



# Improving the Fagacées growth model with an expanded common beech (*Fagus sylvatica* L.) data series from France and Germany

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## Abstract

• **Key message** The Fagacées growth model was originally designed for application in the Northern half of France. It is a robust model with potential applicability to a larger area, though this potential has not yet been verified. We added new data to the original parameterization data set and our results show that the Fagacées formalism can be generalized.

• **Context** The Fagacées growth and yield model was designed for the management of pure even-aged stands of European beech and served as a prototype to build models for other tree species.

• **Aims** The objective of this study was to improve the growth components of the Fagacées model with additional data from North-Western France to South-Western Germany.

• **Material and methods** Our model was calibrated on several forest inventory data sets. The first one (F) is the original data set that was used to elaborate the equations in the Fagacées model. The second one (F+) is the original data set extended with additional measurements on the same sites and on new sites in Northern France. The third (G) adds complementary data from a forest network in Southwestern Germany. The last one (A) is the aggregate of all these data sets.

• **Results** Fitting the original model equations on the extended F+ dataset led us to modify the equation for stand basal area increment. This new equation also fit the German dataset well. The other equations could be applied to all datasets, some with the same parameter values and some after recalibrating according to the dataset.

• **Conclusion** We conclude that the general form of the model's equations is appropriate for application to other regions, but that a recalibration of the equations is preferable in order to reflect local conditions. The advantage of our approach is that fewer data are required to recalibrate an existing equation than to establish an entirely new one.

**Keywords** *Fagus sylvatica* L. · Growth model · Model calibration · France · Germany

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**Contribution of the co-authors** Gilles Le Moguédec and François Ningre wrote the manuscript; Gilles Le Moguédec and Sidonie Artru supervised the statistical treatment of the data; François Ningre conducted the experiment, managed the data; Axel Albrecht was particularly influential in the development of the discussion

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## 1 Introduction

Over the last decades, a large number of empirical growth-and-yield models have been developed to support forest management decisions and forestry research. Most of these models are designed to predict stand and tree development and their response to silvicultural treatments. They differ in the type of forests studied (even/uneven-aged forests, mixed/pure stands...) and in modeling approach (whole-stand, individual-tree, distance-dependent/independent models...).

In fact, model design cannot be separated from the context for which the models are built or from the user's objectives (Vanclay 1994; Weiskittel et al. 2011). Unlike empirical models, mechanistic approaches allow models to be directly applied to situations different from those for which the parameterization was performed since such models describe the ecophysiological processes leading to the observed effects (Guan et al. 1997; Parysow and

Gertner 1997). In both cases, however, extrapolating the use of a model to other contexts relies on the hypothesis that the underlying phenomena are regular enough.

It is therefore relatively common to find several models developed for the same tree species. Reciprocally, once a model has been designed for a particular species, it may be extended to another species by retaining the general structure of the model and the initial form of the equations. Many examples of these two cases can be found in the FORMODELS database of the European Forest Institute ([http://www.iefc.net/fr/formodels\\_database\\_forest\\_modeles\\_liste/](http://www.iefc.net/fr/formodels_database_forest_modeles_liste/)).

When adapting a model to a new species, the necessity to recalibrate certain parameters is obvious. Another way to extend a model would be to adapt it to a given locality within its original validity area. In this case, recalibration becomes an integral part of the model's development and evaluation (Vanclay 1994). Methods such as cross-validation can be used, notably to assess possible bias. However, sufficient independent data are necessary to guarantee the efficiency of such methods and some concern has been expressed as to whether cross-validation is an appropriate method for model evaluation and improvement (Kozak and Kozak 2003).

A model can also be extended to a new geographic area. In this case, not only should the parameter values be recalibrated, the algebraic form of the equations should also be reconsidered since the new area may have different forest conditions which the former equations may no longer represent.

Nevertheless, the recalibration of a growth model for the purpose of applying it to other regions is actually quite rare, even if though it may be necessary (Vanclay and Skovsgaard 1997) or possible (Albrecht et al. 2009; Albrecht et al. 2010; Lacerte 2006; Schmid et al. 2006). The lack of available long-term tree data based on frequent remeasurements is often the main obstacle.

The Fagacées growth and yield model was designed by Dhôte during the 1990s (Dhôte 1991) for the management of pure even-aged stands of common beech (*Fagus sylvatica* L.), which is the most important broadleaved tree species in Central Europe (Köble and Seufert 2001).

The model incorporated all the data available at the time from experimental trials located in northern France. These data represent only a few sites but they are distributed over a large geographical zone and a large part of the common beech distribution range in France.

The model's main originality is that individual-tree diameter growth is organized in a top-down approach; that is, the main equations are established at the stand scale (Le Moguédec and Dhôte 2012). This approach makes the model robust, i.e., it will not have an aberrant behavior when it is extrapolated beyond the domain for which it was originally validated.

Moreover, the Fagacées model served as a prototype to build models for other tree species such as *Quercus petraea* Liebl. (Dhôte 1999), *Abies alba* Mill. (Bontemps et al. 2009) and *Eucalyptus* (Saint-André et al. 2002). In each of these

examples, the original growth equations were easily adapted to other species with only minor modifications in the algebraic form of the basic growth equations.

This family of forest models is frequently used by the French National Forest Office (ONF) to establish silvicultural guidelines (Jarret 2004; Pilard-Landeau and Simon 2008; Sardin 2008, 2012, 2013) and has more recently helped researchers study carbon storage (Fortin et al. 2012), forest growth and windstorm damage in beech forests (Fortin et al. 2014).

However, though the Fagacées model (in its version for *Fagus sylvatica* L.) is applied in France beyond its original validity zone—for example, in the Pyrenées Mountains (Sardin 2013)—there are no long-term experimental data available in those regions to locally recalibrate the equations. Thus, the performance of the model under these conditions has never been assessed.

Our objectives were (i) to validate the model by adding new data from different geographic regions to the original parameterization data set, i.e., to assess whether the algebraic form of an equation is still appropriate after fitting that equation to extended data and to improve the model by removing potential bias in the original version; and (ii) to check whether the parameter estimates changed significantly when the basic equations were recalibrated with extended data sets from the same geographic region.

In this study, we focus on the Fagacées equations for height and diameter increment, which are at the core of the model.

## 2 Materials and methods

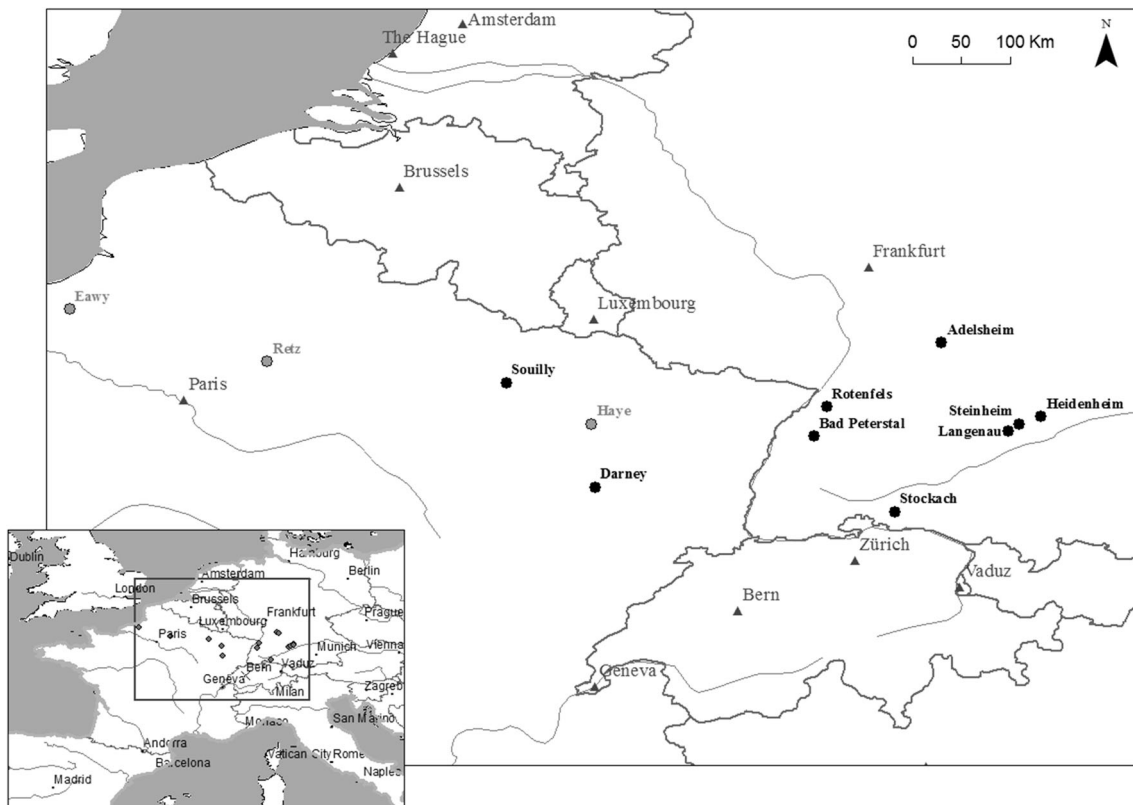
### 2.1 Data description

The data used in this study come from mostly pure even-aged stands of naturally regenerated common beech (*Fagus sylvatica* L.). The studied stands were selected from two networks of permanent thinning trials located at similar latitudes in Northern France and South-Western Germany (Fig. 1) (Dhôte 1996; Hein et al. 2007; Klädtke 2002).

Altogether, the data cover a significant east-to-west gradient and a wide range of biogeographical and ecological conditions (Table 1).

Climatic conditions in the study area vary from an oceanic climate in Normandy to a semi-continental climate in Lorraine and Baden-Württemberg with an intermediate climate in Picardy and the North-Eastern Paris Basin, the latter characterized by lower precipitation than the other climates and high average atmospheric humidity (Dhôte 1996).

The two networks (French and German) mainly differ in altitude, with only slight differences in average annual temperatures and in May-to-September temperatures and precipitation. The French network ranges from 140 to 440 m in altitude and the German network from 237 to 671 m. The average annual temperature is 8.9 °C for France and 7.8 °C for Germany. The



**Fig. 1** Geographical location of the inventoried French and the German stands

average May-to-September temperature is 14.8 °C in France and 14.4 °C in Germany. The average May-to-September precipitation is 485 mm in France and 449 mm in Germany.

Both the German and French networks present similar, and relatively high, levels of site index, revealing high general productivity conditions (Bontemps et al. 2007; Hein 2007). The French network presents much higher variability, especially in terms of age range, plot area (Table 2a), and silvicultural treatment (Fig. 2).

