



# Predicting individual-tree growth of central European tree species as a function of site, stand, management, nutrient, and climate effects

Brigitte Rohner<sup>1</sup> · Peter Waldner<sup>2</sup> · Heike Lischke<sup>3</sup> · Marco Ferretti<sup>1</sup> · Esther Thürig<sup>1</sup>

Received: 19 May 2017 / Revised: 31 October 2017 / Accepted: 6 November 2017 / Published online: 30 November 2017  
© Springer-Verlag GmbH Germany, part of Springer Nature 2017

## Abstract

We used data from representatively sampled trees to identify key drivers of tree growth for central European tree species. Nonlinear mixed models were fitted to individual-tree basal area increments (BAI) from the Swiss national forest inventory. Data from 1983 to 2006 were used for model fitting and data from 2009 to 2013 for model evaluation. We considered 23 potential explanatory variables specifying individual-tree characteristics, site and stand conditions, management, climate, and nitrogen deposition. Model selection was processed separately for *Picea abies*, *Abies alba*, *Pinus* sp., *Larix* sp., other conifers, *Fagus sylvatica*, *Quercus* sp., *Fraxinus* sp./*Acer* sp., and other broadleaves. The selected models explained 56–70% of the BAI variance in the model fitting dataset and 21–64% in the evaluation dataset. While some variables were relevant for all species, the combination of further variables differed among the species, reflecting their physiological properties. In general, BAI was positively related to DBH and temperature and negatively related to basal area of larger trees, stand density, mean DBH of the 100 thickest trees per ha, slope, and soil pH. For most species, harvesting had a positive effect on BAI. In general, nitrogen deposition was positively related to BAI, except for spruce and fir, for which the inverse effect was found. Increasing drought reduced BAI for most species, except for pine and oak. These BAI models incorporate many influencing factors while representing large spatial extents, making them useful for both nationwide scenario analyses and deepening the understanding of the main drivers modulating tree growth throughout central Europe.

**Keywords** Basal area increment · Empirical growth models · Growth function · National forest inventory · Tree growth · Switzerland

---

Communicated by Hans Pretzsch.

---

**Electronic supplementary material** The online version of this article (<https://doi.org/10.1007/s10342-017-1087-7>) contains supplementary material, which is available to authorized users.

---

✉ Brigitte Rohner  
brigitte.rohner@wsl.ch

- <sup>1</sup> Forest Resources and Management, Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland
- <sup>2</sup> Forest Soils and Biogeochemistry, Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland
- <sup>3</sup> Landscape Dynamics, Swiss Federal Institute for Forest, Snow and Landscape Research WSL, Zürcherstrasse 111, 8903 Birmensdorf, Switzerland

## Introduction

Identifying factors that may affect tree growth is crucial in economic, ecological, and political terms (e.g. Lindner et al. 2010; Nabuurs et al. 2013, 2017) and has implications for management scenario analyses and future management strategies (e.g. Canadell and Raupach 2008; Lindner 2000). Tree growth is influenced by site conditions (e.g. geography, topography, soil properties, nutrient availability, see, for example, Lévesque et al. 2016; King et al. 2013; Oberhuber and Kofler 2000; Rohner et al. 2016), climate (Fritts 1976), competition and management (Biging and Dobbertin 1995), and nitrogen (N) deposition (Bedison and McNeil 2009; Laubhann et al. 2009), while the effect of other factors, like air pollutants including tropospheric ozone, is uncertain (e.g. Wang et al. 2016). The significance of individual drivers may vary depending on tree species and the site-specific realization of the driver of concern. Disentangling the effect (size and direction) of individual drivers over a population

of trees is therefore a complex matter that requires (1) representative, unbiased growth data covering multiple species and (2) covering large gradients of the various drivers, and (3) an appropriate modelling approach able to simultaneously consider many drivers and control their possible multicollinearity.

As for (1), statistically representative growth data over large populations of forest trees can be obtained from National Forest Inventories (NFIs). In Switzerland, the NFI is a probabilistic-based survey that has been carried out across the entire country since 1983–1985 and repeated on a ca. 10-year basis (see below). This guarantees an unbiased sample of the Swiss forest tree population.

Regarding (2), as NFIs cover entire countries on a systematic basis, they capture large gradients of many drivers (see Table 1 for the range of variability of the various drivers considered in this study). In Switzerland, these gradients are often of the same amplitude as those that occur at the continental scale.

Finally, concerning (3), the modelling approach is important in view of the possible use of derived tree growth functions in forest development models such as succession models (Bugmann 2001) or management scenario simulators (Barreiro et al. 2016). In addition, a deeper understanding of tree-growth-related ecological processes may be intended.

Empirical forest scenario models have traditionally been prepared to estimate future forest development based on statistical inferences combined with management strategies (Barreiro et al. 2016; Weiskittel et al. 2011). These models have proven useful in several contexts, for example, to compare different management strategies (Thürig and Kaufmann 2010; Werner et al. 2010), to estimate the potential timber supply (Barreiro et al. 2016; Verkerk et al. 2011), and to predict carbon sequestration (Groen et al. 2013). Forest scenario models have often been developed based on data from NFIs (Barreiro et al. 2016; Peng 2000) to provide representative inferences over large spatial extents (e.g. PROGNAUS for Austria—Monserud et al. (1997), MASSIMO for Switzerland—Kaufmann (2001b), Thürig et al. (2005), and EFIS-CEN for the European scale—Nabuurs et al. (1997)).

In the past, empirical forest scenario models have mostly considered drivers related to site, stand, and management under the assumption of constant environmental conditions. Effects of climate change and nutrient deposition on forests (Ciais et al. 2005; Laubhann et al. 2009; Lindner et al. 2010; Solberg et al. 2009), however, render such an assumption questionable. Other empirical individual-tree diameter or basal area growth functions accounting for climate and/or nutrient deposition effects have usually focused on one tree species and/or on data from ad hoc selected sites (e.g. Adame et al. 2008; Crecente-Campo et al. 2010; Trasobares et al. 2016; Zeng et al. 2017). In Laubhann et al. (2009), empirical models for several species (*Fagus sylvatica*,

*Quercus petraea* and *Q. robur*, *Pinus sylvestris*, and *Picea abies*) were fitted to data from plots of the pan-European EU and ICP-Forests intensive monitoring programme (Level II plots), which is not a statistically representative sample of European forests (Ferretti and Chiarucci 2003).

With this study, we aimed to overcome the above-mentioned limitations in terms of categories of drivers, number of species, and representativeness of the tree population. Our objective was to simultaneously quantify the effects of many different drivers (stand, management, site, climate, and N-deposition—see below) on tree growth for common European tree species. We investigated

1. which combination of 23 potential explanatory variables best predicts individual-tree basal area increment,
2. how the effect size varies among the variables, and
3. how these results vary among tree species.

The analysis is based on nonlinear mixed-effects models (Pinheiro and Bates 2000) fitted to data from the Swiss NFI. Results are thus representative of Switzerland's large environmental variability, which supports their inclusion in nationwide scenario analyses and helps to provide a deeper understanding of the main drivers modulating tree growth, also in other parts of central Europe.

## Materials and methods

### Growth data

The analyses were based on single-tree growth data collected as part of the Swiss NFI (for details see Brassel and Lischke 2001, [www.lfi.ch](http://www.lfi.ch)). The Swiss NFI comprises more than 6000 permanent plots located on a systematic grid (1.4 km × 1.4 km) covering Switzerland, leading to a dataset that is representative of the whole country. The plots are composed of two concentric circles with areas of 200 and 500 m<sup>2</sup>, respectively. Within the inner circle, all trees with a diameter at breast height (DBH) ≥ 12 cm are recorded, whereas within the remaining area of the outer circle, trees with a DBH ≥ 36 cm are recorded. By recording the exact geolocation of the trees, their identification in subsequent inventories is ensured. In addition to individual-tree characteristics, a wealth of information regarding site, stand, and silvicultural intervention is collected per plot. So far, three inventory campaigns have been completed: NFI 1 took place between 1983 and 1985, NFI 2 between 1993 and 1995, and NFI 3 between 2004 and 2006. Since 2009, a continuous inventory has been conducted by monitoring a representative sub-grid of one-ninth of the plots every year (NFI 4). We used data from NFI 1–3 for model fitting and data from NFI 3–4 (until 2013) for model evaluation.

