stress (Muller *et al.*, 2011) also was not considered in this study. Although remaining unquantified at the regional scale, this process may explain part of the reported decline of LAImax along water stress gradients. Our incomplete representation of the mechanisms driving C allocation, together with the site idiosyncrasies that were not accounted for in C supply modelling (e.g. insect outbreaks), are likely responsible for the substantial part of growth variability that remains unexplained by CASTANEA.

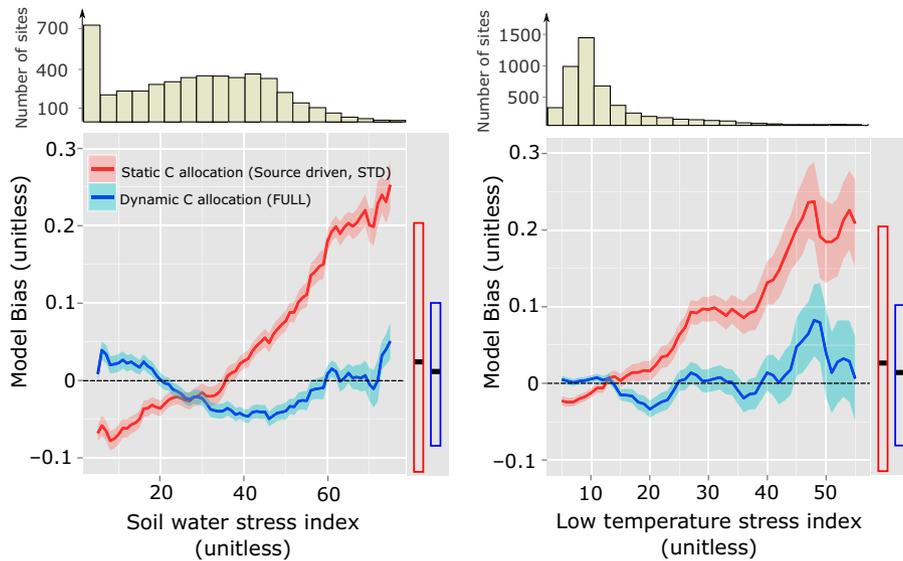


Fig. 6 Bias affecting the predictions of the STD (carbon (C) source driven) and FULL (C sink–source driven) versions of CASTANEA at the national forest inventory (NFI) evaluation sites (all species included). The soil water and low temperature stress index are site average values. The histograms indicate the distributions of soil water stress index (SWS) (left) and low temperature stress index (LTS) (right) in the NFI evaluation dataset. The SWS is an annual bioclimatic index that integrates the water balance and the soil water holding capacity of the site (see main text). The LTS is the number of days with air temperature below 6°C. The continuous lines are moving averages of the model average bias along the SWS and LTS gradients (coloured areas are \pm SEM). Positive and negative bias indicates that the model over- and underestimate wood growth, respectively. The box plots indicate the median, and the first and third quartiles of the bias distribution of the STD (red) and FULL (blue) versions: the average bias of both STD and FULL versions were not statistically different from zero.