All the data used in this study include the same information collected on identified individual-trees: species, status (alive, dead, dry, windfall, [...], thinned, missing, ...) and diameter [...] at breast height (dbh); in addition, trees height was measured on a subsample on each plot.

The original data used to build the Fagacées model included all the inventories carried out before 1990 in the 13 original plots located in five forests (Eawy, Retz, Haye, Souilly, and Darney) ranging from Northwestern to Northeastern France (Table 2a). The new enlarged data set includes the inventories carried out on these same original plots after 1990, and inventories on 48 additional plots located in the same forests. Thus, the total French network was brought up to 61 plots (11 trials). Within this network, the number of inventories carried out between 1904 and 2009 differs among plots (from one to 22 inventories with intervals ranging from 1 to 16 years). In this paper, we refer to the original data set as “F” and to the extended data set (original + additional measurements on the same sites and on new sites) as “F+”.

The German network is composed of 26 plots from two experimental networks, called “Altherr” and “Merkel” after the founders of the experiments, both located in Southwestern Germany. The Altherr network is composed of 20 plots and the Merkel network is composed of six plots (Table 2b). As in the French network, the number of inventories differs among plots: between 1949 and 2009, 8 to 11 inventories with intervals ranging from 2 to 8 years were carried out. We refer to this German data set as “G”.

We compiled four data sets from these raw data: the original data set from which the Fagacées model was established (“F”), the same data completed with additional measurements (“F+”), the separate German data set (“G”), and all the data grouped together (“A”).

For the French “F+” network, a total of 105,166 dbh measurements and 5,051 height measurements (4.9% of the dbh measurements) were collected on 14,982 beech trees. For the original “F” data set, there were 48,228 dbh and 2,315 height measurements. For the German network, a total of 40,613 dbh measurements and 12,104 height measurements (30% of the dbh measurements) were carried out on 7,947 beech trees (Table 3).

## 2.2 Fagacées growth model structure and equations

In this study, we focus only on the growth components of the Fagacées model, a detailed presentation of which can be found in Dhôte (1991) and Le Moguédec and Dhôte (2012).

**Table 1** Environmental description of experimental sites. Climatic variables cover the period 1961–90. Sources : database Digitalis (Bertrand et al. 2011) for French plots and Deutscher Wetterdienst (DWD) for German plots

Country	Location (Department)	Experimental site	Altitude (m)	Mean annual temperature (°C)	Mean annual precipitation (mm)	Mean annual May-September temperature (°C)	Mean annual May-September precipitation (mm)
Germany	Meuse Seine-Maritime Vosges	Souilly	315	8,6	971	14,5	525
		Eawy «CampCusson»	180	9,1	875	14,0	459
		Damey «Clinal :20 plots»	440	8,5	1039	14,8	577
	Vosges Meurthe-et-Moselle Meurthe-et-Moselle Aisne Aisne	Damey «Sainte Marie»	392	8,8	999	15,1	558
		Haye «Charlemagne»	397	8,2	947	14,4	522
		Haye «Chavigny»	382,5	8,3	945	14,4	521
		Haye «Epiceas»	403	8,2	951	14,4	523
		Retz «Mortefert»	150	9,6	731	15,2	411
		Retz «Pré Des Seigneurs»	140	9,7	727	15,3	409
		Retz «Chrétienne»	155	9,6	730	15,2	409
Retz «Faîte»	186	9,4	759	14,9	421		
Country	Location	Experimental site	Altitude (m)	Mean annual temperature (°C)	Mean annual precipitation (mm)	Mean annual May-September temperature (°C)	Mean annual May-September precipitation (mm)
Germany (Baden-Württemberg)	Adelsheim	«Bu 223»	343	8,7	894	15,3	370
		Adelsheim	325	8,6	894	15,1	371
	Adelsheim	«Bu 224»	323	8,8	844	15,4	382
		«Bu 225»	616	6,9	919	13,5	421
	Steinheim	«Bu 226»	661	7,2	899	13,8	436
		Langenau	654	7,1	907	13,7	448
	Langenau	«Bu 227»	671	7,1	907	13,7	448
		«Bu 228»	611	7,0	916	13,7	451
	Heidenheim	«Bu 229»	587	7,0	917	13,7	454
		«Bu 230»	237	9,7	1132	16,2	490
	Heidenheim	«Bu 231»	593	8,0	1629	13,1	717
		Rotenfels	532	8,2	787	15,2	406
	Bad-Peterstal	«Bu 237»					
		«Bu 238»					
	Stockach	«Bu 239»					
		«Bu 239»					

**Table 2a** French study sites and experimental plot characteristics

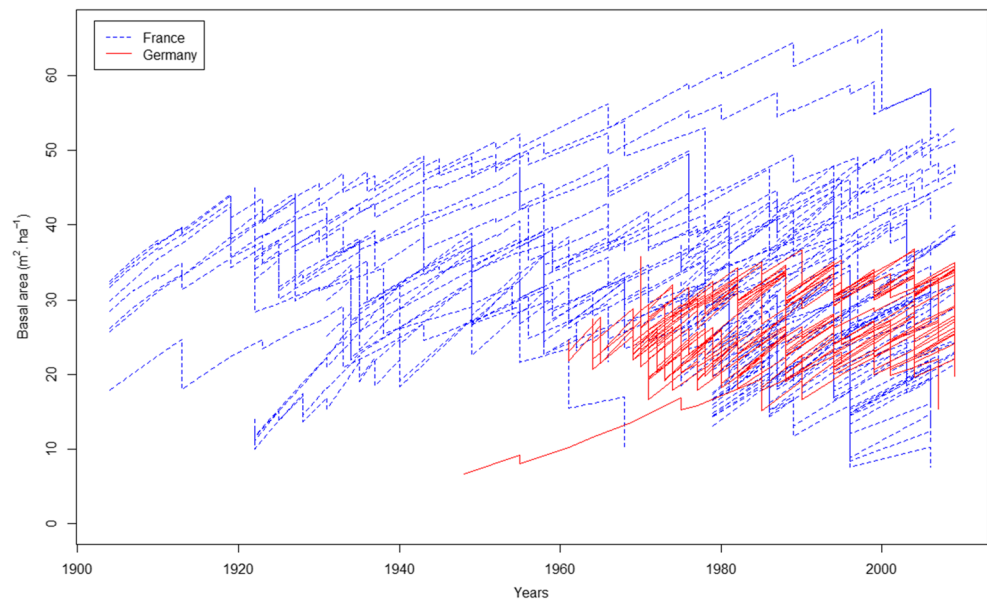
Country	Location (Department)	Experimental site	Plot	Set of plots <sup>1</sup>	Plot size (ha)	Study period	Age at first-last inventory	Number of inventories	Delta years	Density (per hectare) at first-last inventory	Percentage of Beech at site index (top height at 100 years)	
France	Meuse	Souilly	A (1 to 4)	Ad	0.8	1975 – 2009	47–81	16	34	3075–505	91–99	34.9
			B (1 to 4)	Ad	0.8	1975 – 2009	47–81	16	34	6125–2320	84–82	37.7
		C (1 to 4)	Ad	0.8	1975 – 2009	47–81	16	34	3825–940	91–97	38.6	
			Ad	0.8	1975 – 2009	47–81	16	34	5095–1875	99–96	38.0	
	Seine-Maritime	Eawy « CampCusson »	1	Or	1	1931 – 2009	51–129	14	78	510–87	100–100	33.0
			2	Or	1	1931 – 2009	51–129	14	78	805–158	99–100	
		3	Or	1	1931 – 2009	51–129	14	78	242–81	98–100		
			4	Or	1	1931 – 2009	51–129	14	78	751–191	95–97	
	Vosges	Damey « Clinal: 20 plots »	1 to 20	Ad	0.05	1979 – 2006	64–91	8	27	740–402	98–99	31.4
			1	Ad	1	1966	78	1	0	639	74	33.0
	Vosges	Damey « Sainte Marie »	2	Ad	1	1962	74	1	0	638	79	
			3	Ad	1	1958–1966	70–78	3	8	1134–519	83–83	
Meurthe-et-Moselle	Haye « Charlemagne »	1	Or	0.25	1904–1997	49–142	18	93	1472–232	94–100	33.9	
		2	Or	0.25	1904–1997	49–142	18	93	1352–156	97–100		
		3	Or	0.25	1904–2006	49–151	20	102	1816–344	92–100		
Meurthe-et-Moselle	Haye « Chavigny »	1	Or	0.2	1904–1995	47–138	18	91	1480–225	95–100	34.0	
		2	Or	0.2	1904–1995	47–138	18	91	1295–155	97–100		
		2	Ad	0.25	1904–2006	48–150	22	102	952–184	76–100	31.0	
Meurthe-et-Moselle	Haye « Epiceas »	2	Ad	0.25	1904–2006	48–150	22	102	532–68	57–42		
		3	Ad	0.25	1904–2006	48–150	22	102	1340–344	78–99		
		3	Ad	0.25	1904–2006	48–150	22	102	135–35	96–100	28.9	
Aisne	Retz « Montefert »	1	Ad	1	1922–1968	165–211	9	46	247–105	95–98	33.8	
		1	Ad	1	1922–1968	127–173	9	46				
Aisne	Retz « Pré Des Seigneurs »	1	Ad	0.25	1922–1978	62–118	10	56	608–120	92–100	36.4	
		2	Ad	0.25	1922–1978	62–118	10	56	468–196	82–96		
		3	Ad	0.25	1922–1978	62–118	10	56	532–332	88–99		
		4	Ad	0.5	1922–1978	62–118	10	56	578–76	85–96		
Aisne	Retz « Faite »	1	Or	0.2	1922–2006	35–119	15	84	2255–190	97–100	33.7	
		2	Or	0.2	1922–2006	35–119	15	84	2465–210	98–100		
		3	Or	0.2	1922–2006	35–119	15	84	2325–230	98–100		
		4	Or	0.2	1922–2006	35–119	15	84	2065–195	98–100		