**Table 1** Overview of potential explanatory variables

	Acronym	Unit	Mean	SD	5% quantile	95% quantile	Resolution	Source	Group of competing variables	Competing variables selected (yes: ✓, no:×)
Diameter at breast height	DBH	cm	31.4	14.8	13	57	Individual tree	Abegg et al. (2014)	–	–
Basal area of larger trees	BAL	m <sup>2</sup> ha <sup>-1</sup>	21.6	16.1	0	51	Individual tree	Abegg et al. (2014)	–	–
Stand basal area	BA	m <sup>2</sup> ha <sup>-1</sup>	39.0	17.1	1.5	69	Plot	Abegg et al. (2014)	A	×
Stand density index	SDI	–	742	304	311	1279	Plot	Abegg et al. (2014), according to Reineke (1933)	A	✓
Mean of the 100 largest diameters per ha	DDOM	cm	41.9	10.6	25	59	Plot	Abegg et al. (2014)	–	–
Uneven structure compared to even structure	Forest type	–	–	–	–	–	Plot	Abegg et al. (2014)	–	–
Individual-tree harvesting effect	–	–	–	–	–	–	Individual tree	Calculated based on data from Abegg et al. (2014), according to Thirig et al. (2005)	B	×
Plot-level harvesting effect	–	–	0.01	0.03	0.00	0.08	Plot	Calculated based on data from Abegg et al. (2014)	B	✓
Slope	–	%	46.2	27.7	6	93	Plot	Abegg et al. (2014)	C	✓
Eastness	–	–	–0.02	0.69	–0.99	0.98	Plot	Abegg et al. (2014)	C	✓
Northness	–	–	0.06	0.72	–0.98	0.99	Plot	Abegg et al. (2014)	C	✓
Curvature	–	–	0.00	0.28	–0.43	0.45	Plot	Abegg et al. (2014)	C	✓
Soil quality	–	–	3211	1396	686	5346	Plot	Abegg et al. (2014), according to Keller (1978)	C	×
Available water capacity	AWC	mm	177	62	100	254	Plot	Remund et al. (2014)	–	–
pH	–	–	5.1	1.4	3.1	7.2	Plot	Abegg et al. (2014)	–	–
N-deposition	–	kg ha <sup>-1</sup> year <sup>-1</sup>	27.0	10.4	11.9	46.2	Plot	Rihm (1996), Thimonier et al. (2005)	–	–
Altitude	–	m a.s.l.	1027	417.7	475	1788	Plot	Abegg et al. (2014)	D	×
Temperature	–	°C	6.9	2.2	2.6	9.7	Plot	Remund et al. (2014)	D	✓
Degree days	–	°C d	1504	460	725	2136	Plot	Calculated based on data from Remund et al. (2014)	D	×
Precipitation	–	mm	1399	346	864	1990	Plot	Remund et al. (2014)	E	×
ETa/ETp	–	–	0.975	0.035	0.918	0.999	Plot	Remund et al. (2014)	E	✓
Drought stress	–	–	0.023	0.043	0.000	0.099	Plot	Calculated according to Bugmann and Cramer (1998) based on data from Remund et al. (2014) and Abegg et al. (2014)	E	×
Global radiation	–	Wm <sup>-2</sup>	1586	149	1372	1889	Plot	Remund et al. (2014)	–	–

Groups of highly correlated variables that represent the same physiological processes (referred to as ‘competing variables’) are indicated by upper-case letters A–E

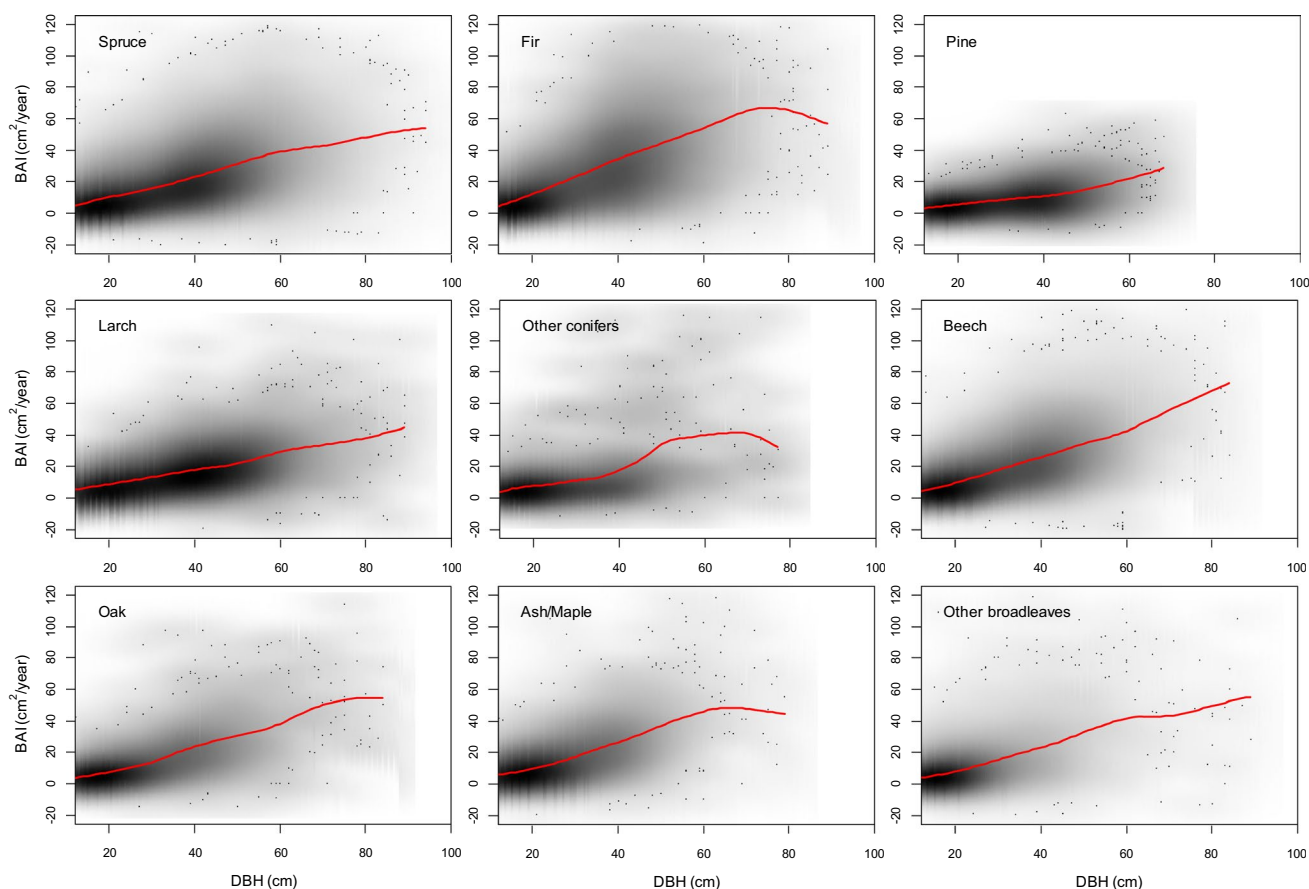
We modelled tree growth by defining individual-tree basal area increment (BAI) as the target variable. BAIs were calculated from DBH measurements of two consecutive NFIs. Due to slightly varying interval lengths, mean annual BAI was calculated by dividing BAI calculated from two consecutive inventories by the number of growing seasons between the inventories. The largest and the smallest 0.01% of these BAI values were excluded from the analyses as outliers ( $\text{BAI} \leq -241$  and  $\text{BAI} \geq 293 \text{ cm}^2 \text{ year}^{-1}$ ), resulting in a total of 86,262 BAI values for model fitting (Fig. 1).

## Explanatory variables

We considered 23 potential explanatory variables to model possible effects on BAI (Table 1) and grouped them into three main categories: (1) tree- and stand-related variables, (2) site-related variables, and (3) climate- and N-deposition-related variables.

## Tree- and stand-related variables

Tree- and stand-related variables included the individual DBH and the basal area of trees thicker than the target tree on the same plot (basal area of larger trees, BAL; Monserud and Sterba 1996), which is an indicator of the competition the target tree experiences. Stands were characterized by the stand basal area per ha (BA) and the stand density index (SDI) according to Reineke (1933). In addition, the mean DBH of the 100 thickest trees per ha (DDOM) was included as a general description of a stand's development stage. These individual-tree and stand variables were calculated based on measurements conducted at the beginning of the inventory intervals. Management was considered, on the one hand, by a dummy variable 'forest type' that differentiated between even-aged high forests and uneven-aged forests (including both coppices and uneven-aged high forests). On the other hand, two variables specifying harvesting effects were defined at the individual-tree level and at the plot level. For the former, a release effect was defined as



**Fig. 1** Basal area increment (BAI) data used for model fitting. For each species or species group, the measured BAI values are plotted against the diameter at breast height (DBH) at the beginning of the inventory interval. The greyscale indicates the density of the points

(darker grey represents more points). The 100 points with the lowest regional density are plotted individually (some lie outside of the plotting area). A smoothing spline with 20 knots is shown as a red line

dummy variable: if a tree belonging to the overstorey was removed, its nearest neighbour was assumed to benefit from this removal (cf. Thürig et al. 2005). For the latter, a release effect was defined as a proportion: if a tree belonging to the overstorey was removed, all remaining trees on the plot were assumed to benefit; the extent of this release effect was assumed to be inversely proportional to the number of remaining trees, i.e. if one tree remained on the plot, the variable took the value 1 and if ten trees remained on the plot, it took the value 0.1.