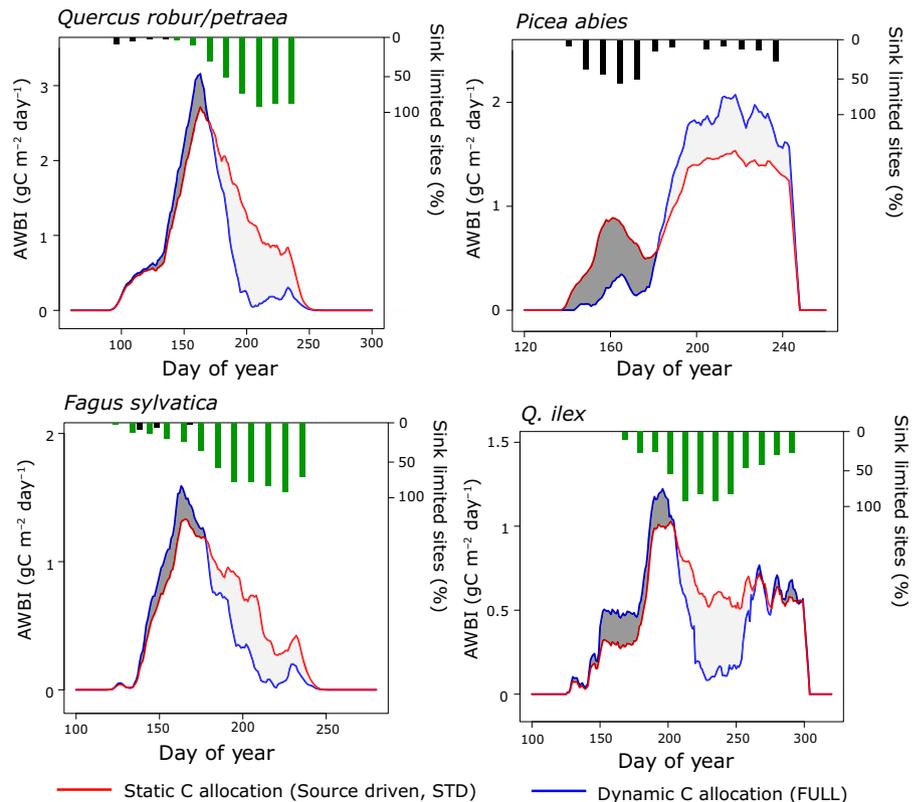


Fig. 7 Comparison of the seasonal wood growth patterns simulated by the STD (carbon (C) source driven) and FULL (C sink–source driven) versions of CASTANEA. For each species, a third of the studied site-years was selected: we retained the years with the highest environmental control of C allocation to wood, that is, with the longest period of allocation cessation (Eqn 6). The bar-plots are the proportion of site-years with no wood growth because of the modulation of sink demand by low temperature (black bars) or water stress (green bars). Grey shaded areas highlight discrepancies between the outputs of the model versions.

Most importantly, the interplay between C reserve pool and structural compartments, which likely plays a crucial role in determining source–sink interaction in trees, is not simulated

explicitly in CASTANEA. Previous modelling attempts (Richardson *et al.*, 2013; Schiestl-Aalto *et al.*, 2015) used C allocation schemes that explicitly account for the impact of C reserve

dynamic on growth – that is, where growth results from C fluxes originating from the reserve pool. However, the reserve measurements that are required to calibrate such models remain scarce, which has so far prevented large-scale studies. We therefore chose to model growth as fractions of net C supply (NPP, Eqn 2), the environmental modulations of C allocation being accounted for through temporal fluctuations of the allocation coefficients (Fig. 1). Under the assumption that CASTANEA is able to predict C supply at our different study sites (see, e.g., Delpierre *et al.*, 2009b, 2012), this approach indeed allowed us to evaluate our modelling of C allocation against leaf and wood growth data, available at large scales.

The processes that underlie the environmental lag effects often found in annual tree growth series remain poorly known. Both source- (e.g. active replenishment of the C reserve pool) and sink-related (e.g. lagged modulation of bud formation) processes could indeed explain the negative effect of previous year's water stress on the C allocation to leaves and wood that we report here (Eqns 1, 5). Further research is therefore needed to unravel and quantify the drivers of C allocation, using seasonal measurements of reserve pool and sink activities (Schiestl-Aalto *et al.*, 2015). Moreover, a significant fraction of the C accumulated in the reserve pool could be sequestered, rather than stored (Sala *et al.*, 2012). This could have important implications for our understanding of C allocation, but is not considered in the current version of CASTANEA. In this regard, isotope tracking techniques may provide crucial data, documenting both the age and fate of C reserves (Richardson *et al.*, 2013).

Conclusions

We used annual to semi-decadal measurements to inform CASTANEA about the environmental modulations of C allocation to leaves and wood. In this regard, it is worth recalling that PBMs used at large scales usually are evaluated against wood biomass stocks (Zaehle *et al.*, 2006; Bellassen *et al.*, 2011a) or allometric scaling metrics (Wolf *et al.*, 2011; Smith *et al.*, 2014), which poorly describe the partitioning of C among the ecosystem pools (Litton *et al.*, 2007). Our results therefore pinpoint the need to calibrate and evaluate PBMs using annual growth data, additionally to stand biomass measurements. Moreover, we call for a thorough calibration and evaluation of PBMs at finer (i.e. seasonal) timescales, which have remained largely overlooked to date, in order to gain greater insight into the processes that drive the allocation of C to wood (Cuny *et al.*, 2015; Schiestl-Aalto *et al.*, 2015; Delpierre *et al.*, 2016a) and, more generally, the forest C cycle. The modelling of the environmental control of C allocation significantly improved the ability of CASTANEA to predict the year-to-year and spatial variability of aboveground forest growth. This calls for introducing these fundamental growth drivers, especially the overlooked environmental modulations of wood sink demand (Körner, 2015), in the C allocation scheme of the current-generation PBMs. The implications of the environmental control of C allocation for the simulations of current and future forest productivity are a crucial challenge for modellers.

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Author contributions

J.G., C.F., E.D., N.K.M-SP. and N.D. designed the study; G.H., K.S. and J-M.O. provided part of the data; J.G. conducted the analyses, with the help of C.F., G.M., G.H. and N.D.; and J.G. wrote the manuscript, with significant inputs from all the authors.

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Supporting Information

Additional Supporting Information may be found online in the Supporting Information tab for this article:

Notes S1 Description of the CASTANEA model.

Notes S2 Description of the datasets.

Notes S3 Presentation and spatial dependences of the FAPARmax measured at the NFI sites.

Notes S4 Calibration procedure.

Notes S5 Prior and posterior distributions of the optimized parameters.

Notes S6 Performance criteria.

Notes S7 Evaluation of the CASTANEA model by age classes using the NFI wood growth evaluation dataset.

Notes S8 Temporal evaluation (year to year) of the CASTANEA model (FULL version) using the RENECOFOR and Puéchabon aboveground wood growth datasets (nonstandardized data).

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