Or Original plot used to build Fagacées; Ad additional plot

Table 2b German study sites and experimental plot characteristics

Country	Location	Network	Experimental site	Plot size (ha)	Study period	Age at first-last inventory	Number of inventories	Delta years	Density (per hectare) at first-last inventory	Percentage of beech at first-last inventory	Percentage of beech at site index (m) (top height at 100 years)
Germany (Baden-Württemberg)	Adelsheim	Altherr	«Bu 223 »	1	1969–2009	54–94	9	40	1086–257	84–97	33.2
			« Bu 224 »	2	1969–2009	54–94	9	40	1064–307	82–88	
			« Bu 225 »	2	1969–2009	63–103	9	40	995–255	90–93	31.4
	Steinheim		« Bu 226 »	2	1969–2009	58–98	9	40	1188–428	90–93	
			« Bu 227 »	1	1971–2009	74–112	8	38	503–148	89–97	34.0
			« Bu 228 »	2	1971–2009	74–112	8	38	523–210	96–99	
	Langenau		« Bu 229 »	1	1971–2009	78–116	9	38	808–288	96–100	30.4
			« Bu 230 »	2	1971–2009	78–116	9	38	652–334	91–99	
			« Bu 231 »	3	1971–2009	78–116	9	38	712–204	94–97	
	Heidenheim		« Bu 232 »	1	1971–2009	69–107	9	38	892–303	91–100	33.3
			« Bu 233 »	2	1971–2009	69–107	9	38	1064–250	90–100	
			« Bu 234 »	1	1970–2009	62–101	9	39	1398–340	92–99	34.4
Heidenheim		« Bu 235 »	2	1970–2009	62–101	9	39	1447–1057	90–100		
		« Bu 236 »	3	1970–2009	62–101	9	39	4750–436	89–99	33.1	
		« Bu 237 »	1	1970–2009	70–109	9	39	2929–964	94–99		
Heidenheim		« Bu 238 »	2	1970–2009	70–109	9	39	726–180	94–98		
		« Bu 239 »	1	1971–2009	88–126	9	38	1083–487	98–100	28.6	
		« Bu 240 »	2	1971–2009	88–126	9	38	1160–577	99–100		
Rotenfels	Merkel	« Bu 241 »	1	1971–2009	78–116	8	38	725–400	87–93	29.8	
		« Bu 242 »	2	1971–2009	78–116	8	38	745–225	96–100		
		« Bu 243 »	1	1964–2007	62–105	9	43	361–100	29–100	35.6	
Bad-Peterstal		« Bu 244 »	2	1964–2007	62–105	9	43	1160–290	32–94		
		« Bu 245 »	3	1964–2007	62–105	9	43	363–137	31–100		
		« Bu 246 »	1	1948–1995	47–94	10	46	150–114	88–100	32.9	
Stockach		« Bu 247 »	1	1961–2007	50–96	11	46	1188–120	35–100	32.9	
		« Bu 248 »	2	1961–2007	51–97	11	46	964–124	28–97		

**Fig. 2** Comparison of changes in stand basal area in the French (blue dashed lines) and German (red solid line) networks



The Fagacées model has a simple organization (see Fig. 3), defined by a limited set of equations with few variables and parameters. All the notations and definitions of the equation variables and parameters are presented in Table 4.

Stand growth is mainly driven by the top-height curve, which is unaffected by thinning (except for very low stand density). An important assumption of the model is that the top-height curve is almost independent from forestry practices. However, this curve is parameterized by its value at age 100, that is used as a site index.

The main originality of the Fagacées model is that it presents a top-down organization with two levels: the whole-stand level and the individual-tree level. At stand level stand growth, or the sum of the individual-tree basal area increment values, is defined by the product of the stand area ( $S$ ) and the stand basal area increment ( $\Delta G$ ). After that, stand growth is distributed among the trees within the stand by an intermediate Eq. (1) where  $\delta g$  is the individual basal area increment.

$$\frac{1}{10000} \sum_{trees} \delta g(\sigma) = \Delta G \cdot S \quad (1)$$

This equation depends on a parameter  $\sigma$ , that represents the minimum diameter for radial growth. This threshold is numerically adjusted at every step to balance global growth and the sum of the individual growths as in Eq. (6).

### 2.2.1 Stand basal area increment

In the Fagacées model, basal area growth (Eq. 2) is modeled using the potential x modifier method (Reed et al. 2001). The potential  $f_1$  expresses the maximum potential stand growth

and the multiplicative modifier  $f_2$  expresses the reduction in maximum growth related to density index. In Eq. (4) below, only trees whose diameter exceeds a given threshold are used. The density index is computed as the sum of those diameters divided by the plot size (Eq. 5).

$$\Delta G = f_1(\Delta H_0) \cdot f_2(\Sigma_\sigma) \quad (2)$$

With

$$f_1(\Delta H_0) = p_1 + p_2 \cdot \Delta H_0 \quad (3)$$

$$f_2(\Sigma_\sigma) = 1 - e^{-(r_1+r_3)\Sigma_\sigma} \quad (4)$$

$$\Sigma_\sigma = \frac{1}{S} \sum_{d_{130} \geq \sigma} d_{130} \quad (5)$$

where  $\Delta H_0$  is the top height increment, and  $p_1, p_2, r_1, r_2,$  and  $r_3$  are parameters to be estimated.

### 2.2.2 Individual-tree basal area increment

The basal area increment for a given tree is expressed by Eq. (6).

$$\delta g = \gamma \cdot \max(d_{130} - \sigma; 0) \quad (6)$$

With

$$\gamma = f_1(\Delta H_0) \cdot (r_3 + r_1 \cdot e^{-r_2 \cdot \Sigma_\sigma}) \quad (7)$$

Only trees whose diameter exceeds the threshold  $\sigma$  at the current step will grow (Fig. 4). The  $\gamma$  parameter represents the potential maximum diameter increment of a given tree. In the model, individual-tree basal increment is computed in 3-year steps.

**Table 3** Number of measurements performed on the France (F), extended France (F+) Germany (G) and All (A) data sets

	France (F) <i>original</i> <i>calibration data</i>	France (F+)	Germany (G)	All (A) <i>all data</i> <i>sets grouped</i> <i>together</i>
Plots	13	<b>61</b>	<b>26</b>	<b>87</b>
Inventories	173	<b>753</b>	<b>235</b>	<b>988</b>
dbh	49139	<b>112669</b>	<b>52702</b>	<b>165371</b>
<i>Beech only</i>	<i>48228</i>	<i>105166</i>	<i>40613</i>	<i>145779</i>
Height	2315	<b>5152</b>	<b>12641</b>	<b>17793</b>
<i>Beech only</i>	<i>2315</i>	<i>5051</i>	<i>12104</i>	<i>17155</i>

### 2.2.3 Individual-tree height

The tree height is computed from the tree diameter following the allometric relation below (Eq. 8):

**Table 4** Main notations and units used in this article

Symbol	Description	Unit
$d_{130}$	Tree diameter at 1.30 meters	cm
$h$	Height of a tree	m
$H_o$	Top height of the stand	m
$G$	Basal area of the stand	$m^2 ha^{-1}$
$g$	Basal area of the tree	$cm^2$
$\sigma$	Threshold diameter for individual growth	cm
$\Sigma_\sigma$	Density index	$cm ha^{-1}$
$\gamma$	Maximum potential diameter increment	cm
$\gamma_a$	Annual maximum potential diameter increment	$cm year^{-1}$
$\Delta H_o$	Top height increment	$m year^{-1}$
$\Delta T$	Time interval	year
$\Delta G$	Annual stand basal area increment	$m^2 ha^{-1} year^{-1}$
$\delta g$	Annual tree basal area increment	$cm^2 year^{-1}$
$S$	Plot size	ha
	Parameters used for the allometric relation for individual height	
$q_1$		$m cm^{-1}$
$q_2$		-
	Parameters used for increment of basal area	
$p_1$		$m^2 ha^{-1} year^{-1}$
$p_2$		$m ha^{-1}$
$p_3$		$m ha^{-1} year^{-1}$
$r_1$ to $r_3$		$ha cm^{-1}$
$r_{1+3}$		$ha cm^{-1}$
$l_o$		cm
$l_1$		$m^{-1}$
$l_2$		$year m^{-1}$
$l$		$year^{-1}$

$$h = 1.30 + \frac{\alpha(d_{130}) - \sqrt{\alpha^2(d_{130}) - 4\pi q_1 q_2 (H_o - 1.30) \cdot d_{130}}}{2q_2} \quad (8)$$

$$\text{with } \alpha(d_{130}) = H_o - 1.30 + \pi q_1 \cdot d_{130} \quad (9)$$

## 2.3 Statistical methods

All graphic and statistical analyses were performed with the statistical software R version 3.1.0 (R Core Team (2014)).

### 2.3.1 Calibration of the equations

We calibrated our model with single-tree height and dbh information from the French and German inventories. Top height ( $H_o$ ), diameter threshold ( $\sigma$ ), density index ( $\Sigma_\sigma$ ), and maximum growth in diameter ( $\gamma$ ) were determined from these individual tree data.

We used nonlinear regressions (nls) to estimate our growth model equation parameters. We used the parameter values from the original version of the Fagacées model as initial values to fit the model. For stand level equations (Eq. 2, Eq. 3, Eq. 4), the observations were weighted by plot area. We tested the quantitative part of the model (including verifications for normality, homoscedasticity, and independence of residuals) according to graphical criteria and set the level of significance at  $\alpha = 0.05$  for statistical tests. Due to heteroscedasticity, Eq. (7) was fitted on log-transformed data. Log-transforming makes it possible to estimate and test parameters but a bias correction must be applied when using the model for predictions on back-transformed data (Baskerville 1972).

All the equations were successively and independently fitted to all our data sets.

At each inventory date, we obtained an estimate and the standard deviation for  $\sigma^1$  and  $\gamma$  from Eq. (6). This allowed us to weight  $\gamma$  by its precision (more exactly by the squared inverse of the standard deviation) in order to adjust Eq. (7).