### Site-related variables

Site-related variables included topography (slope, altitude, curvature, and aspect) and soil characteristics (soil quality index, available water capacity, and pH). Aspect was transformed to the continuous variables eastness [ $\sin(2\pi \times \text{azimuth}/360)$ ] and northness [ $\cos(2\pi \times \text{azimuth}/360)$ ]. Regarding soil characteristics, the soil quality index according to Keller (1978) was considered; this index combines information about altitude, aspect, relief, geology, etc. In addition, available water capacity at 1 m soil depth (AWC; Remund et al. 2014) and the pH-value of the upper soil layer were included as potential site-related explanatory variables.

### Climate and N-deposition-related variables

While all tree-, stand- and site-related variables were derived from direct on-site observations/measurements, we also considered other predictors (N-deposition, climate) for which data from direct measurements were not available for the NFI plots. Use of estimated predictors for climate (e.g. Laubhann et al. 2009) and N-deposition (e.g. Magnani et al. 2007) in observational studies is quite common, although estimates can be affected by considerable uncertainties. For this study, we assumed that the large number of sites ( $n > 6000$ ), for which estimates were prepared, mitigated the effect of inherent uncertainties on the output.

Atmospheric nitrogen (N) deposition was estimated for NFI plots for the reference years 1990, 2000, and 2010 using a modelling approach combining emission inventories, statistical dispersion models, spatially interpolated monitoring data from 5-year periods (1988–1992, 1998–2002, and 2008–2012), and inferential deposition models for each N compound (e.g. gaseous  $\text{NH}_3$ ,  $\text{NO}_2$  and dissolved  $\text{NH}_4^+$  and  $\text{NO}_3^-$ ; updated from Thimonier et al. 2005). The resulting N-deposition values for the reference years 1990, 2000, and 2010 were considered as potential explanatory variables for the intervals NFI 1–2, NFI 2–3, and NFI 3–4, respectively (uncertainties about  $\pm 20\%$  to  $30\%$ ).

Several climatic and bioclimatic variables were taken into consideration as possible explanatory variables. For each NFI plot, the variables temperature, precipitation, the ratio

between actual and potential evapotranspiration ( $\text{ET}_a/\text{ET}_p$ ;  $\text{ET}_p$  calculated according to Romanenko 1961), and global radiation were provided in monthly resolution for the time span 1982–2012 by Remund et al. (2014). Based on these temperature and precipitation data, as well as slope and aspect data, we calculated monthly degree days (for a threshold of  $5.5\text{ }^\circ\text{C}$ ) and drought stress according to Bugmann and Cramer (1998). The way the climatic and bioclimatic variables were calculated from the monthly data was based on Rohner et al. (2016), where climatic variables were strongly related to multiannual BAI if whole-year conditions (instead of parts of the years) and means within the multiyear periods (instead of extremes) were considered. Accordingly, we first calculated means over the physiological years (October of the previous year to September of the current year) and subsequently averaged these annual values over the inventory intervals.

### Model formulation

For modelling individual-tree BAI, we fitted nonlinear mixed-effects models with covariates (Pinheiro and Bates 2000). The models were based on the following formulation according to Teck and Hilt (1991) and Quicke et al. (1994), which is implemented in the Swiss Forest Scenario Model ‘MASSIMO’ (Kaufmann 2001a, b) and was evaluated by Thürig et al. (2005):

$$\text{BAI} = e^{b_1 \times (1 - e^{b_2 \times \text{DBH}})} \times e^{b_3} + \epsilon,$$

where  $b_1$ – $b_3$  are the coefficients to be estimated and  $\epsilon$  is the residual error. Coefficient  $b_3$  was modelled as a function of  $i$  explanatory variables  $V_{1,\dots,i}$  according to:

$$b_3 = \beta_0 + \beta_1 V_1 + \dots + \beta_i V_i + b_{\text{plot}},$$

where  $\beta_0$  is an estimated fixed intercept,  $\beta_{1,\dots,i}$  are the model coefficients estimated for the included explanatory variables, and  $b_{\text{plot}}$  is a random intercept with NFI plots as grouping factor, which takes into account the grouped structure of the data (several trees per plot). All numerical variables not distributed around zero (except DBH) were centred and scaled before being included in the models to enhance comparability among the estimated coefficients. The means and standard deviations used for scaling and centring are shown in Table 1. To fit the models, we used the package *nlme* (Pinheiro et al. 2016) in the statistical software environment R (R Core Team 2013).

### Model selection

To avoid including highly correlated variables representing the same physiological processes in the model, we first performed a pre-selection among what we refer to hereafter as ‘competing variables’. This pre-selection was based on the



whole model fitting dataset (all species combined). As competing variables, we considered the following combinations: (1) BA versus SDI, (2) individual-tree versus plot-level harvesting effects, (3) soil quality according to Keller (1978) versus a group of variables containing slope, eastness, northness, and curvature, (4) altitude versus temperature versus degree days, and (5) precipitation versus ETa/ETp versus drought stress according to Bugmann and Cramer (1998, Table 1). For the pre-selection, we fitted separate models for all combinations containing one variable per group of competing variables ( $2 \times 2 \times 2 \times 3 \times 3 = 72$  combinations; see Online Resource 1), including all variables that were not among the competing variables. These models were compared based on the Akaike information criterion (AIC) and the corrected Akaike information criterion (AICc), which is unbiased for finite sample sizes (Burnham and Anderson 2002). The model with the lowest AIC and AICc was used as the full model for the subsequent model selection process.

For the actual model selection process, we used a stepwise backward approach starting from the aforementioned full model. Step by step, the variable whose exclusion resulted in the strongest reduction of the AIC was excluded from the model. DBH was not involved in the model selection process; it was included in all cases because of the model formulation. Model selection was finished if excluding additional variables did not reduce the AIC further. This selection procedure was repeated using the AICc as alternative exclusion criterion.

The stepwise backward selection was done separately for *P. abies* (spruce, 34,552 data points), *Abies alba* (fir, 10,430 data points), *Pinus* sp. (pine, 3722 data points), *Larix* sp. (larch, 3901 data points), other conifers (992 data points), *F. sylvatica* (beech, 17,791 data points), *Quercus* sp. (oak, 2082 data points), *Fraxinus* sp. and *Acer* sp. (ash/maple 5770 data points), and other broadleaves (7022 data points).

## Model evaluation

The selected models were evaluated by (1) conducting a sensitivity analysis and (2) comparing observations and model predictions. In the sensitivity analysis, the estimated effects of the explanatory variables on BAI were investigated by varying every selected explanatory variable within its range, while fixing all the others at their respective mean values. The comparison of observations and model predictions was conducted, on the one hand, based on the dataset used to fit the models. This approach can be seen as an evaluation of the ability of the model to predict BAI under current (model development stage) conditions. On the other hand, observations and model predictions were compared based on data from NFI 3–4, which had not been used for fitting the models. This additional evaluation can be seen as a first step ‘into the future’, and

it comes close to an application of the BAI models within scenario models. For both datasets, observations were compared to (1) model predictions based on the fixed and random effects—as it is possible for plots already present in the fitting step—and (2) model predictions based on the fixed effects only—as it is possible for new plots. For comparing observed and predicted BAI, we calculated the root mean square error (RMSE), the Pearson’s correlation coefficient ( $r$ ), and its square ( $r^2$ ) as an indicator of the explained variance in BAI.

## Results

### Key drivers of individual-tree BAI

After the pre-selection of competing variables (see AIC and AICc values in Online Resource 1), the following variables were included in the full model (besides the variables that were part of the full model anyway, Table 1): (1) SDI, (2) plot-level harvesting effect, (3) the variable group containing slope, eastness, northness, and curvature, (4) temperature, and (5) ETa/ETp. The pairwise correlations between all variables of the full model are indicated in Online Resource 2 (all  $\leq |0.63|$ , 88 of 91 correlations  $< |0.5|$ ). The subsequent species-specific backward selection resulted—irrespective of whether AIC or AICc were used—in the variable combinations shown in Table 2 (model coefficients at the original unscaled and uncentred scale of the variables are shown in Online Resource 3). Whereas some variables were included in all or most of the selected models (e.g. BAL and slope), other variables were only included for a few species (e.g. aspect variables and global radiation). A summary of the inclusion of the variables and the direction of the estimated effects is given in Table 3.

### Tree- and stand-related variables

DBH, BAL, and SDI were the most important drivers in this group. As expected, BAI significantly increased with increasing DBH (Table 2). The BAI of most species decreased with increasing BAL, SDI, and DDOM. However, BAL was not included in the selected model for oak, SDI was not included in the selected models for ‘other conifers’ and beech, and DDOM was not included in the selected models for pine, larch, and ‘other conifers’. Spruce, fir, and all broadleaved species showed increased BAI after harvesting of competitors. In uneven-aged forests, the BAI of pine was greater and the BAI of larch and ash/maple was smaller compared to that in even-aged forests.