### 2.3.2 Top-height estimation ( $H_o$ )

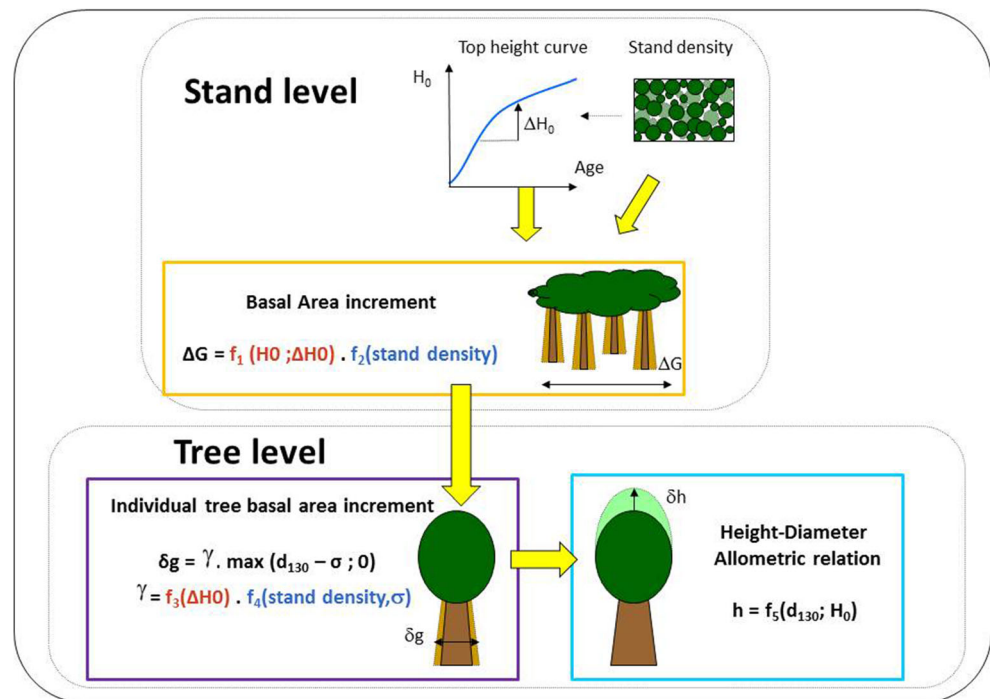
The measurements cover a period from 1904 to 2009. The first height measurements were mainly of felled trees, but the measurement method gradually shifted to standing trees and this became the only method by the mid-twentieth century. Of course, bias and precision may have changed as a result, but we did not detect any real difference.

The main consequence of the change in methodology concerns the representativeness of the trees measured in height, as they are only those that have been thinned. For this reason, we did not use the top height indicated in the data (when avail-

<sup>1</sup> The  $\sigma$  parameter was numerically adjusted to balance Eq. (1). We used the bootstrap method to estimate the standard deviation of the parameter  $\sigma$ .



**Fig. 3** Diagram of the Fagacées model. The three boxes represent the growth component of the model: basal area increment, individual-tree increment and the allometric height-diameter relationship. Source: Le Moguédec and Dhôte 2012



able) but instead used another methodology based on simulations of the height of all trees for all plots according to the observed relationship between individual height and diameter.

We applied a standard definition of top height, that is the average height of the 100 largest-diameter trees per hectare. As a consequence, if the stand size was  $n$  ares, only the  $n$  biggest trees were used for the top-height computation.

For each plot, individual height measurements were used to fit a non-parametric regression (LOESS method), with stand age and individual diameter as predictors. This model was then used to simulate a height with respect to the prediction variance for each tree for which no height measurement was available at a given date. We thus obtained a height value, either measured or simulated, for each tree at each date. The top height at each date was then computed from these values.

### 3 Results

The parameters of the equations are interdependent. First, we computed all the variations between two successive inventories ( $\delta g$ ,  $\Delta G$ ,  $\Delta H_0$ ). Then the corresponding  $\sigma$  and  $\gamma$  values were numerically adjusted at each step according to Eq. (1) and Eq. (6). From these values, we fitted the stand basal area increment model according to Eq. (2) and its dependencies. We then used the result to fit the individual basal area increment (Eq. 7). Finally, we fitted the Eq. (8) for individual height-diameter relationships.

For each set of equations, we first fitted the original Fagacées model equations on all the data sets (including the original one),

then checked for potential fit problems on the new data sets (“F+”, “G” and “A”). In some situations, we had to modify the original equation. In these cases, we verified that the new equations could be applied to the original data set “F”.

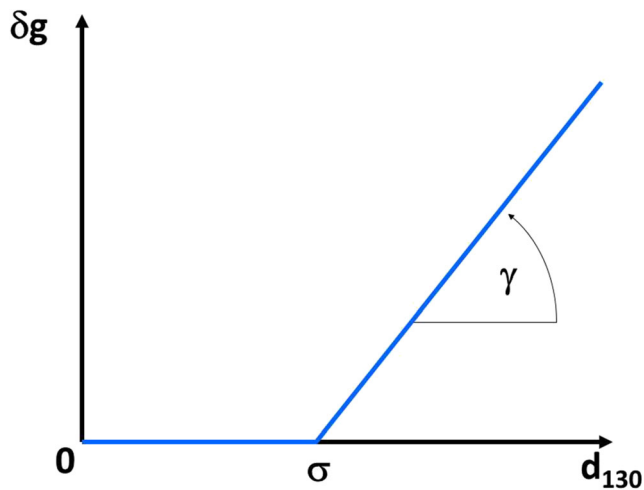
#### 3.1 Stand basal area increment (Eq. 2)

Equation (2) expresses the stand basal area increment  $\Delta G$  as the product of a potential growth ( $f_1$ , Eq. 3) and a modifier ( $f_2$ , Eq. 4).

Simply observing Eq. (4) reveals that the model is over-parameterized; the  $r_1$  and  $r_3$  parameters cannot be estimated independently. In practice, to fit  $f_2$ , we first merged the  $r_1$  and  $r_3$  parameters into one parameter  $r_{1+3}$  (Eq. 10). This Eq. (10) fits all the data sets well. Parameter values remained within the same order of magnitude (Table 5). Parameters  $r_1$  and  $r_3$  can then be separated only later, in Eq. (7)

$$f_2(\Sigma\sigma) = 1 - e^{-(r_{1+3})\Sigma\sigma} \quad (10)$$

We then fitted Eqs. (3) and (10) using Eq. (2). The resulting parameters are significant for all our data sets. However, the graphical examination of the residuals for top height showed a clear negative linear tendency for all cases other than the original data set “F”, (Fig. 5 shows the residuals for data set “F+”). Since this trend did not occur with the original Fagacées calibration data set “F”, we added the variable top height to Eq. (3), which represents the potential part of the basal area increment function of Eq. (2). Therefore, Eq. (3) was replaced by Eq. (11).



**Fig. 4** Modeling individual-tree basal area increment ( $\delta g$ ) in relation with diameter. Source: Le Moguédec and Dhôte 2012

$$f_1(\Delta H_0, H_0) = p_1 + p_2 \cdot \Delta H_0 - p_3 \cdot H_0 \quad (11)$$

Finally, Eq. (11) for  $f_1$  and Eq. (10) for  $f_2$  were used to fit the basal area increment. The model performance improved: as no residual trends are visible. Graphical examination of the residuals showed that they follow a normal distribution and show no systematic bias (Appendix Fig. 10 and Appendix Fig. 11). All the  $p$  values were significant ( $p < 10^{-2}$ ) except for parameter  $p_2$  ( $p = 0.417$ ) in data set “G” (Table 5). For parameters  $p_1$ ,  $p_2$ , and  $p_3$ , the standard errors associated to the data set “G” were systematically larger than those associated to the data set “F+”. This was due to the small number of inventories in the data set “G”. We suppose that with a similar number of inventories, the standard errors would have been comparable between estimations from data sets “G” and “F+”.

The parameter values (Eq. 10 and Eq. 11) estimated for the data sets “F+” and “G” were not significantly different. We used the bootstrap method (Huet et al. 1992) to examine the differences in parameter values between these two data sets. However, without recalibration, Eq. (2) for the data set “G” would have resulted in a systematic bias of  $0.06 \text{ m}^2 \text{ ha}^{-1} \text{ year}^{-1}$  on average (or an 8% relative bias), which would have led to systematic underestimations at the stand level (Fig. 6). Figure 12 in Appendix compares the predictions from both parameterization with observed values.

### 3.2 Individual-tree basal area increment

Individual-tree increment is dependent on the potential maximum diameter increment  $\gamma$  and the threshold diameter for individual growth  $\sigma$ .

In addition, the  $\gamma$  coefficient defined by Eq. (7) is dependent on the density index, top height growth, and three other parameters ( $r_1$ ,  $r_2$ ,  $r_3$ ). We therefore fit individual tree increment by

adjusting  $\gamma$ . We used the result of Eq. (10), which gives an estimation of the parameter  $r_{1+3}$ , as a constraint to fit Eq. (7).

The  $\gamma$  coefficient was originally fitted for use in simulations with a 3-year time-step. Due to the irregular time intervals in our datasets (1 to 16 years), we also fitted an annual maximum potential diameter increment  $\gamma_a$  (Eq. 12).

We found no clear tendency between  $\gamma_a$  and the predictor variables implicated in Eq. (7) of the original model for any of our datasets. However, graphical examination of the relation between  $\gamma_a$  annual increment and various other predictor variables revealed a relation between  $\gamma_a$  and the time interval between inventories  $\Delta T$  (Fig. 7).

This finding led us to replace the original expression of the  $\gamma$  parameter (Eq. 7) with a new Eq. (12), which depends on top height  $H_0$ , top height increment  $\Delta H_0$ , and time interval between two successive inventories  $\Delta T$ . Four new parameters  $l$ ,  $l_0$ ,  $l_1$ , and  $l_2$  were then estimated.

$$\gamma_a = l_0 \cdot \frac{e^{l_1 \cdot H_0 + l_2 \cdot \Delta H_0}}{(\Delta T)^l} + \varepsilon \quad (12)$$

We then fitted this new equation to the “F+” and “G” data sets separately. The model fit converged in both cases and the residuals followed a Gaussian distribution. We detected no clear trends or heteroscedasticity for the residuals (results not shown).

The estimated parameter values for the two data sets were not significantly different (Table 6) (for the same reasons mentioned previously for the parameters of Eq. 10 and Eq. 11).

As noted earlier for Eq. (2), not recalibrating Eq. (12) for the German data would have resulted in a systematic bias of  $0.008 \text{ cm/year}$  on average (23.4% of the relative bias) (Fig. 8).

### 3.3 Height-diameter allometric relationships

Height versus diameter showed a nonlinear relationship within all data sets (Fig. 9). The different scatterplots could be superimposed, with the same central tendency and a similar dispersion, although the German data seem more concentrated around the tendency. The fitted models confirmed this observation; they produced parameter values very close to each other in the different adjustments (Eq. 8, Table 7). The height-diameter relationship was very similar across the different data sets. However, because of the large number of data at the tree level, the parameter values were significantly different.

## 4 Discussion

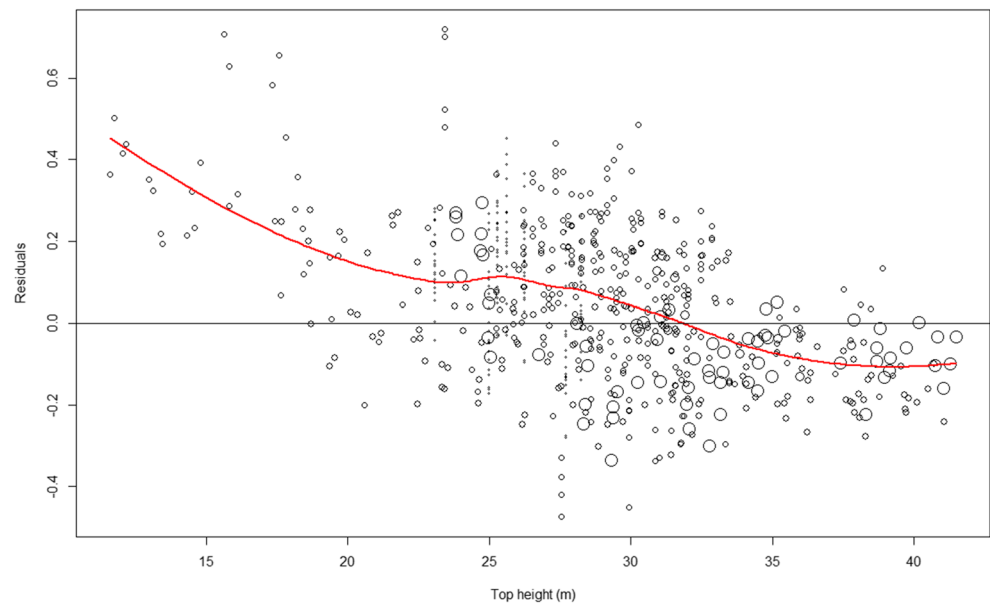
The objective of this study was to improve the growth component of the Fagacées model by including additional data from North-Western France and South-Western Germany. The additional data contains three times as many dbh

**Table 5** Parameter values and associated standard errors (Std Error) and residual standard deviation ( $\sigma\epsilon$ ) of the stand basal area increment ( $\Delta G$ ) equation fitted by R function "nls" (nonlinear least squares) on the France (F), extended France (F+) Germany (G) and All (A) data sets. The column France (F) represents equations and the parameter values from the original version of the Fagacées model fitted on the Original France data set. For parameter units refer to Table 4

Dataset	Parameter	P1	P2	P3	r <sub>1</sub>	r <sub>2</sub>	r <sub>1+3</sub>	$\sigma_\epsilon$	Equations number
<b>France (F)</b> original calibration data	Value	0.1512	2.0525	—	$3.66 \times 10^{-4}$	$1.67 \times 10^{-4}$	—	—	Eq.3; Eq.4
	value {*}	1.34	$4.74 \times 10^{-2}$	$2.33 \times 10^{-2}$	—	—	$2.8 \times 10^{-4}$	—	Eq.10; Eq.11
	estimate upper	1.41	$11.85 \times 10^{-2}$	$2.55 \times 10^{-2}$	—	—	$3.38 \times 10^{-4}$	$7.14 \times 10^{-2}$	
<b>Germany (G)</b>	Std Error	1.49	$18.94 \times 10^{-2}$	$2.78 \times 10^{-2}$	—	—	$4.24 \times 10^{-4}$	—	
	p-value	$3.87 \times 10^{-2}$	$3.61 \times 10^{-2}$	$1.15 \times 10^{-3}$	—	—	$3.04 \times 10^{-5}$	—	
	value {*}	$2.08 \times 10^{-160}$	$1.10 \times 10^{-3}$	$5.8 \times 10^{-82}$	—	—	$1.68 \times 10^{-26}$	—	
<b>All (A)</b> all data sets grouped together	Std Error	1.42	$-8.8 \times 10^{-2}$	$2.2 \times 10^{-2}$	—	—	$2.12 \times 10^{-4}$	—	
	p-value	1.57	$6.2 \times 10^{-2}$	$2.66 \times 10^{-2}$	—	—	$2.55 \times 10^{-4}$	$6.06 \times 10^{-2}$	
	value {*}	1.72	$21.29 \times 10^{-2}$	$3.12 \times 10^{-2}$	—	—	$3.07 \times 10^{-4}$	—	
95% confidence intervals	Std Error	$7.58 \times 10^{-2}$	$7.63 \times 10^{-2}$	$2.37 \times 10^{-3}$	—	—	$2.64 \times 10^{-5}$	—	
	p-value	$1.07 \times 10^{-51}$	0.42	$4.43 \times 10^{-23}$	—	—	$2.08 \times 10^{-18}$	—	
	value {*}	1.39	$6.45 \times 10^{-2}$	$2.43 \times 10^{-2}$	—	—	$2.92 \times 10^{-4}$	—	
Approximate 95% confidence intervals	Std Error	1.45	$12.9 \times 10^{-2}$	$2.64 \times 10^{-2}$	—	—	$3.33 \times 10^{-4}$	$7.09 \times 10^{-2}$	
	p-value	1.52	$19.34 \times 10^{-2}$	$2.84 \times 10^{-2}$	—	—	$3.85 \times 10^{-4}$	—	
	value {*}	$3.49 \times 10^{-2}$	$3.28 \times 10^{-2}$	$1.04 \times 10^{-3}$	—	—	$2.38 \times 10^{-5}$	—	
Approximate 95% confidence intervals	Std Error	$3.34 \times 10^{-209}$	$9.18 \times 10^{-5}$	$4.34 \times 10^{-106}$	—	—	$2.3 \times 10^{-40}$	—	
	p-value	—	—	—	—	—	—	—	

{\*} Approximate 95% confidence intervals

**Fig. 5** Residuals of the original Fagacées stand basal area increment (Eq. 2) adjusted for the French data set (F+), versus top height (the circled areas are proportional in size to the weight of the points in the regression)



measurements as the original data, which strengthens the reliability of the tested relationships.

The additional French data were not only limited to additional inventories on the original plots, but also included measurements from new plots, representing a broader range of environmental conditions (for example, higher altitudes in the Darney sites) and of stand development stages (see the Retz “Mortefert” site characteristics).

On average, the German plots are located at higher altitudes than the French plots and cover a greater range of altitudes. This is not surprising since the Fagacées model was originally designed for lowland beech forests. However, for other characteristics such as stand age and silvicultural treatment, the German stands were less diverse than the French ones, although the diversity remained important. Both the French

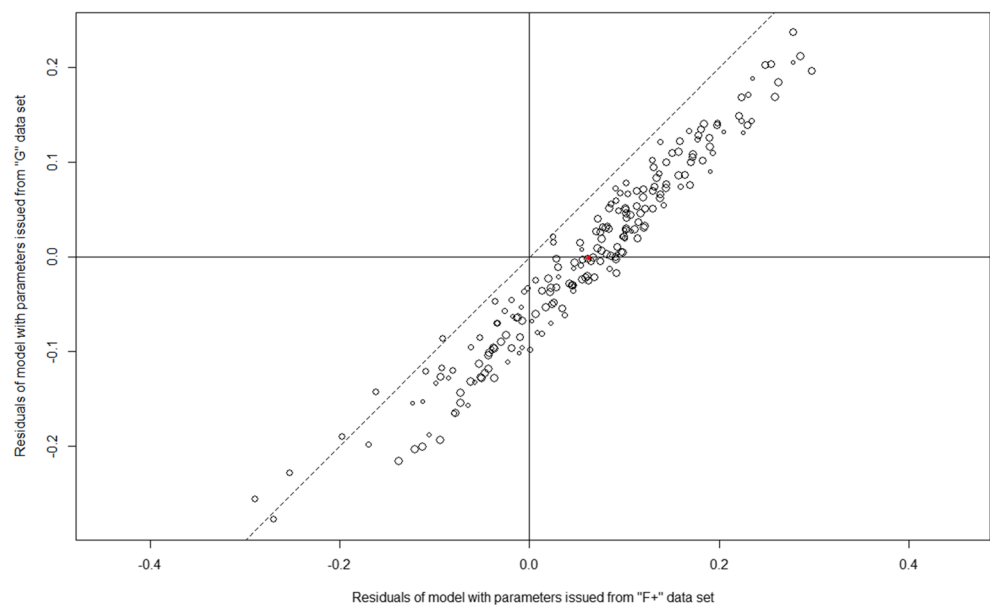
and German stands had quite high site index values. This is not that surprising since silviculture often focuses on potential-high-yield areas.

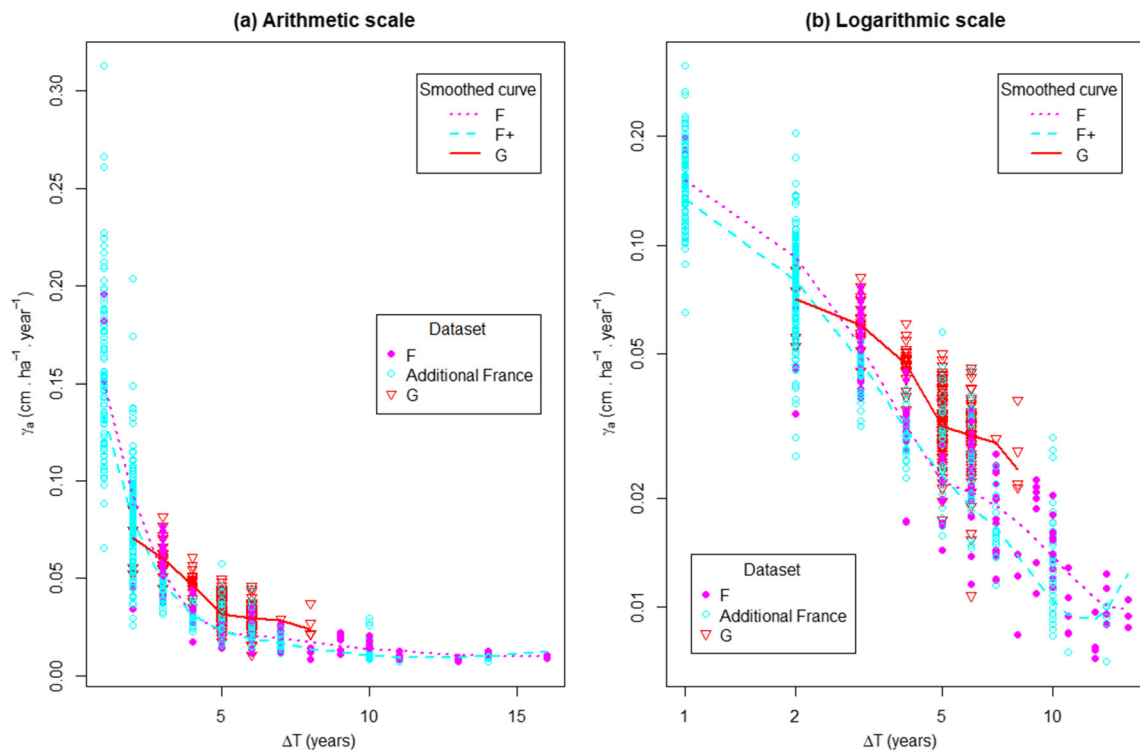
In the German and French networks, silviculture is undoubtedly the most important factor, above genetics or the environment. The Fagacées model was based on the assumption that the interactions between silviculture and the environment were secondary (Dhôte 1991). This is still the case for the updated version including our additional data.