**Table 2** Estimated coefficients of the selected models

	Spruce (34,552)	Fir (10,430)	Pine (3722)	Larch (3901)	Other conifers (992)	Beech (17,791)	Oak (2082)	Ash/Maple (5770)	Other broadleaves (7022)
$b_1$	3.563 ± 0.071***	4.450 ± 0.131***	2.496 ± 0.184***	2.903 ± 0.245***	3.338 ± 0.887***	4.180 ± 0.082***	4.623 ± 0.194***	3.165 ± 0.149***	3.881 ± 0.136***
$b_2$ (DBH)	-0.048 ± 0.002***	-0.049 ± 0.002***	-0.030 ± 0.006***	-0.050 ± 0.006***	-0.069 ± 0.018***	-0.048 ± 0.002***	-0.031 ± 0.003***	-0.029 ± 0.003***	-0.044 ± 0.003***
Intercept of $b_3$	0.133 ± 0.081*	-0.450 ± 0.151**	0.557 ± 0.201**	0.494 ± 0.279*	-0.101 ± 0.941 0.914	-0.346 ± 0.096***	-0.479 ± 0.250*	0.942 ± 0.111***	-0.303 ± 0.145*
Basal area of larger trees	-0.166 ± 0.007***	-0.123 ± 0.013***	-0.204 ± 0.025***	-0.204 ± 0.020***	-0.363 ± 0.049***	-0.116 ± 0.010***	-0.116 ± 0.010***	-0.211 ± 0.024***	-0.149 ± 0.025***
Stand density index	-0.070 ± 0.007***	-0.101 ± 0.013***	-0.059 ± 0.028*	-0.073 ± 0.020***			-0.049 ± 0.030 0.104	0.039 ± 0.018*	-0.107 ± 0.026***
Mean of the 100 largest diameters per ha	-0.054 ± 0.009***	-0.031 ± 0.016*				-0.132 ± 0.011***	-0.171 ± 0.030***	-0.039 ± 0.023*	-0.084 ± 0.027**
Plot-level harvesting effect	0.019 ± 0.003***	0.007 ± 0.004*				0.020 ± 0.003***	0.033 ± 0.007***	0.027 ± 0.007***	0.031 ± 0.010**
Uneven structure compared to even structure			0.138 ± 0.044**	-0.046 ± 0.031 0.140				-0.051 ± 0.0284*	
Slope	-0.083 ± 0.010***	-0.177 ± 0.017***	-0.077 ± 0.030*	-0.112 ± 0.023***	-0.233 ± 0.073**	-0.152 ± 0.011***	-0.150 ± 0.032***	-0.107 ± 0.019***	-0.173 ± 0.024***
Eastness			0.067 ± 0.041 0.105			0.037 ± 0.015*			
Northness	0.037 ± 0.011***					0.034 ± 0.014*			
Curvature	0.124 ± 0.033***				-0.126 ± 0.081 0.121	0.079 ± 0.035*		-0.108 ± 0.057*	
Available water capacity	0.029 ± 0.008***					0.060 ± 0.014***	0.099 ± 0.041*		0.042 ± 0.031 0.168
pH	-0.064 ± 0.009***	-0.077 ± 0.015***	-0.094 ± 0.027***	0.036 ± 0.022 0.103	-0.089 ± 0.060 0.139	-0.047 ± 0.011***	-0.0915 ± 0.030**	-0.093 ± 0.018***	
N-Deposition	-0.043 ± 0.008***	-0.050 ± 0.013***	0.064 ± 0.026*		0.130 ± 0.054*	0.082 ± 0.011***	0.115 ± 0.033***	0.067 ± 0.018***	0.126 ± 0.028***
Temperature	0.231 ± 0.012***	0.250 ± 0.024***	0.121 ± 0.024***		0.128 ± 0.052*	0.147 ± 0.020***	0.145 ± 0.062*	0.129 ± 0.033***	
ETA/ETp	0.096 ± 0.011***	0.192 ± 0.026***	0.092 ± 0.018***			0.046 ± 0.016**		0.042 ± 0.024*	0.039 ± 0.015*
Global radiation	0.046 ± 0.010***	0.063 ± 0.022**	0.038 ± 0.021*						
Standard deviation of random intercept for $b_3$	0.367	0.394	0.489	0.416	0.457	0.368	0.393	0.408	0.506

The estimated coefficients ± standard error and  $p$  value (\*  $p \leq 0.1$ , \*\*  $p \leq 0.01$ , \*\*\*  $p \leq 0.001$ ) are indicated for the variables included in the selected models. The number of data points used to fit the models is stated in brackets in the table header. Estimated coefficients at the original scale of the variables (unscald and uncentred) are shown in Online Resource 3

**Table 3** Summary of inclusion of the explanatory variables in the selected models and the direction of their estimated effects (i.e. the sign of the estimated coefficients (except  $b_2$ ), see Table 2)

Variable	Number of species for which the variable was selected	Number of estimated positive effects	Number of estimated negative effects
$b_2$ (DBH)	9	9	0
Basal area of larger trees	8	0	8
Stand density index	7	1	6
Mean of the 100 largest diameters per ha	6	0	6
Plot-level harvesting effect	6	6	0
Uneven structure compared to even structure	3	1	2
Slope	9	0	9
Eastness	2	2	0
Northness	3	2	1
Curvature	3	2	1
Available water capacity	4	4	0
pH	8	1	7
N-deposition	8	6	2
Temperature	7	7	0
ETa/ETp	6	6	0
Global radiation	3	3	0

**Table 4** Explained BAI variance and root mean square error of the selected models

	Spruce (34,552)	Fir (10,430)	Pine (3722)	Larch (3901)	Other conifers (992)	Beech (17,791)	Oak (2082)	Ash/Maple (5770)	Other broadleaves (7022)
Explained BAI variance in model fitting dataset	0.60	0.70	0.56	0.61	0.69	0.69	0.67	0.67	0.58
Root mean square error in model fitting dataset ( $\text{cm}^2 \text{ year}^{-1}$ )	11.9	14.1	6.2	9.6	12.3	9.6	10.5	8.9	9.7
Explained BAI variance in evaluation dataset	0.37	0.53	0.21	0.27	0.64	0.43	0.43	0.45	0.27
Root mean square error in evaluation dataset ( $\text{cm}^2 \text{ year}^{-1}$ )	17.8	21.2	11.7	15.8	18.4	15.8	19.8	13.9	13.6

The number of data points used to fit the models is stated in brackets in the table header

### Site-related variables

Slope and—to a lower extent—soil pH were the most important drivers in this group. All species had a lower BAI on steeper slopes. However, the other topographical variables (eastness, northness, and curvature) were included in the selected models only for a few species. BAI of all species except larch and ‘other broadleaves’ decreased with increasing pH. BAI of spruce, beech, oak, and ‘other conifers’ increased with increasing AWC.

### Climate- and N-deposition-related variables

N-deposition and temperature were the most important drivers of this group. N-Deposition had a positive effect on the BAI of most species, but a negative effect on the BAI of spruce and fir. For most species, BAI increased with increasing temperature and increasing ETa/ETp. Temperature, however, was not included in the selected models for pine and ‘other broadleaves’, and ETa/ETp was not included in the selected models for pine, ‘other conifers’, and oak. Whereas global radiation had a positive effect on the BAI of spruce, fir, and larch, it was not included in any of the selected models for the broadleaved species.



## Model evaluation

The effect size, i.e. the estimated coefficients, varied considerably among the variables in the selected models (Table 2). In general, BAL and temperature had comparably large effect sizes, while the pH effect and the harvesting effect were comparatively low. Slope had the largest effect size of all variables in the selected models for beech and ‘other broadleaves’, but it had a comparatively low effect size in the selected models for spruce and pine. As an example, Fig. 2 shows the sensitivity analysis for beech, i.e. how the selected variables affect BAI and how the effect size varies among the selected variables. The sensitivity analyses for the other tree species are shown in Online Resource 4.

For the dataset used to fit the models (NFI 1–3), the comparison of observations and model predictions is presented in Fig. 3. The correlation coefficients ( $r$ ) between observations and predictions based on the fixed effects varied from 0.49 for pine to 0.71 for ‘other conifers’. Including the random effects always increased  $r$  (30% on average), resulting in values between 0.75 (pine) and 0.84 (fir). Consequently, the models including the random effects explained 56–70% of the BAI variance in the dataset used for model fitting (Table 4).

The comparison of model predictions and observations for the evaluation dataset (NFI 3–4) is shown in Fig. 4. In general, the  $r$  values were lower than those for the dataset used for model fitting, irrespective of whether the predictions were based only on the fixed effects (on average 14% lower in the evaluation than the model fitting dataset) or on both the fixed and the random effects (on average 22% lower in the evaluation than in the model fitting dataset). For the evaluation dataset, the  $r$  between observations and predictions varied more among the species than for the model fitting dataset. If predictions were based on the fixed effects,  $r$  varied from 0.3 for pine to 0.8 for ‘other conifers’ (the only  $r$  value that was higher for the evaluation dataset than for the model fitting dataset). If the random effects were additionally included,  $r$  increased by 18% on average, resulting in values between 0.45 (pine) and 0.8 (‘other conifers’) with a mean of 0.62. Hence, the models including the random effects explained 21–64% of the BAI variance in the evaluation dataset (Table 4).

## Discussion

### Methodological aspects

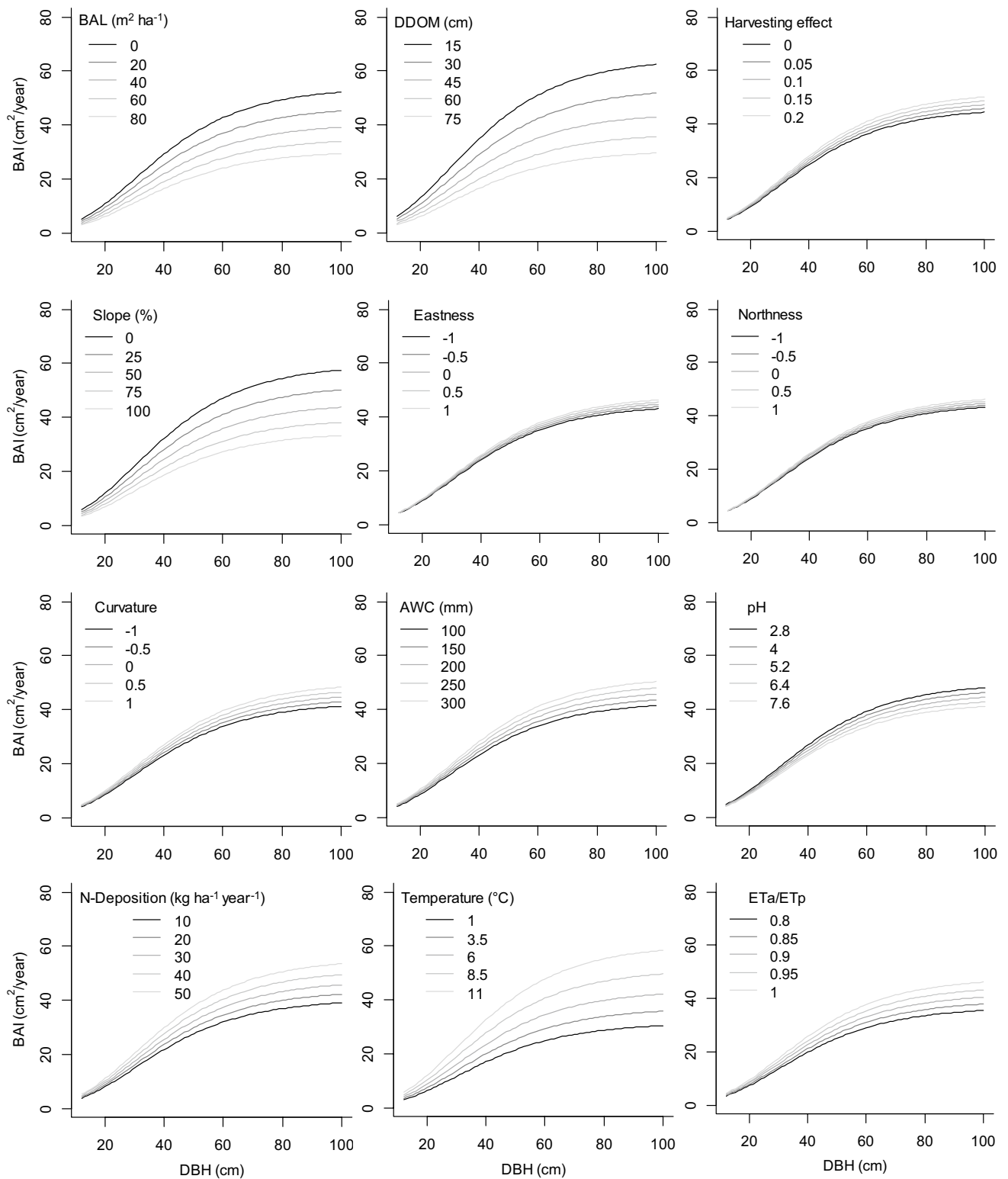
Forest inventories offer a robust empirical basis for developing tree growth models for spatially representative scenario analyses (Brassel and Lischke 2001). All in all, the performance of the selected models was reasonably good (see Table 4), although with species-specific differences.

In general, model predictions were better for species with wide ranges of BAI values (e.g. fir) than for species with a rather narrow BAI range (e.g. pine and larch). The fact that BAI predictions were generally better if random effects were included is not surprising, since the random effects capture further site and stand effects not explicitly included as fixed effects.

Although a wide range of potential influences on BAI was considered in the present study, further growth-influencing factors are definitely conceivable, such as more detailed soil information (e.g. soil nutrients; Lévesque et al. 2016) or quantitative measures of tree health in general and pathogen and insect infestations in particular (cf. Rolland et al. 2001). However, such information is rarely available over large areas and was not available at the NFI plot level for the present study. If such information becomes available in the future, its inclusion could potentially improve the BAI functions presented here. In addition, further studies focusing on interactions among the included variables would be desirable.

In the way the explanatory climatic variables were calculated here—mean values over the inventory intervals—variability from year to year is not considered. The approach of using mean values of climatic variables to investigate climate effects on growth has been used previously (Condés and García-Robredo 2012; Nothdurft et al. 2012). In Rohner et al. (2016), the question of whether means or extremes of climatic variables should be chosen for modelling multiannual tree growth was explicitly addressed. The results of this study indicated means as a reasonable choice, with this choice being generally less important than the decision of including information from the whole year or parts of the year only. Rohner et al. (2016) further showed that effects of climatic variables on BAI were insensitive to the timing of the intervals (i.e. in which year an inventory took place). The use of climate means in empirical tree growth models at multiannual resolutions is further supported by the fact that short-term negative growth responses to climatic extremes are often followed by periods of increased growth (Pretzsch et al. 2013).

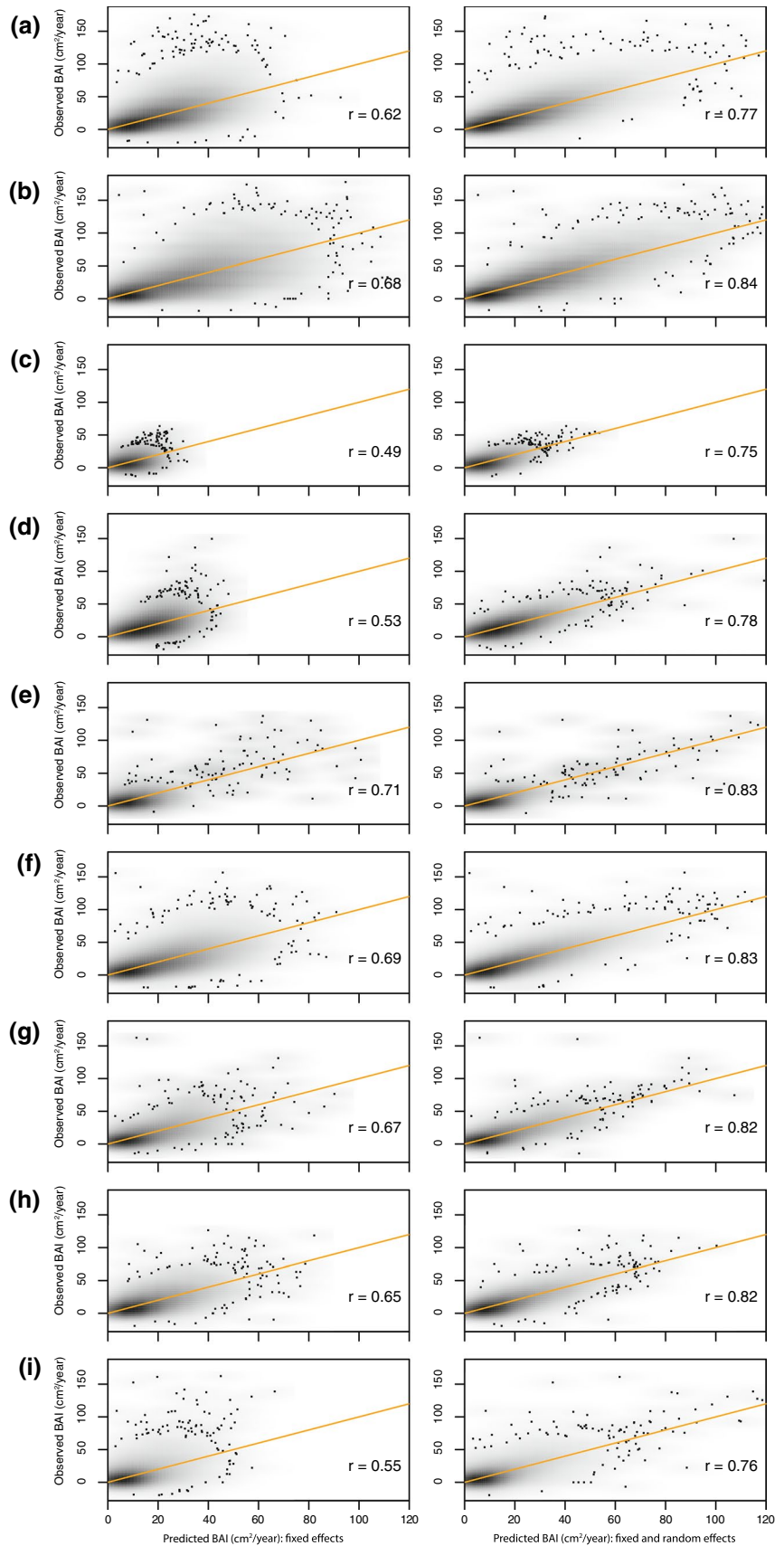
The identified drivers of BAI are based on the present range of the included explanatory variables, and extrapolations beyond this range should be interpreted with caution. In particular, sites with temperatures and ETa/ETp values at the edge of the current distribution (i.e. the warmest and driest sites of the sample) are expected to exhibit conditions in the future that are not represented in the present sample. Thus, if the growth functions are intended to be used in scenario analyses, the results for such sites should be checked carefully. Restricting scenario analyses to the coming few decades may limit the risks associated with extrapolation.