The targeted improvements to the original Fagacées model concern the growth equations as much as their parameters. The results we obtained can be classified according to three situations.

The first situation corresponds to the height-diameter allometric Eqs. (8) and (9). The form of these equations remained the same and the parameter values were very similar between the “F,” “F+”,

**Fig. 6** Comparison of the residuals of the stand basal area increment equation (Eq. 2) for the German data set according to parameterization (the red point is the center of gravity of the point cloud, the circle areas are proportional in size to the weight of the points in the regression)





**Fig. 7** Annual potential maximal diameter increment ( $\gamma_a$ ) versus the time between two successive inventories, on a linear scale (a) and a log-log scale (b). “Additional France” corresponds only to the additional measurements in F+ data set

“G”, or “A” data sets. Due to the large number of data, however, the parameter values were significantly different. Therefore, if enough data are available, it may be better to recalibrate the allometric equations. Yet, the allometric height-diameter relationship appears to be transferable to new regions without recalibration.

This important result suggests either that our different data sets were quite homogeneous regarding climatic or site conditions, or that the basic allometric assumptions correctly accounted for the changes in climatic and site conditions included in the enlarged French-German data. It should be noted

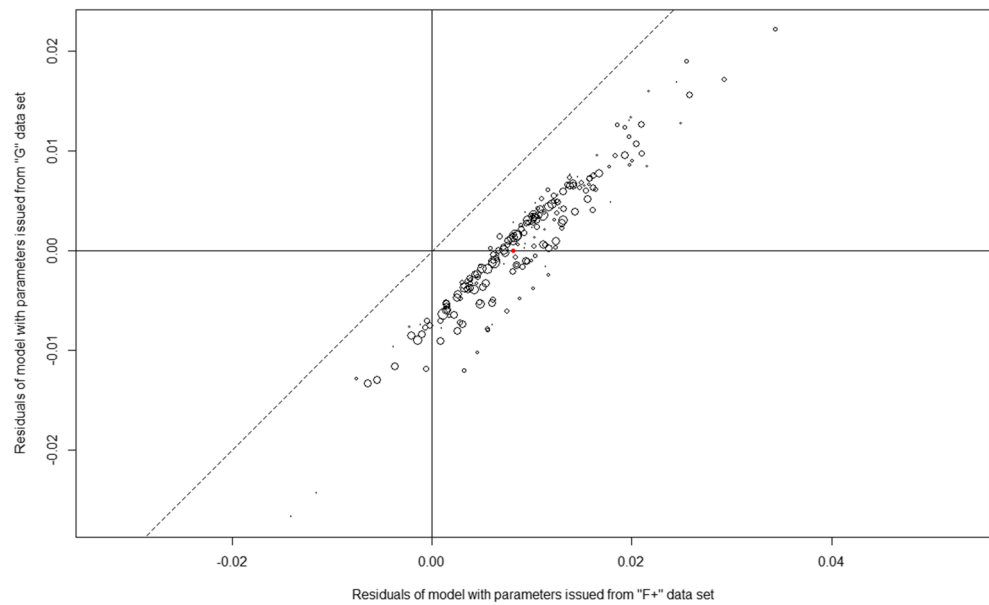
**Table 6** Parameter values and associated standard errors (Std Error) and residual standard deviation ( $\sigma_\epsilon$ ) of the annual maximum potential diameter increment ( $\gamma_a$ ) equation (Eq. 12) fitted by R function “nls”

(nonlinear least squares) on the extended France (F+), Germany (G) and All (A) data sets. For parameter units refer to Table 4

Dataset		Parameter		l	l <sub>0</sub>	l <sub>1</sub>	l <sub>2</sub>	$\sigma_\epsilon$	
France (F+)	value	lower	{*}	1.01	$21.28 \times 10^{-2}$	$-2.27 \times 10^{-2}$	$0.38 \times 10^{-2}$	—	
		estimate		1.04	$23.6 \times 10^{-2}$	$-1.96 \times 10^{-2}$	$10.19 \times 10^{-2}$	$5.28 \times 10^{-3}$	
		upper		1.07	$26.15 \times 10^{-2}$	$-1.64 \times 10^{-2}$	$19.89 \times 10^{-2}$	—	
	Std Error			$1.46 \times 10^{-2}$	$1.24 \times 10^{-2}$	$1.60 \times 10^{-3}$	$5.05 \times 10^{-2}$	—	
		p-value			$8.56 \times 10^{-313}$	$1.84 \times 10^{-64}$	$5.29 \times 10^{-31}$	0.044	—
Germany (G)	value	lower	{*}	0.83	$22.8 \times 10^{-2}$	$-3.09 \times 10^{-2}$	$-12.07 \times 10^{-2}$	—	
		estimate		0.94	$28.94 \times 10^{-2}$	$-2.31 \times 10^{-2}$	$12.33 \times 10^{-2}$	$6.2 \times 10^{-3}$	
		upper		1.05	$36.64 \times 10^{-2}$	$-1.54 \times 10^{-2}$	$36.61 \times 10^{-2}$	—	
	Std Error			$5.64 \times 10^{-2}$	$3.48 \times 10^{-2}$	$3.95 \times 10^{-3}$	$12.33 \times 10^{-2}$	—	
		p-value			$6.5 \times 10^{-40}$	$1.26 \times 10^{-14}$	$1.94 \times 10^{-8}$	0.3183	—
All (A) all data sets grouped together	value	lower	{*}	0.95	$19.65 \times 10^{-2}$	$-2.02 \times 10^{-2}$	$5.91 \times 10^{-2}$	—	
		estimate		0.98	$21.89 \times 10^{-2}$	$-1.69 \times 10^{-2}$	$16.33 \times 10^{-2}$	$6.52 \times 10^{-3}$	
		upper		1.01	$24.36 \times 10^{-2}$	$-1.37 \times 10^{-2}$	$26.64 \times 10^{-2}$	—	
	Std Error			$1.57 \times 10^{-2}$	$1.22 \times 10^{-2}$	$1.68 \times 10^{-3}$	$5.43 \times 10^{-2}$	—	
		p-value			$9.88 \times 10^{-324}$	$1.9 \times 10^{-61}$	$1.46 \times 10^{-22}$	$2.7 \times 10^{-3}$	—

{\*} Approximate 95% confidence intervals

**Fig. 8** Comparison of the residuals of the  $\gamma_a$  equation (Eq. 12) for the German data set according to parameterization (the red point is the center of gravity of the point cloud, the circle areas are proportional in size to the weight of the observations in the regression)



that the stand densities represented in our data were mostly medium values, with a few extreme densities for the French data (Fig. 2). Indeed, many authors have demonstrated the influence of stand density on height-diameter allometric stability (Lopez Sanchez et al. 2003; Castado Dorada et al. 2005; Sharma and Parton 2007; Fortin et al. 2009).

The second situation corresponds to the basal area increment Eq. (2). This equation is the most important one in the model since it drives all stand growth. In the original version of the Fagacées model, basal area increment was computed from Eqs. (3) and (10).

Equation (10) fits all the data sets well, and the parameter values remained within the same order of magnitude.

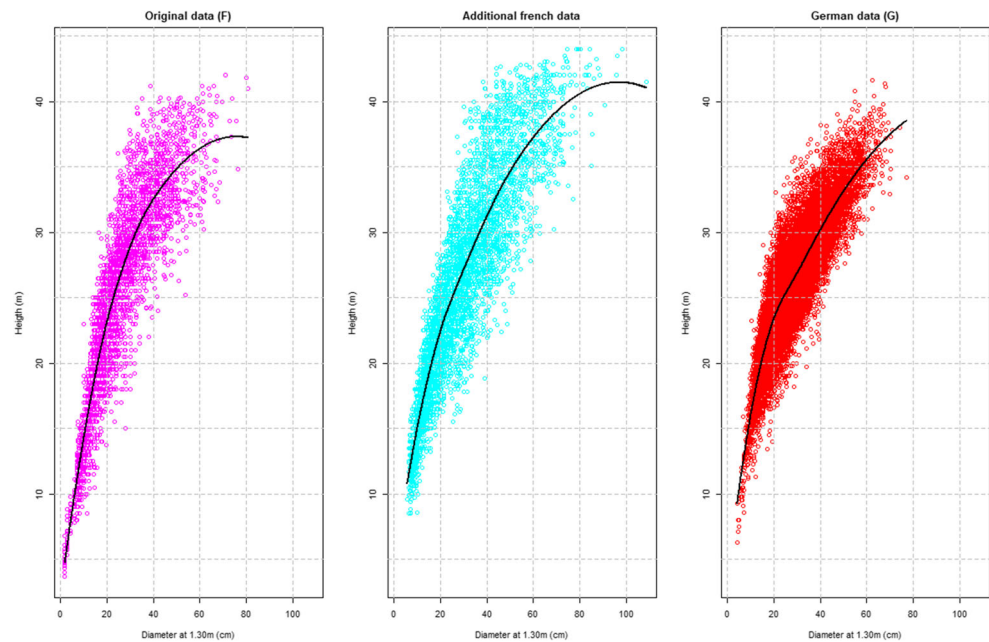
The extension of data set “F” to “F+”, required to introduce a new variable (top height) to the fl potential (Eq. 3), which led to Eq. (11). This modification was based on the graphical investigation of the residuals and can be seen as a simple extension of the original equation. Interestingly, this new equation is identical to the one used for oak in the original version of the Fagacées model (Le Moguédec and Dhôte 2012). Equation (11) fits the “G” data set data well and produces parameter values in the same order of magnitude as the “F+” data set. Especially for young stages of stand development, including top height avoids a substantial underestimation of stand basal area increment (around 20% for stands with a 17-m top height).