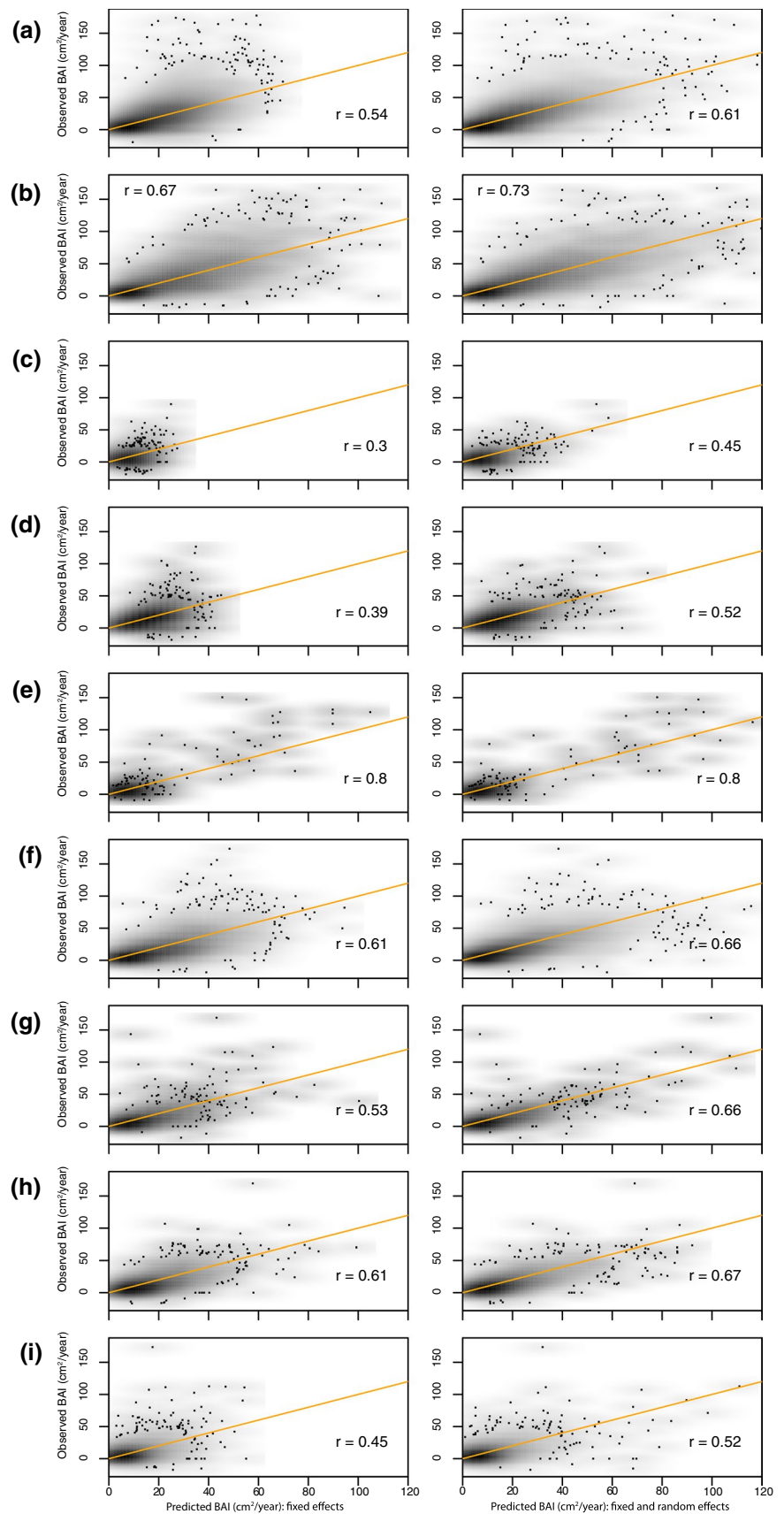
**Fig. 2** Sensitivity to the included variables in the selected model for beech. The relationship between basal area increment (BAI) and diameter at breast height (DBH) was predicted by varying one

explanatory variable at a time, while the other variables were fixed at their mean values. The sensitivity analysis for the other species and species groups is presented in Online Resource 4

**Fig. 3** Comparison of observed and predicted basal area increments (BAI) based on the dataset used for model fitting (NFI 1–3). Predictions were based on the fixed effects (left) or on the fixed and the random effects (right) of the selected models (Tables 2, 3) for **a** spruce, **b** fir, **c** pine, **d** larch, **e** other conifers, **f** beech, **g** oak, **h** ash/maple, and **i** other broadleaves. The grey-scale indicates the density of the points (darker grey represents more points). The 100 points with the lowest regional density are plotted individually. The Pearson correlation coefficient ( $r$ ) between observed and predicted BAI is indicated for each comparison



**Fig. 4** Comparison of observed and predicted basal area increments (BAI) based on the evaluation dataset (NFI 3–4). Predictions were based on the fixed effects (left) or on the fixed and the random effects (right) of the selected models (Tables 2, 3) for **a** spruce, **b** fir, **c** pine, **d** larch, **e** other conifers, **f** beech, **g** oak, **h** ash/maple, and **i** other broadleaves. The grey-scale indicates the density of the points (darker grey represents more points). The 100 points with the lowest regional density are plotted individually. The Pearson correlation coefficient ( $r$ ) between observed and predicted BAI is indicated for each comparison



To enhance comparability among the estimated coefficients, variables were centred and scaled before fitting the models. However, we would like to emphasize that this comparability has some limitations even if the variables are scaled and centred. Since the datasets differ among the species, coefficients can only be directly interpreted regarding relative effect size within the selected models (per species), but not among them.

### Drivers of individual-tree BAI

Table 3 summarizes the inclusion of the selected explanatory variables in the models. The variables BAL, SDI, slope, pH, N-deposition, and temperature were included in most of the species-specific models (7–9 models, Table 3), while forest type, aspect, curvature, AWC, and global radiation were included only in a few models (2–4 models, Table 3).

### Tree- and stand-related variables

BAI was larger for smaller BAL (8 of 9 species), lower SDI (6 of 9 species), and lower DDOM (6 of 9 species). These results may be interpreted as a consequence of the struggle for resources. However, the estimated effect size of DDOM was comparably low, possibly because DDOM—a rather general description of a stand's development stage—may affect individual-tree BAI less directly than, for example, BAL, which is determined at the individual-tree level. The negative effects of BAL, SDI, and DDOM are in line with the positive harvesting effect, which was identified for 6 of the 9 investigated species. A possible reason for this harvesting effect being comparatively small may be the fact that it integrates possible growth responses of all remaining trees on a plot, including trees not growing in proximity to removed trees. Nevertheless, the pre-selection of competing variables indicated that this plot-level-based descriptor of the harvesting effect is still preferable to the descriptor related to the one tree closest to where a tree was removed.

In the present study, both the competition index BAL and the harvesting effect were defined independently from the species of the trees included in the calculation of these variables. Consequently, possible species mixture effects on BAI were not considered, although recent studies have indicated their potential importance for productivity (e.g. Condés et al. 2013; Mina et al. 2017; Paquette and Messier 2011; Pretzsch et al. 2010). Furthermore, we defined BAL according to Monserud and Sterba (1996), i.e. in absolute values. However, in a study setting in which the DBH distribution varies strongly among the investigated plots, relative measures (e.g. Schröder and Von Gadow 1999; Stage 1973) could be more informative. More sophisticated, species-mixture-dependent variables quantifying the competitive situation carry the potential to explain additional variability

in BAI. Thus, future investigations in this direction would be desirable.

### Site-related variables

Slope had the most consistent negative effect on BAI, indicating harsher growth conditions on steeper slopes for all investigated tree species. This may be a consequence of shallow soils and high wind exposure on comparatively steep slopes. A negative relationship between slope and BAI was already discussed by Monserud and Sterba (1996) for trees growing in Austria, even though they identified a significant effect only for spruce, beech, black pine (*Pinus nigra*), and a species group containing several broadleaved species, but not for fir, larch, Scots pine (*Pinus sylvestris*), stone pine (*Pinus cembra*), and oak. Apart from slope, the other variables related to topography played a rather limited role in predicting BAI.

Regarding soil conditions, our results indicate a positive effect of AWC on the BAI of some species (Table 2), and a general, negative effect of pH values on the BAI of most species. Why most species showed decreasing BAI with increasing pH is not clear. It is conceivable that this negative effect resulted from the fact that pH was determined for the upper soil layer only, and thus may provide little indication of the soil chemical status in the whole rooting zone. A further possible explanation is that shallow soils formed over calcareous rocks may indeed exhibit high pH values but only limited rooting depths.

### Climate- and N-deposition-related variables

For most tree species, greater N-deposition corresponded to larger BAI. This result confirms the stimulating effect of N-deposition on tree growth already described by Bedison and McNeil (2009), Etzold et al. (2014), Ferretti et al. (2014), Laubhann et al. (2009), Magnani et al. (2007), and Solberg et al. (2009) based on data from permanent monitoring plots and eddy-covariance sites. The inverse effect was observed for spruce and fir. A possible explanation for this result may be that spruce and fir grew disproportionately often at sites with comparably high N-deposition values (95% quantile of 47.0 kg ha<sup>-1</sup> year<sup>-1</sup> for spruce and 51.6 kg ha<sup>-1</sup> year<sup>-1</sup> for fir), where already negative saturation effects through, for example, soil acidification may occur (Aber et al. 1998). Furthermore, the uncertainty of the modelled N-deposition estimates may affect the coefficient estimates. Hence, the species-specific effects of N-deposition on BAI we identified here remain to be confirmed.

As far as climate is concerned, temperature and ETa/ETp were the most important drivers of BAI. Increased tree growth under higher temperatures is a well-known relationship from observations along elevation gradients



(Ellenberg 2009; King et al. 2013). Similarly, the positive temperature coefficients included in most of the selected models likely reflect temperature variability in space rather than in time. As for ETa/ETp, BAI generally increased with increasing water availability for most of the examined species. This finding is not surprising and confirms results from previous studies showing positive relationships between ETa/ETp and growth of spruce, fir, and beech in the Swiss lowlands (Graf Pannatier et al. 2007).

### Species-specific considerations

Besides DBH (which is inherent in the model formulation), there were few variables that displayed a generalized, consistent pattern (e.g. slope). For the remaining variables, there was always a species-specific pattern reflecting physiological properties of the individual investigated species.

In contrast to models for most of the other species, SDI was not included in the selected model for beech. This result is in line with the comparatively high shade-tolerance that has previously been described for beech (Ellenberg 2009). In contrast, the negative effect of SDI in the selected oak model may reflect the relatively low competitiveness of oaks (Ellenberg 2009; Rohner et al. 2012). However, the fact that BAL was not included in the selected oak model is rather surprising. This unexpected result may be explained by the management history of this species in Europe: for centuries, oak was facilitated in semi-open stands serving as pastures for feeding pigs with acorns or through coppice-with-standards management (Haneca et al. 2009), but these management strategies have been largely replaced by high forest management (Bürgi 1999). Consequently, a certain proportion of the recorded oaks feature—as remnants of earlier times—disproportionally low BAL values (median BAL  $14.6 \text{ m}^2 \text{ ha}^{-1}$  for oak compared with  $19.2 \text{ m}^2 \text{ ha}^{-1}$  for all species together).

Larch was the only species for which N-deposition was not included in the selected model. This result may be related to the fact that larch was almost exclusively recorded at sites with comparably low N-deposition values (median N-deposition:  $14.6 \text{ kg ha}^{-1} \text{ year}^{-1}$  for larch compared to  $25.8 \text{ kg ha}^{-1} \text{ year}^{-1}$  for all species together), although even these deposition levels may be high enough to enhance larch growth.

Regarding the considered climate variables, the comparably high drought tolerance that has been ascribed to pine and oak (Contran et al. 2012; Ellenberg 2009) was confirmed by the results of the present study. In particular, the drought index ETa/ETp proved to be relevant for most species but had no effect on the BAI of pine and oak.

### Conclusions

In the present study, a variety of effects on BAI were quantified simultaneously for nine species or species groups, including the most frequent tree species in central Europe. While most identified effects were plausible and well reflected species-specific physiological properties, the effects of pH and N-deposition remain to be confirmed in further studies.

The key results of the present study are thus species-specific growth models involving tree, site, stand, management, climate, and N-deposition variables. As a next step, these growth models may be incorporated into empirical forest scenario models (such as MASSIMO; Kaufmann 2001b) to, for example, improve their approach for considering climate change effects. While the fixed effects of the growth models could be applied to investigate independent sites, analyses based on the Swiss NFI could additionally include the random effects, resulting in an even higher proportion of explained BAI variance. Incorporating the growth models into forest scenario models may pave the way for a better understanding of tree (and forest) responses to the suite of potential influencing factors, and for analyses of scenarios that assume changing environmental conditions with respect to climate, N-deposition and other potentially important drivers. Such scenario analyses will potentially support resource managers and decision makers by helping them design adequate management strategies and policies.

**Acknowledgements** We would like to thank Jan Remund for providing the climate data and Beat Rihm for modelling and providing the N-deposition data. For many fruitful discussions, we are grateful to Edgar Kaufmann, Jürgen Zell, and Golo Stadelmann. This study was funded by the Swiss Federal Office for the Environment FOEN and the Swiss Federal Institute for Forest, Snow and Landscape Research WSL as part of the research programme ‘Forests and Climate Change’.

### References

- Aber J et al (1998) Nitrogen saturation in temperate forest ecosystems. *BioScience* 48:921–934
- Adame P, Hynynen J, Cañellas I, Del Río M (2008) Individual-tree diameter growth model for rebollo oak (*Quercus pyrenaica* Willd.) coppices. *For Ecol Manag* 255:1011–1022
- Abegg M et al (2014) Fourth national forest inventory—result tables and maps on the Internet for the NFI 2009–2013 (NFI4b). Published online 06/11/2014 Available from World Wide Web. <http://www.lfich/resultate/>
- Barreiro S et al (2016) Overview of methods and tools for evaluating future woody biomass availability in European countries. *Ann For Sci*. <https://doi.org/10.1007/s13595-016-0564-3>
- Bedison JE, McNeil BE (2009) Is the growth of temperate forest trees enhanced along an ambient nitrogen deposition gradient? *Ecology* 90:1736–1742