**Table 7** Parameters values and associated standard errors (Std Error) and residual standard deviation ( $\sigma_\epsilon$ ) of the individual height growth equation (Eq. 8) fitted on the extended France (F+), Germany (G) and All (A) data sets. All *p*-values are far smaller than 0.01. For parameter units refer to Table 4

Dataset	Parameter		q1	q2	$\sigma_\epsilon$
France (F+)	value {*}	lower	$4.16 \times 10^{-1}$	$9.79 \times 10^{-1}$	—
		estimate	$4.2 \times 10^{-1}$	$9.8 \times 10^{-1}$	1.79
		upper	$4.24 \times 10^{-1}$	$9.82 \times 10^{-1}$	—
	Std Error		$1.79 \times 10^{-3}$	$7.25 \times 10^{-4}$	—
	<i>p</i> -value		$< 2.23 \times 10^{-308}$	$< 2.23 \times 10^{-308}$	—
	Germany (G)	value {*}	lower	$4.32 \times 10^{-1}$	$9.81 \times 10^{-1}$
estimate			$4.34 \times 10^{-1}$	$9.82 \times 10^{-1}$	1.58
upper			$4.36 \times 10^{-1}$	$9.83 \times 10^{-1}$	—
Std Error			$1.2 \times 10^{-3}$	$4.66 \times 10^{-4}$	—
<i>p</i> -value			$< 2.23 \times 10^{-308}$	$< 2.23 \times 10^{-308}$	—
All (A) all data sets grouped together		value {*}	lower	$4.27 \times 10^{-1}$	$9.8 \times 10^{-1}$
	estimate		$4.29 \times 10^{-1}$	$9.81 \times 10^{-1}$	1.66
	upper		$4.31 \times 10^{-1}$	$9.82 \times 10^{-1}$	—
	Std Error		$1.01 \times 10^{-3}$	$3.99 \times 10^{-4}$	—
	<i>p</i> -value		$< 2.23 \times 10^{-308}$	$< 2.23 \times 10^{-308}$	—

\* Approximate 95% confidence intervals

**Fig. 9** Scatter plot of height versus diameter at breast height (dbh) for the original calibrated data set (F), the additional France data set, and the German (G) data set. “Additional France” corresponds only to the additional measurements in the F+ data set. Black line represents the result of a nonparametric adjustment (LOESS method) on the data



Since Eq. (11) contains one additional term compared to Eq. (3), it can be seen as a generalization of Eq. (3). Equation (11) was adapted to all the data sets, including the original one “F”. Again, parameter values remained within the same order of magnitude.

In this situation, the equations remained unchanged but their parameters, although not significantly different, had to be recalibrated when the model was applied to a new region; otherwise, a bias would have been introduced. The same result was obtained by Albrecht for the SILVA model (Albrecht et al. 2009).

The third situation concerns the adjustment of the potential maximum diameter increment  $\gamma$  (Eq. 7). In this case, we had to build an entirely new equation including the time interval between two inventories to fit all the data sets (Eq. 12). The adjusted equation models an average annual maximum potential diameter increment rather than a maximal growth efficiency in 3-year-time-steps as defined by Dhôte (1991) in the original Fagacées version. This adjustment was necessary because the additional French data contained many short time intervals between two successive inventories. This type of situation was rare for the original data set “F”.

These short measurement intervals were not a reaction to thinning operations so the observed trend for  $\gamma_a$  is not linked to thinnings. Annual maximum potential diameter increment  $\gamma_a$  stabilizes after 3 years. This justifies a posteriori the 3-year time-step used in our simulations. Shortening this time interval would imply modifying the Fagacées equations accordingly.

In this third situation, even the algebraic form of the equation had to be modified. Parameter values for the different data sets were of the same magnitude and not significantly

different. Hence, a new calibration was necessary for each data set to avoid introducing an unacceptable relative bias.

In all three situations, different adjustments were made for the different datasets. It was only preferable in the first situation but necessary for the last two. We unsuccessfully attempted to model the parameter variations with global stand characteristics such as geographical position (Western-Eastern gradient, altitude) and climatic variables (average temperatures, annual, and May-to-September precipitation). No trend was found for local variations in parameter values. This means that, even if the same equations can be generalized, parameter values should be adjusted for the specific geographical area considered.

We suppose that no clear trend was found because the model already included top height, and changes in top height over time could reflect local variations. For example, top height at age 100 is classically used to determine the fertility or site index, and, in itself, summarizes the local pedoclimatic conditions.

Including top height in the Fagacées model is an advantage since this variable already reflects most of the pertinent information on growth conditions. Even so, as we have shown, Fagacées equations with top height must still be recalibrated when they are applied outside the origin model’s zone.

The biases related to our new equations seem weak in terms of absolute values. If linear functions are applied, the cumulated bias after several iterations would only be proportional to the total length of the simulation period. However, if the functions are nonlinear and present convexities, the cumulated bias can become much more accentuated.

Since basal area is regulated in the model by growth at the stand level, the bias would have no consequences on average

individual-tree growth, only on growth distribution among all the stems in the stand.

These biases are therefore not insignificant and equations should be recalibrated for each new situation.

## 5 Conclusion

The results of our investigation support the robustness and reliability of the growth component of the Fagacées model. We established that it is possible to parameterize the original equations for different site conditions. Indeed, even though the new data sets included large variations in site index, age, and stand density, the algebraic form of the equations could be kept and the estimated parameter values remained within the same order of magnitude.

The ease with which we were able to adapt the Fagacées model to the Baden-Württemberg stands makes us optimistic about its possible extension to other regions. However, a new calibration would be necessary in each case.

As soon as data from inventories for different development phases or new sites are available, the models can be recalibrated. Data from national forest inventories could be used for such a purpose.

The Fagacées model has also successfully been adapted to several other species (sessile oak, silver fir, eucalyptus).

Its adaptability both to other regions and to other species indicates that the Fagacées formalism should be considered as very generic for applications to growth and yield modeling of pure even-aged stands.

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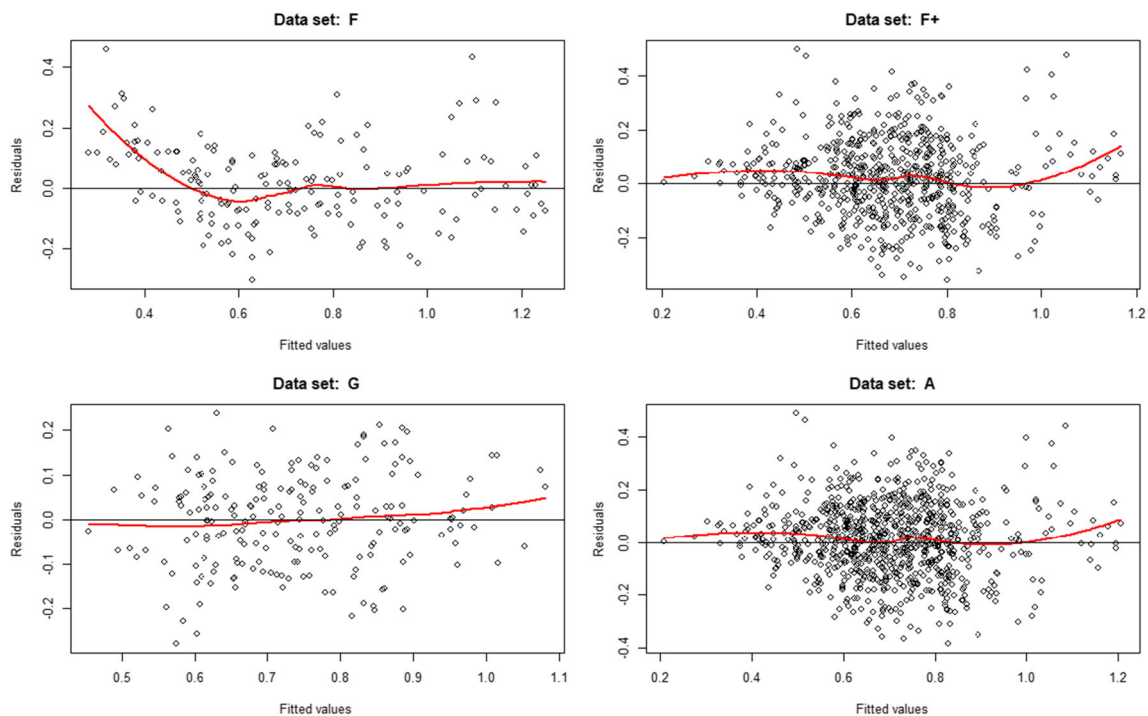
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**Data availability** Dataset is available from the corresponding author on reasonable request.

## Declarations

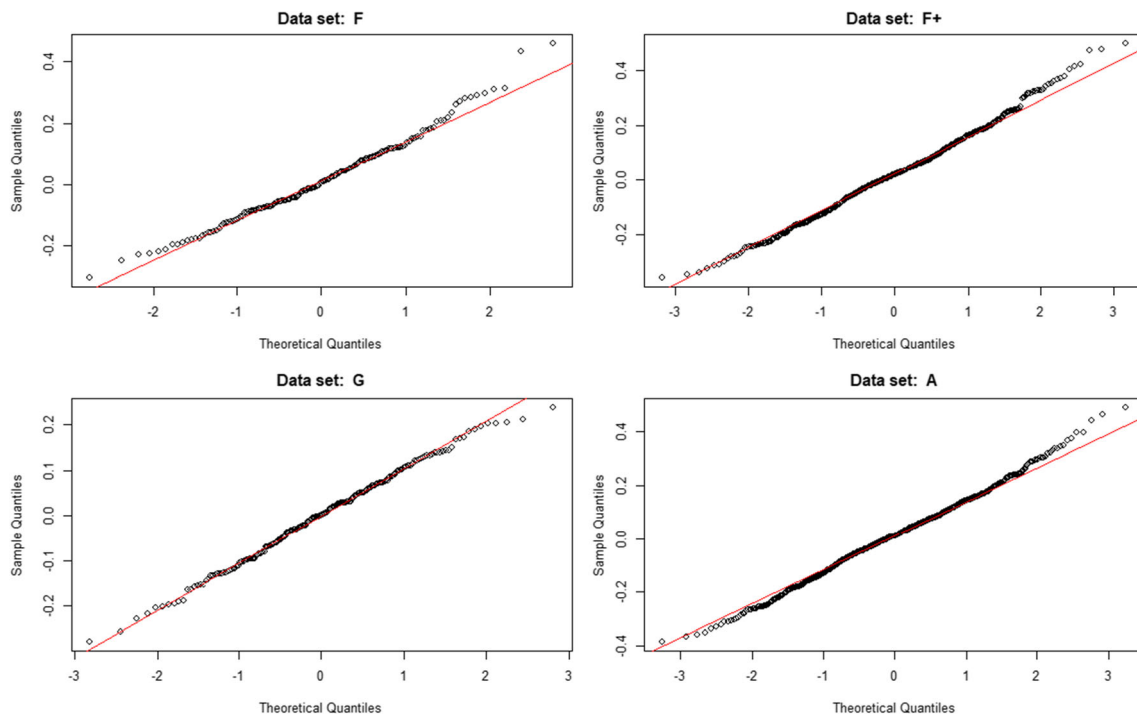
**Conflict of interest** The authors declare no conflict of interest.