- Biging GS, Dobbertin M (1995) Evaluation of competition indices in individual tree growth models. *For Sci* 41:360–377
- Brassel P, Lischke H (eds) (2001) Swiss national forest inventory: methods and models of the second assessment. Swiss Federal Research Institute WSL, Birmensdorf
- Bugmann H (2001) A review of forest gap models. *Clim Change* 51:259–305
- Bugmann H, Cramer W (1998) Improving the behaviour of forest gap models along drought gradients. *For Ecol Manag* 103:247–263
- Bürgi M (1999) A case study of forest change in the Swiss lowlands. *Landsc Ecol* 14:567–575
- Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer, New York
- Canadell JG, Raupach MR (2008) Managing forests for climate change mitigation. *Science* 320:1456–1457
- Ciais P et al (2005) Europe-wide reduction in primary productivity caused by the heat and drought in 2003. *Nature* 437:529–533
- Condés S, García-Robredo F (2012) An empirical mixed model to quantify climate influence on the growth of *Pinus halepensis* Mill. stands in South-Eastern Spain. *For Ecol Manag* 284:59–68
- Condés S, Del Río M, Sterba H (2013) Mixing effect on volume growth of *Fagus sylvatica* and *Pinus sylvestris* is modulated by stand density. *For Ecol Manag* 292:86–95
- Contran N, Günthardt-Goerg MS, Kuster TM, Cerana R, Crosti P, Paoletti E (2012) Physiological and biochemical responses of *Quercus pubescens* to air warming and drought on acidic and calcareous soils. *Plant Biol*. <https://doi.org/10.1111/j1438-8677201200627x>
- Crecente-Campo F, Soares P, Tomé M, Diéguez-Aranda U (2010) Modelling annual individual-tree growth and mortality of Scots pine with data obtained at irregular measurement intervals and containing missing observations. *For Ecol Manag* 260:1965–1974
- Ellenberg H (2009) Vegetation ecology of central Europe, 4th edn. Cambridge University Press, Cambridge
- Etzold S, Waldner P, Thimonier A, Schmitt M, Dobbertin M (2014) Tree growth in Swiss forests between 1995 and 2010 in relation to climate and stand conditions: recent disturbances matter. *For Ecol Manag* 311:41–55
- Ferretti M, Chiarucci A (2003) Design concepts adopted in long-term forest monitoring programs in Europe—problems for the future? *Sci Tot Environ* 310:171–178
- Ferretti M et al (2014) On the tracks of Nitrogen deposition effects on temperate forests at their southern European range—an observational study from Italy. *Global Change Biol* 20:3423–3438
- Fritts HC (1976) Tree rings and climate. Academic, London
- Graf Pannatier E, Dobbertin M, Schmitt M, Thimonier A, Waldner P (2007) Effects of the drought 2003 on forests in Swiss level II plots. In: Eichhorn J (ed) Symposium: forests in a changing environment—results of 20 years ICP forest monitoring, Göttingen, 25–28.10.2006. J.D. Sauerländer's Verlag, Frankfurt a.M., pp 128–135
- Groen TA et al (2013) What causes differences between national estimates of forest management carbon emissions and removals compared to estimates of large-scale models? *Environ Sci Policy* 33:222–232
- Haneca K, Čufar K, Beeckman H (2009) Oaks, tree-rings and wooden cultural heritage: a review of the main characteristics and applications of oak dendrochronology in Europe. *J Archaeol Sci* 36:1–11
- Kaufmann E (2001a) Estimation of standing timber, growth and cut. In: Brassel P, Lischke H (eds) Swiss national forest inventory: methods and models of the second assessment. Swiss Federal Research Institute WSL, Birmensdorf, pp 162–196
- Kaufmann E (2001b) Prognosis and management scenarios. In: Brassel P, Lischke H (eds) Swiss national forest inventory: methods and models of the second assessment. Swiss Federal Research Institute WSL, Birmensdorf, pp 197–206
- Keller W (1978) Einfacher ertragskundlicher Bonitätsschlüssel für Waldbestände in der Schweiz. Mitteilungen der Eidgenössischen Forschungsanstalt für Wald, Schnee und Landschaft 54
- King GM, Gugerli F, Fonti P, Frank DC (2013) Tree growth response along an elevational gradient: climate or genetics? *Oecologia*. <https://doi.org/10.1007/s00442-013-2696-6>
- Laubhann D, Sterba H, Reinds GJ, De Vries W (2009) The impact of atmospheric deposition and climate on forest growth in European monitoring plots: an individual tree growth model. *For Ecol Manag* 258:1751–1761
- Lévesque M, Walthert L, Weber P (2016) Soil nutrients influence growth response of temperate tree species to drought. *J Ecol* 104:377–387
- Lindner M (2000) Developing adaptive forest management strategies to cope with climate change. *Tree Physiol* 20:299–307
- Lindner M et al (2010) Climate change impacts, adaptive capacity, and vulnerability of European forest ecosystems. *For Ecol Manag* 259:698–709
- Magnani F et al (2007) The human footprint in the carbon cycle of temperate and boreal forests. *Nature* 447:848–850
- Mina M, Huber MO, Forrester DI, Thürig E, Rohner B (2017) Multiple factors modulate tree growth complementarity in central European mixed forests. *J Ecol*. <https://doi.org/10.1111/1365-2745.12846>
- Monserud RA, Sterba H (1996) A basal area increment model for individual trees growing in even- and uneven-aged forest stands in Austria. *For Ecol Manag* 80:57–80
- Monserud RA, Sterba H, Hasenauer H (1997) The single-tree stand growth simulator PROGNAUS. In: Proceedings of the forest vegetation simulator conference, vol 373, pp 50–56
- Nabuurs GJ, Päävinen R, Sallnäs O, Kupka I (1997) A large scale forestry scenario model as a planning tool for European forests. In: Moiseev NA, von Gadow K, Krott M (eds) Planning and decision making for forest management in the market economy. IUFRO conference, Pushkino, Moscow, 25–29 Sept 1996. Cuvillier Verlag, Göttingen, pp 89–102
- Nabuurs G-J, Lindner M, Verkerk PJ, Gunia K, Deda P, Michalak R, Grassi G (2013) First signs of carbon sink saturation in European forest biomass. *Nat Clim Change* 3:792–796
- Nabuurs G-J, Arets EJMM, Schelhaas M-J (2017) European forests show no carbon debt, only a long parity effect. *For Policy Econ* 75:120–125
- Nothdurft A, Wolf T, Ringeler A, Böhner J, Saborowski J (2012) Spatio-temporal prediction of site index based on forest inventories and climate change. *For Ecol Manag* 279:97–111
- Oberhuber W, Kofler W (2000) Topographic influences on radial growth of Scots pine (*Pinus sylvestris* L.) at small spatial scales. *Plant Ecol* 146:231–240
- Paquette A, Messier C (2011) The effect of biodiversity on tree productivity: from temperate to boreal forests. *Glob Ecol Biogeogr* 20:170–180
- Peng C (2000) Growth and yield models for uneven-aged stands: past, present and future. *For Ecol Manag* 132:259–279
- Pinheiro JC, Bates DM (2000) Mixed-effects models in S and S-PLUS. Statistics and computing. Springer, New York
- Pinheiro J, Bates D, DebRoy S, Sarkar D, R Core Team (2016) nlme: linear and nonlinear mixed effects models. R package version 3.1-128
- Pretzsch H et al (2010) Comparison between the productivity of pure and mixed stands of Norway spruce and European beech along an ecological gradient. *Ann For Sci* 67:712
- Pretzsch H, Schütze G, Uhl E (2013) Resistance of European tree species to drought stress in mixed versus pure forests: evidence of stress release by inter-specific facilitation. *Plant Biol* 15:483–495
- Quicke HE, Meldahl RS, Kush JS (1994) Basal area growth of individual trees: a model derived from a regional longleaf pine growth study. *For Sci* 40:528–542

- R Core Team (2013) R: a language and environment for statistical computing. R Foundation for Statistical Computing. Vienna. <http://www.R-project.org>
- Reineke LH (1933) Perfecting a stand-density index for even-aged forests. *J Agric Res* 46:627–638
- Remund J, Rihm B, Huguenin-Landl B (2014) Klimadaten für die Waldmodellierung für das 20. und 21. Jahrhundert. Meteotest, Bern
- Rihm B (1996) Critical loads of nitrogen and their exceedances: eutrophying atmospheric depositions: report on mapping critical loads of nitrogen for Switzerland, produced within the work programme under the Convention on Long-Range Transboundary Air Pollution of the United Nations Economic Commission for Europe (UNECE). Federal Office of Environment, Forests and Landscape (FOEFL), Berne
- Rohner B, Bigler C, Wunder J, Brang P, Bugmann H (2012) Fifty years of natural succession in Swiss forest reserves: changes in stand structure and mortality rates of oak and beech. *J Veg Sci* 23:892–905
- Rohner B, Weber P, Thürig E (2016) Bridging tree rings and forest inventories: how climate effects on spruce and beech growth aggregate over time. *For Ecol Manag* 360:159–169
- Rolland C, Baltensweiler W, Petitcolas V (2001) The potential for using *Larix decidua* ring widths in reconstructions of larch budmoth (*Zeiraphera diniana*) outbreak history: dendrochronological estimates compared with insect surveys. *Trees* 15:414–424
- Romanenko VA (1961) Computation of the autumn soil moisture using a universal relationship for a large area. In: Proceedings of the Ukrainian hydrometeorological research institute, no 3, Kiev
- Schröder J, von Gadow K (1999) Testing a new competition index for Maritime pine in northwestern Spain. *Can J For Res* 29:280–283
- Solberg S et al (2009) Analyses of the impact of changes in atmospheric deposition and climate on forest growth in European monitoring plots: a stand growth approach. *For Ecol Manag* 258:1735–1750
- Stage AR (1973) Prognosis model for stand development. US Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station, Ogden, Utah
- Teck RM, Hilt DE (1991) Individual-tree diameter growth model for the Northeastern United States. Radnor, Pennsylvania
- Thimonier A, Schmitt M, Waldner P, Rihm B (2005) Atmospheric deposition on Swiss long-term forest ecosystem research (LWF) plots. *Environ Monit Assess* 104:81–118
- Thürig E, Kaufmann E (2010) Increasing carbon sinks through forest management: a model-based comparison for Switzerland with its Eastern Plateau and Eastern Alps. *Eur J For Res* 129:563–572
- Thürig E, Kaufmann E, Frisullo R, Bugmann H (2005) Evaluation of the growth function of an empirical forest scenario model. *For Ecol Manag* 204:51–66
- Trasobares A, Zingg A, Walthert L, Bigler C (2016) A climate-sensitive empirical growth and yield model for forest management planning of even-aged beech stands. *Eur J For Res* 135:263–282
- Verkerk PJ, Anttila P, Eggers J, Lindner M, Asikainen A (2011) The realisable potential supply of woody biomass from forests in the European Union. *For Ecol Manag* 261:2007–2015
- Wang B, Shugart HH, Shuman JK, Lerdau MT (2016) Forests and ozone: productivity, carbon storage, and feedbacks. *Sci Rep* 6:22133. <https://doi.org/10.1038/srep22133>
- Weiskittel AR, Hann DW, Kershaw JA Jr, Vanclay JK (2011) Forest growth and yield modeling. Wiley, Chichester
- Werner F, Taverna R, Hofer P, Thürig E, Kaufmann E (2010) National and global greenhouse gas dynamics of different forest management and wood use scenarios: a model-based assessment. *Environ Sci Policy* 13:72–85
- Zeng W, Duo H, Lei X, Chen X, Wang X, Pu Y, Zou W (2017) Individual tree biomass equations and growth models sensitive to climate variables for *Larix* spp. in China. *Eur J For Res* 136:233–249