## Appendix



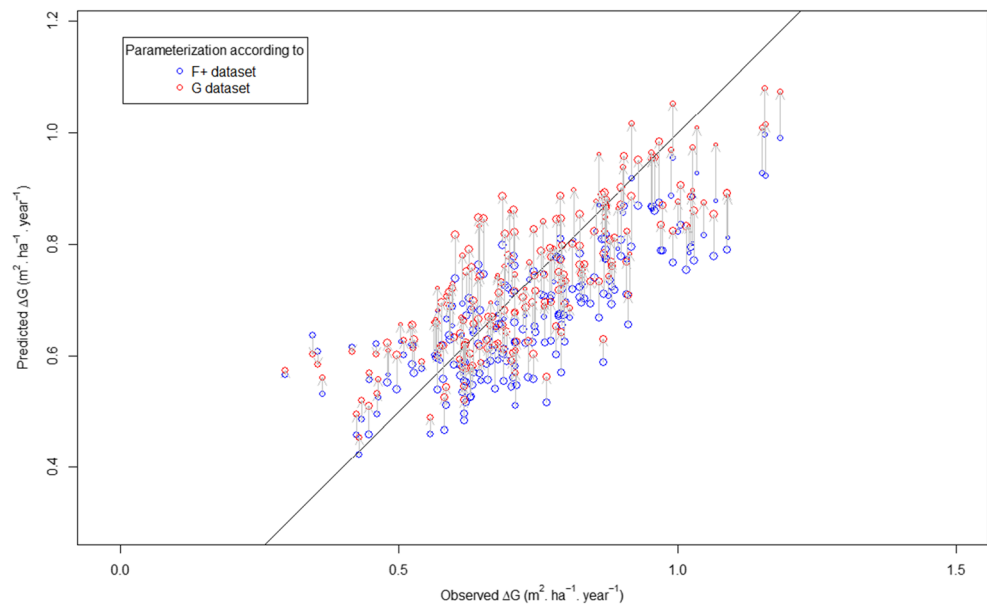
**Fig. 10** Residuals versus fitted values of the model for stand basal areal annual increment fitted separately on each data set





**Fig. 11** Normal quantile-quantile plot of the residuals of the model for stand basal area annual increment fitted separately on each data set

**Fig. 12** Comparison of predictions to observed values on dataset G, according to the parameterization from dataset F+ (in blue) and from dataset G (in red). The grey arrows show the evolution of predictions from F+ to G parameterization



## References

- Albrecht A, Hein S, Kohnle U, Biber P (2009) Evaluierung des Waldwachstumssimulators SILVA 2.2 anhand langfristiger ertragskundlicher Versuchsflächen in Baden-Württemberg. Allgemeine Forst- und Jagdzeitung 180(3/4):55–64
- Albrecht A, Kohnle U, Nagel J (2010) Parametrisierung und Evaluierung von BWinPro für Baden-Württemberg anhand von waldwachstumskundlichen Versuchsflächendaten. Tagungsband der Jahrestagung der Sektion Ertragskunde im DVFFA vom 17.-19.05.2010 in Körbecke, 11-26
- Baskerville GL (1972) Use of logarithmic regression in the estimation of plant biomass. *Can J For Res* 2:49–53
- Bertrand R, Lenoir J, Piedallu C, Riofrio-Dillon G, de Ruffray P, Vidal C, Pierrat J-C, Gegout J-C (2011) Changes in plant community composition lag behind climate warming in lowland forests. *Nature* 479: 517–520
- Bontemps J-D, Longuetaud F, Mothe F, Perez V, Rittié D, Saint-André L, Seynave I (2009) AbiA1- un simulateur de croissance-production de

- type arbre indépendant des distances (MAID) pour les peuplements purs et réguliers de Sapin pectiné (*Abies alba* Mill.) dans les massifs des Vosges et du Jura. Rapport de modélisation et de présentation du simulateur. Document interne du laboratoire LERFoB (UMR 1092 INRA-ENGREF).
- Bontemps J-D, Duplat P, Hervé J-C, Dhôte J-F, 2007. Croissance en hauteur dominante du Hêtre dans le Nord de la France – Des courbes de référence qui intègrent les tendances à long terme. *Rendez-Vous Techniques*, ONF, Hors-série n°2 “Gestion des hêtraies”, 39-47.
- Castedo Dorado F, Barrio Anta M, Parresol BR, Álvarez Gonzales JG (2005) A stochastic height-diameter model for maritime pine ecoregions in Galicia (northwestern Spain). *Ann For Sci* 62:455–465
- Dhôte J-F (1991) Modélisation de la croissance des peuplements réguliers de hêtre: dynamique des hiérarchies sociales et facteurs de production. *Ann For Sci* 48:389–416
- Dhôte J-F (1996) A model of even-aged beech stands productivity with processbased interpretations. *Ann For Sci* 53:1–20
- Dhôte J-F (1999) Compétition entre classes sociales chez le Chêne sessile et le Hêtre. *Rev For Fr* 51:309–325
- Fortin M, Bernier S, Saucier J-P, Labbé F (2009) Une relation hauteur-diamètre tenant compte de l'influence de la station et du climat pour 20 espèces commerciales du Québec. Gouvernement du Québec. Ministère des Ressources naturelles et de la Faune. Direction de la recherche forestière. Mémoire de recherche forestière n°153, 23pp
- Fortin M, Ningre F, Robert N, Mothe F (2012) Quantifying the impact of forest management on the carbon balance of the forest-wood product chain: a case study applied to even-aged oak stands in France. *For Ecol Manag* 279:176–188
- Fortin M, Albrecht A, Kohnle U, Ningre F (2014) The impact of wind-storm damage in the assessment of the carbon balance in even-aged *Fagus sylvatica* L. stands. *Forests* 5(4):784–801. <https://doi.org/10.3390/f5040784>
- Guan B, Gertner GZ, Parysow P (1997) A framework for uncertainty assessment of mechanistic forest growth models: a neural network example. *Ecol Model* 8:47–58
- Hein S, Lenk E, Klädtke J, Kohnle U (2007) Z-Baum orientierte Auslesedurchforstung in Buche (*Fagus sylvatica* L.): Auswirkungen auf Qualität, Sortenstruktur und Wertleistung. *Allgemeine Forst-und Jagdzeitung* 178:1–20
- Huet S, Jolivet E, Messéan A (1992) La régression non-linéaire ; méthodes et applications en biologie. Ed. INRA, Collection « mieux comprendre », Paris, 236p.
- Jarret P (2004) Chênaies atlantiques. Guide des sylvicultures. Office National des Forêts, Paris, 335 p
- Klädtke J (2002) Wachstum großkroniger Buchen und waldbauliche Konsequenzen. *Forstarchiv* 73:211–217
- Köble R, Seufert G (2001) Novel maps for forest tree species in Europe. Proceedings of the 8th European Symposium on the Physico-Chemical Behaviour of Air Pollutants : « A Changing Atmosphere », Torino (IT) 17-20 September 2001
- Kozak A, Kozak R (2003) Does cross validation provide additional information in the evaluation of regression models? *Can. J For Res* 33(6):976–987
- Lacerte V, Larocque GR, Woods M, Parton WJ and Penner M (2006) Calibration of the forest vegetation simulator (FVS) model for the main forest species of Ontario, Canada. *Ecol Model* 199 (3) pp 336–349. <https://doi.org/10.1016/j.ecolmodel.2006.05.028>
- Le Moguédec G, Dhôte J-F (2012) Fagacées: a tree-centered growth and yield model for sessile oak (*Quercus petraea* L.) and common beech (*Fagus sylvatica* L.). *Ann For Sci* 69:257–269
- Lopez Sanchez CA, Gorgoso Varela J, Castedo Dorado F, Rojo Alboreca A, Rodriguez Soalleiro R, Álvarez Gonzales JG, Sanchez Rodriguez F (2003) A height-diameter model for Pinus radiata D. Don in Galicia (Northwest Spain). *Ann For Sci* 60:237–245
- Parysow P, Gertner GZ (1997) Virtual experimentation: conceptual models and hypothesis testing of ecological scenarios. *Ecol Model* 95:59–71
- Pilard-Landeau B, Simon E (2008) Guide des sylvicultures - La hêtraie Nord Atlantique. ONF, Direction Territoriale Ile de France Nord-Ouest, Direction Forêt, 154 pp
- R Core Team (2014) version 3.1.0. R: a language and environment for statistical computing, R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org/>
- Reed D, Tomé M, Araújo MC and Jones E (2001) A re-examination of potential \* modifier dimensional growth models. In Proc. IUFRO S4.11 conference on Forest Biometry, Modelling and Information Science, 25-29 June 2001, Uni. of Greenwich, London, U.K.
- Saint-André L, Laclau J-P, Bouillet J-P, Deleporte P, Miabala A, Ognouabi N, Baillères H, Nouvellon Y, Moukinois R (2002) Integrative modelling approach to assess the sustainability of the Eucalyptus plantations in Congo. Fourth Workshop IUFRO S5.01.04, Harrison Hot Springs, British Columbia, Canada, September 8-15, 11 p.
- Sardin T (2008) Chênaies continentales. Guide des sylvicultures, Office National des Forêts, Paris, 455 p
- Sardin T (2012) Massif vosgien : sapin, épicéa et pin sylvestre. Guide des sylvicultures, Office National des Forêts, Paris, 132 p
- Sardin T (2013) Hêtraies et hêtraies sapinières des Pyrénées. Guide des sylvicultures, Office National des Forêts, Paris, 100 p
- Schmid S, Zingg A, Biber P, Bugmann H (2006) Evaluation of the forest growth model SILVA along an elevational gradient in Switzerland. *Eur J For Res* 125:43–55
- Sharma M, Parton J (2007) Height-diameter equations for boreal tree species in Ontario using a mixed-effects modeling approach. *For Ecol Manag* 249:187–198
- Vanclay JK (1994) Modelling forest growth and yield: applications to mixed tropical forests. CAB International, Wallingford, UK, 312 p
- Vanclay JK, Skovsgaard JP (1997) Evaluating forest growth models. *Ecol Model* 98:1–12

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